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# Empathy: Its ultimate and proximate bases

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**Abstract:** There is disagreement in the literature about the exact nature of the phenomenon of empathy. There are emotional, cognitive, and conditioning views, applying in varying degrees across species. An adequate description of the ultimate and proximate mechanism can integrate these views. Proximately, the perception of an object's state activates the subject's corresponding representations, which in turn activate somatic and autonomic responses. This mechanism supports basic behaviors (e.g., alarm, social facilitation, vicariousness of emotions, mother-infant responsiveness, and the modeling of competitors and predators) that are crucial for the reproductive success of animals living in groups. The Perception-Action Model (PAM), together with an understanding of how representations change with experience, can explain the major empirical effects in the literature (similarity, familiarity, past experience, explicit teaching, and salience). It can also predict a variety of empathy disorders. The interaction between the PAM and prefrontal functioning can also explain different levels of empathy across species and age groups. This view can advance our evolutionary understanding of empathy beyond inclusive fitness and reciprocal altruism and can explain different levels of empathy across individuals, species, stages of development, and situations.

**Keywords:** altruism; cognitive empathy; comparative; emotion; emotional contagion; empathy; evolution; human; perception-action; perspective taking

## 1. Introduction

The concept empathy has had a difficult history, marked by disagreement and discrepancy. Although it has been studied for hundreds of years, with contributions from philosophy, theology, developmental psychology, social and personality psychology, ethology, and neuroscience, the field suffers from a lack of consensus regarding the nature of the phenomenon. Despite this disagreement, the empirical data on empathy are very consistent, across a wide range of species. Consider the following examples:

An albino rat sees a distressed conspecific suspended in the air by a harness; he presses a bar to lower the rat back to safe ground, staying close to and oriented toward him (Rice & Gainer 1962). Another rat sees a distressed conspecific receiving electric shocks and does not press the bar to terminate the shock, he instead "retreat[s] to the corner . . . farthest from the distressed, squeaking, and dancing animal and crouch[es] there, motionless" (Rice 1964, p. 167). The response of a rat to shock of a conspecific occurs without any prior experience with shock, is stronger after prior experience with shock, and strongest when prior shock occurred at the same time as to the conspecific (Church 1959).

In an experiment with rhesus monkeys, subjects were trained to pull two chains that delivered different amounts of food. The experimenters then altered the situation so that pulling the chain with the larger reward caused a monkey in sight of the subject to be shocked. After the subjects witnessed the shock of the conspecific, two-thirds preferred the nonshock chain even though it resulted in half as many rewards. Of the remaining third, one stopped pulling the chains altogether for 5 days and another for 12 days after witnessing the shock of the object. These monkeys were literally starving themselves to prevent the shock to the conspecific. Starvation was induced more by visual than auditory cues, was more likely in animals that had experienced shock themselves, and was enhanced by familiarity with the shocked individual (Masserman et al. 1964).

Human infants orient to the distress of others, often responding with their own distress cries from infancy to 14 months (e.g., Sagi & Hoffman 1976; Ungerer 1990; Zahn-Waxler & Radke-Yarrow 1982). After the first year, children start to show helping behaviors, even when they have become distressed. They also imitate the distress behaviors of the other, possibly "trying on" the expressions to better understand them (Zahn-Waxler et al. 1977, in Thompson 1987). With age, the level of personal distress decreases while appropriateness of helping behaviors increases (e.g., Zahn-Waxler et al. 1983).

These examples, all from empirical reports, show that individuals of many species are distressed by the distress of a conspecific and will act to terminate the object's distress, even incurring risk to themselves. Humans and other animals exhibit the same robust effects of familiarity, past experience, and cue salience (Table 1), and parallels exist be-

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tween the development of empathy in young humans and the phylogenetic emergence of empathy (de Waal 1996; Hoffman 1990, respectively). These facts suggest that empathy is a phylogenetically continuous phenomenon, as suggested by Charles Darwin more than a century ago (1871/1982).

The goal of this theoretical review is to present data across disciplines so that the continuity is apparent. Moreover, this paper aims to show that consistencies exist because all empathic processes rely on a general perception-action design of the nervous system that has been postulated for over a century, is adaptive for myriad reasons, and exists across species. Recent advances in interdisciplinary research and tools for understanding the brain provide strong support for the Perception-Action Model (PAM), warranting its application to emotional domains. This Perception-Action Model also sheds light on the ultimate level description, placing the emphasis on direct effects on reproductive success from the general design of the nervous system, rather than on indirect effects from helping behaviors. Thus, by fleshing out the phenomenon along both proximate and ultimate levels, and by combining data across fields, a unified story emerges.

Stephanie Preston received her doctorate in Psychology in 2001 from the University of California, Berkeley. Her dissertation investigated the effects of social and metabolic stress on food-hoarding decisions in kangaroo rats. Her interdisciplinary research combines techniques and ideas across fields, and uses naturalistic paradigms, in order to study how emotion and cognition interact to produce behavior. She is currently a postdoctoral fellow at the University of Iowa with Antoine Bechara, doing behavioral, psychophysiological, and brain imaging research on empathy, decision-making, and hoarding.

Frans B. M. de Waal is a Dutch-born ethologist/zoologist renowned for his work on the social intelligence of primates, such as chimpanzees, bonobos, capuchin monkeys, and macaques. His first book, *Chimpanzee Politics* (1982) compared the schmoozing and scheming of chimpanzees involved in power struggles at the Arnhem Zoo with that of human politicians. Ever since, de Waal has drawn parallels between primate and human behavior, from peacemaking and morality to culture. His scientific work, conducted first in the Netherlands and later at NIH-sponsored regional primate centers in the USA, has been published in numerous technical articles in journals such as *Science, Nature, Scientific American,* and outlets specialized in animal behavior and primatology. His award-winning popular books have been translated into more than a dozen different languages. His latest work, *The Ape and the Sushi Master* (Basic Books, 2001), tries to bridge the nature/culture divide. Dr. de Waal is C. H. Candler Professor in the Psychology Department of Emory University and Director of the Living Links Center at the Yerkes Primate Center, Atlanta, Georgia. He is Correspondent Member of the Royal Dutch Academy of Sciences.

### 1.1. Terminology

**1.1.1. Proximate versus ultimate.** Ernst Mayr first created the distinction between proximate and ultimate causes of behavior. According to Mayr, "proximate causes govern the responses of the individual (and his organs) to immediate factors of the environment while ultimate causes are responsible for the evolution of the particular DNA code of information with which every individual of every species is endowed" (Mayr 1961, p. 1503). Causes exist at each of these levels; therefore, theories that refer to different levels are not in conflict. For example, when you help your distressed neighbor, is it because you "feel their pain," or because you will eventually need them to reciprocate? Given Mayr's levels of causality, these hypotheses are not in conflict; the former is a proximate explanation, the latter an ultimate one.

**1.1.2. Definitional distinctions.** Much of the empathy literature focuses on whether empathy is an emotional or cognitive process and distinguishes empathy from emotional contagion, sympathy, and perspective taking (e.g., Eisenberg 1986; Feshbach 1975; Hoffman 1978a; 1982a; Hornblow 1980; Omdahl 1995; Shantz 1975; Wispé 1986). These distinctions are empirically based and help to categorize behavior (Batson et al. 1987; Doherty 1997; Eisenberg et al. 1994; 1998; Eisenberg & Okun 1996; Rice 1964; distinctions summarized in Table 2), but they have been overemphasized to the point of distraction. This overemphasis on definition reflects the deeper problem that empathy lacks a proximate mechanism. Abstract and elusive definitions like "putting oneself in the place of another" or "imaginatively projecting oneself into the situation of another" (Allport 1937; Buchheimer 1963; Demos 1984; Goldie 1999; Smith 1989) indicate an insufficient understanding of the way the nervous system instantiates empathy. Thirty years ago G. W. Allport said it best when he concluded, "the process of *empathy* remains a riddle in social psychology . . . The nature of the mechanism is not yet understood" (Allport 1968, p. 30 from Wispé 1987, original emphasis).

The original German word *Einfühlung*, of which the English "empathy" is Titchener's translation (1909; Wispé 1991, p. 78), literally means "feeling into" (Wispé 1986). *Einfühlung* was thought to result from a process where observers project themselves into the objects they perceive (Lipps 1903; McDougall 1908/1923; Titchener 1909). Theodore Lipps first put forth a mechanistic account of *Einfühlung*, where the perception of an emotional gesture in another directly activates the same emotion in the perceiver, without any intervening labeling, associative, or cognitive perspective-taking processes (Lipps 1903). Two paths have since diverged from the original *Einfühlung*.

Some theories focused on the direct perception aspect, and on the basis of empathy in emotional contagion or imitation (e.g., Brothers 1990; Hatfield et al. 1993; Hume 1888/1990; Levenson 1996; Levenson & Reuf 1992; Nietzsche 1895/1920; Smith 1759/1976; Wermlund 1949). McDougall observes in his *Introduction to Social Psychology* (1908/1923, p. 93) "that the behavior of one animal, upon the excitement of an instinct, immediately evokes similar behavior in those of his fellows who perceive his expressions of excitement." McDougall includes imitation of facial expressions from mother to infant, feelings of tenderness evoked in observers of mother-infant interactions, and the

Table 1. *Cross-species references for five main empathy literature findings. Empathy increases with Familiarity (subject's previous experience with object), Similarity (perceived overlap between subject and object, e.g., species, personality, age, gender), Learning (explicit or implicit teaching), Past experience (with situation of distress), and Salience (strength of perceptual signal, e.g., louder, closer, more realistic, etc.)*

| | Familiarity | Similarity | Learning | Past experience | Salience |
|---|---|---|---|---|---|
| Rats | | | | Church 1959; Watanabe & Ono 1986 | Lavery & Foley 1963; Rice & Gainer 1962 |
| Monkeys | Aureli et al. 1989; Aureli et al. 1997; Cords & Thurnheer 1993; Demaria & Thierry 2001; Masserman et al. 1964; Miller et al. 1959a | Miller et al. 1966; Miller et al. 1967; Miller et al. 1959a | de Waal 1996; de Waal et al. 1996 | Masserman et al. 1964; Miller et al. 1967 | Miller et al. 1959a; Miller & Deets 1976 |
| Apes | O'Connell 1995 | | Yerkes & Yerkes 1929 | Povinelli et al. 1992a | O'Connell, 1995 |
| Human infants | Zahn-Waxler & Radke-Yarrow 1982 | Martin & Clark 1982; Simner 1971 | Capps & Sigman 1996; Thompson 1987 | | Lamb & Zakhireh 1997; Sagi & Hoffman 1976; Simner 1971 |
| Human children | Zahn-Waxler 1982; Zahn-Waxler et al. 1984; Farver & Branstetter 1994; Howes & Farver 1987 | Feshbach & Roe 1968; Rosekrans 1967; Shantz 1975; Smith 1988 | Krebs 1970; Eisenberg et al. 1983; Radke-Yarrow 1983; Trivers 1974; Ungerer 1990; Zahn-Waxler et al. 1979; Zahn-Waxler 1984 | Murphy 1937 | Eisenberg et al. 1990; Eisenberg et al. 1993 |
| Human adults | Cialdini et al. 1997; Sawyer 1966; Stinson & Ickes 1992 | Batson et al. 1981; Krebs 1975; Toi & Batson 1982; Gruen & Mendelson 1986 | | Aronfreed 1968; Gruen & Mendelsohn 1986; Stinson & Ickes 1992 | Aronfreed 1965; Eisenberg et al. 1991; Eisenberg et al. 1994; Gouldner 1960 |

contagious distress evoked in chimpanzees by the distress of a conspecific.

Other theories make use of Lipps' projection, imitation, and imagination, without the direct perception. This makes empathy a high-level, cognitive phenomenon, reserved for humans (e.g., Allport 1961; Deutsch & Maddle 1975; Freud 1922/1945; Mead 1934; Titchener 1915). Even in comparative frameworks, empathy can be synonymous with "perspective taking." In one cooperation paradigm, animals are considered to have empathy if they can perform the task of their human partner after only having observed it during training. The transfer task is successfully done by apes but not monkeys and is interpreted as evidence that only the former have empathy (Povinelli et al. 1992a; 1992c, respectively). The task is not performed between conspecifics, and does not include an emotional component.

Still other theories reject both the direct perception approach and the cognitive approach and suggest that empathy is the result of conditioning (e.g., Allport 1924; Becker 1931; Church 1959; Scheler 1923/1954). In the conditioning view, the distress of another is the Conditioned Stimulus (CS), and the distressor itself is the Unconditioned Stimulus (US). The subject learns that the CS predicts the US, and eventually responds to the distress of the other with distress. Supporting this view, rats pre-trained with a shock paired to the shock of a conspecific significantly decrease bar pressing for the remainder of the experiment (interpreted as anxiety). However, as mentioned above, rats that experience an unpaired shock also decrease bar pressing, just to a lesser degree. Even subjects that never experienced shock decreased bar pressing, but the response habituates quickly (Church 1959). These results were replicated with pigeons (Watanabe & Ono 1986).

Developmental research has incorporated different levels of empathy by tracking changes in the life span (e.g., Eisenberg et al. 1983; Hoffman 1978; Ungerer 1990; Zahn-Waxler & Radke-Yarrow 1982; Zahn-Waxler et al. 1992a). Hoffman (1982a; 2000) outlines a variety of emotional and cognitive processes that are involved in empathy, but a great deal of work needs to be done to clarify why these transitions take place, and how these levels interact.

These different views of empathy can be cohered into a unified whole if a broad view of the perception-action model is taken. The perception-action model is supported when existing behavioral data on empathy is combined with recent data from physiology and functional neuroanatomy.

Table 2. *Usage of terminology by most current researchers divided into main variables of classification updated for a perception-action view of the phenomena*

| Term | Definition | Self-other distinction? | State matching? | Helping? | Synonyms |
|---|---|---|---|---|---|
| Emotional contagion | Subject's state results from the perception of object's state | No | Yes | None | personal distress, vicarious emotion, emotional transfer |
| Sympathy | Subject feels "sorry for" the object. Focused more on object's situation than physical state. | Yes | No | Depends | |
| Empathy | Subject's state results from the attended perception of the object's state. | Yes | At representation level, not necessarily visible. | Increasing with familiarity, similarity, salience. | |
| Cognitive empathy | Subject represents state of object through top-down processes. | Yes | No | Depends | true empathy, perspective-taking |
| Prosocial behaviors | Actions taken to reduce the object's distress. | Usually | Not necessarily | Yes | helping, succorance |

Applying the perception-action mechanism broadly recoheres the discrepant views into a unified whole, and changes the ultimate model.

**1.1.3. An overview of the model.** Throughout, *the object* is referred to as the primary individual who experienced the emotion or state. *The subject* is the individual that secondarily experienced or understood the emotion/state of the object, through empathy. The authors view the term empathy broadly, similar to Hoffman (2000), as: *any process where the attended perception of the object's state generates a state in the subject that is more applicable to the object's state or situation than to the subject's own prior state or situation.*

While Hoffman's (2000) definition of empathy, and that of many others focuses on the *response* of the subject, our definition focuses on the *process.* A process model makes empathy a superordinate category that includes all subclasses of phenomena that share the same mechanism. This includes emotional contagion, sympathy, cognitive empathy, helping behavior, and so on (Fig. 1). These phenomena all share aspects of their underlying process and cannot be totally disentangled (as also suggested by Thompson 1987). All forms of empathy involve some level of emotional contagion and personal distress (if only at the representational level), and helping is never entirely for the sake of the object (if only at the ultimate level). This process model also links empathy to all facilitation behaviors that rely on perception-action (e.g., ideomotor actions, imitation, the yawn reflex, automaticity, priming; see Fig. 1).

A Perception-Action Model of empathy specifically states that *attended perception of the object's state automatically activates the subject's representations of the state, situation, and object, and that activation of these representations automatically primes or generates the associated autonomic and somatic responses, unless inhibited* (see Table 3 for clarification on the terms).

With the Perception-Action Model, whether or not a subject perceives the state of the object depends crucially

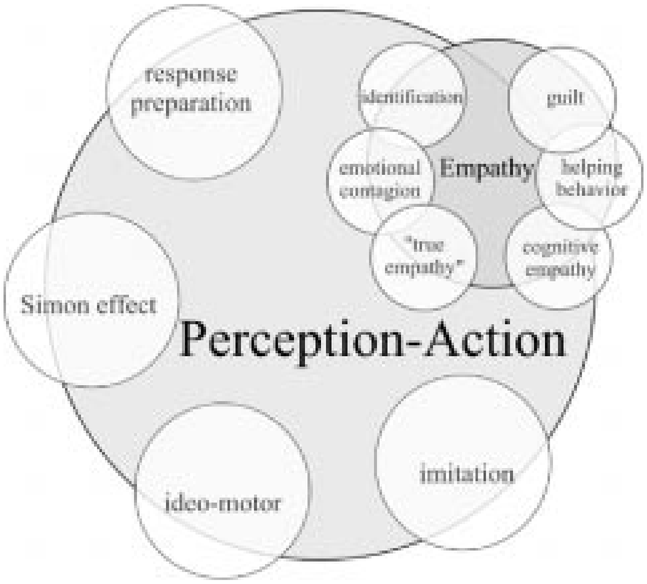


Figure 1. In order to unify the various perspectives, empathy needs to be construed broadly to include all processes that rely on the perception-action mechanism. Thus, perception-action is a superordinate class, which includes two basic level categories, motor behavior and emotional behavior. Both of these basic level categories include subordinate categories of phenomena. Thus, according to the model, various phenomena like emotional contagion, cognitive empathy, guilt, and helping are similar in that they rely on the perception-action mechanism.

Table 3. *Clarification of terms from the summary of the model that are used throughout*

| Term | Meaning |
|---|---|
| Perception-action | From the Perception-Action Hypothesis of motor behavior (Prinz 1987; 1992; 1997). Term "response" used in text to refer to a more general class of phenomena. |
| Attended | Refers to the fact that strong empathic responses require that the subject is attending to the state of the object. Differences in empathy across individuals, age groups, and situations are predictable from levels of attention. |
| Perception | Flexible definition that includes direct activation from the object in the external world, indirect activation from associations with external events or objects, and indirect activation through imagination. |
| Automatically | As a matter of course, unless controlled or inhibited. Does not require conscious and effortful processing. |
| Representation | Parallel distributed patterns of activation that reliably fire in response to a given stimulus. Formed by the combination of developmental tuning biases and connectivity of neurons as well as alterations due to experience. |
| Unless inhibited | Imitative actions are inhibited during observation of action, centrally (from prefrontal inhibition), peripherally (with spinal cord inhibition blocking the motorneurons that execute the action), or both. |

on their interdependence or interrelationship. Interdependence can be temporary and superficial, like when the subject and object must cooperate for a local goal or when the object's distress blocks the goal of the subject. Interdependence can also be long lasting and deep, like the interdependence of family members or spouses that must cooperate for long-term goals spanning a lifetime. The more interrelated the subject and object, the more the subject will attend to the event, the more their similar representations will be activated, and the more likely a response. The more similar the representations of the subject and object, the easier it is to process the state of the object and generate an appropriate response.

There are broadly two types of response: response *with* the object (matching responses as with distress to distress or joy to joy), and response *to* the object (instrumental responses as with consolation to distress or fear to anger). Exemplifying responses with the object, human and nonhuman subjects that correctly identify the emotion of an object have a physiological response that is correlated with the object's state (Levenson & Ruef 1992; Miller et al. 1967, respectively). Exemplifying responses to the object, human subjects that are empathically concerned show a deceleratory heart-rate response to the object of distress (Eisenberg et al. 1990; 1991; 1994) and rhesus macaque subjects show increased heart rate to the approach of a dominant animal (controlling for posture and activity) (Aureli et al. 1999). Since imitation emerges much earlier than prosocial response, and people learn to inhibit and control emotional contagion and imitation, responses with the object should emerge earlier, and with less learning. But, data in the ultimate section attest to the need for experience to fine-tune the circuits for responding with the object as well; thus, a strict division along "nature versus nurture" is not warranted.

The automaticity of overt responses with the object decrease with age and experience, due to many factors, discussed below. These include increased prefrontal functioning, increased segregation of self and other representations, and learned display rules – all of which inhibit the automatic response. In addition, attention can be preemptively allocated when an automatic response is undesirable (determined by current goals and the ability to help). However, covert responses may still occur, even outside of awareness. In orienting studies with infants, even though overt distress can be decreased by distracting or re-orienting attention, distress returns to almost equal levels when the distraction stimulus is removed, and the hormonal stress response may remain throughout (Gunnar et al. 1984; Harman 1994; reviewed in Rothbart et al. 1994). This internal "distress keeper" (Rothbart et al. 1994) may be the mechanism for negative feelings like guilt and remorse that pervade even when attention is shifted. As evidence, trait sympathy is correlated with the probability for entering situations of distress and the susceptibility for guilt and shame after refusing to help (reviewed by Smith 1992).

These processes do not require conscious awareness, but they can be augmented by cognitive capacities in evolution and development so that empathy is possible in the absence of the object of distress, from imagination or effortful processing. For example, if a subject witnesses the distressed state of an object that has been robbed, the subject may feel distressed, and may think about the object, robbery, and feelings of vulnerability and fear. Alternatively, the subject may think of the object or hear of the object's loss, which in turn activates associated thoughts related to the object – robbery and vulnerability – and produces feelings of distress.

The arguments for adaptation and evolution of perception-action processes are presented in the next section "The ultimate bases of empathy." The proximate model follows, with a review of the literature on perception-action in motor behavior, and in emotional behavior (including adult humans, nonhuman animals, human children, and individuals with empathy disorders). Finally, there is a detailed description of the role that representation plays in a perception-action model, explaining the pervasive effects of learning and experience on empathic processes. Cognitive empathy is addressed in the final section as a phenomenon based on the perception-action mechanism, but requiring additional cognitive capacities that develop with the prefrontal cortex.

## 2. The ultimate bases of empathy

Ultimate accounts are notorious for being cursory and speculative. Moreover, previous evolutionary models of empathy did not reference important empirical research available in animals and humans, and dealt only with one aspect or one level of the phenomenon. For example, many have proposed that emotional contagion exists to facilitate the mother-infant bond (Darwin 1998/1872; McDougall 1908/1923; Plutchik 1987). Because emotional contagion is considered related to empathy, the mother-infant bond is transitively used as an evolutionary explanation for empathy. While the mother-infant bond is surely important for developing empathy, this does not allow automatic forms of empathy to be linked with cognitive forms, or explain why we experience empathy for nonoffspring.

Many have proposed that inclusive fitness and reciprocal altruism explain altruism (Axelrod 1984; Hamilton 1964; Maynard Smith 1964; Trivers 1971). Because altruism and empathy are considered related, inclusive fitness and reciprocal altruism are expected to explain empathy. However, inclusive fitness and reciprocal altruism were developed to explain how behaviors that appear "altruistic" could have evolved (like taking care of someone else's offspring or alerting your neighbors to the presence of a predator).

Inclusive fitness, reciprocal altruism, and group esteem are all complementary factors that additively increase the likelihood of helping behaviors. Indeed, empathy, helping, and degree of closeness are correlated with decreasing tendencies from kin to close friends, acquaintances, and strangers (Cialdini et al. 1997), and altruistic behavior in experimental situations is directed at friends more than neutral individuals (Sawyer 1966). But with our model, inclusive fitness and reciprocal altruism did not drive the selection for empathy; they are additional benefits to a highly adaptive nervous system organization.

Perception-action mechanisms emphasize that perception selects elements in the environment that require or suggest a response by the subject. In group-living species, objects that require a response are those that the subject relies upon to attain personal goals; these are usually friends and relatives. Thus, nervous systems that respond automatically with empathy to situations where they must respond, create the appearance of reciprocity, and maximize inclusive fitness. Evidence for the effect of interdependence on empathy, human children are more motivated to help in experiments when there is a responsibility for the object's distress (Chapman et al. 1987). In the primate literature, reconciliations between former opponents are much more likely between kin and friends (de Waal & Yoshihara 1983; reviewed by Kappeler 1992). Species with cooperative kin relationships show higher levels of reconciliation between related individuals than nonrelated individuals (Aureli et al. 1989; 1997; Demaria & Thierry 2001). In chimpanzees, where male alliances are very important for intra and intergroup conflicts, reconciliation is higher among males than females (de Waal 1986a; Goodall 1986b; but see Baker & Smuts 1994). In an experimental situation, macaque pairs trained to cooperate for food dramatically increase their conciliatory tendency (Cords & Thurnheer 1993).

The literature suggests that empathy and helping are determined by the subject's ability to help. Human subjects are more likely to help when the level of need or potential benefit to the object is higher (Aronfreed 1968; note that this is also when the probability of reciprocation by the object is highest, Gouldner 1960). Adult human subjects that are trait sympathetic volunteer to help a distressed object when they expect to have control over the procedure or expect to be able to help the object (Smith 1992). Thus, it may be more accurate to consider helping behavior as the result of a complex cost/benefit analysis on the perceived effectiveness of helping and the effect of helping on short and long-term goals. If the cost is greater than the benefit, attention can be directed away from the distress to control or subvert empathic processing altogether, making the desire to help less likely.

According to a perception-action model, the evolution of a perception-action organization of the nervous system was the precursor to empathy; this organization is adaptive for much more basic reasons than helping behavior. This organization adaptively generates responses from perception, using the same representations to code objects and their associated actions. This is computationally more efficient in terms of the way the information is processed and the storage space it requires. It also facilitates appropriate responses to the environment (like ducking away from a projectile or attacker). Such behavioral tendencies are the keystone of reproductive success.

The general benefit of a response-oriented nervous system laid the groundwork for a perception-action organization. This organization was further refined in group-living animals, because social animals have as much a need to respond with another individual with a matching response as they do to respond to another individual with an instrumental response. This change to the perception-action organization made possible all phenomena that rely on state-matching or social facilitation, including empathy. Thus, affective resonance, state matching, emotional or affective empathy all rely on this transition. Basic information processing components of empathy (such as effects of familiarity, similarity, and experience) were possible as long as there were networks of neurons that changed from experience. But later increases to the prefrontal cortex also augmented these processes to allow empathy to take place in a top-down manner, with more control, and in a broader range of situations. Subsequent sections examine the extent to which perception-action processes exist across species and why these processes are adaptive.

### 2.1. Perception-action processes facilitate group living

McDougall noted that empathy appears to exist in group-living animals, or those with the "gregariousness instinct," because these animals are innately affected by the emotions of others (McDougall 1908/1923). According to McDougall's theory, sympathy "is the cement that binds all animal societies together, renders the actions of all members of a group harmonious, and allows them to reap some of the prime advantages of social life" (McDougall 1908/1923, p. 93).

If one group member sees something dangerous, usually a predator, an alarm call is given and in most cases the group moves away from the source of danger en masse. Thus, the alarm of one individual alarms others. This phenomenon is empirically documented for many species, including ground squirrels (e.g., Sherman 1977), birds (e.g., Powell 1974), and monkeys (e.g., Cheney & Seyfarth 1985). Given this behavior, danger is more likely to be detected even though each individual spends less time on vigilance (Kenward 1978; Powell 1974). The "more eyes" phenomenon allows individuals to spend more time on other activities that promote reproductive success such as feeding and finding mates. The evolutionary importance of detecting and responding to danger is evident in the general design of the nervous sys-

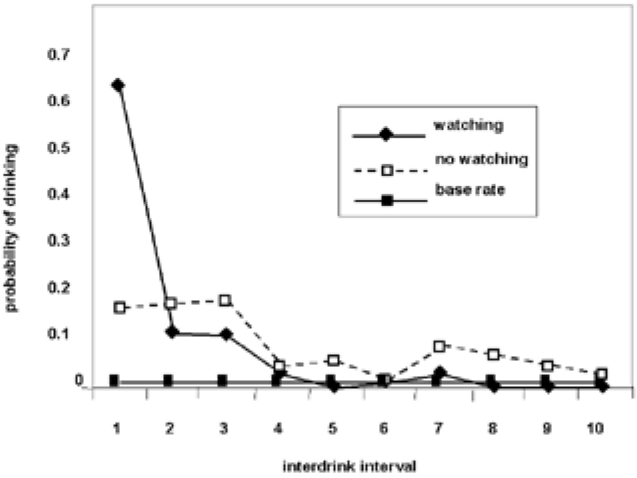


Figure 2. Social facilitation of drinking in captive hyenas (adapted from Glickman et al. 1997).

tem. Response circuits dedicated to the perception of negative emotions, especially fear, have been easy to locate relative to positive ones (e.g., Adolphs et al. 1994; 1995; Ekman et al. 1983; Miller et al. 1966; Scott et al. 1997).

The social facilitation of behavior also relies on the perception-action mechanism, and is evident across group-living animals. For example, hyenas live in tightly bound groups that live, forage, eat, and move together. In social facilitation experiments with hyenas in captivity, when one individual drinks, the probability that an observing individual will drink in the next few minutes is 70%. Even a subject that was not actively attending is 20% more likely to drink than in baseline conditions (Glickman et al. 1997, Fig. 2). Similarly, hyena subjects successfully conditioned to avoid a food resume eating it when placed with other group members that eat the food (Yoerg 1991). The perception-action mechanism explains such examples of social facilitation.

The vicariousness of activity, often seen in group-living animals, is also symptomatic of the innate response to emotion in others. Anecdotally, wild dogs are described as nosing, licking, squeaking, and jumping at each other before the onset of a hunting expedition (van Lawick-Goodall & van Lawick-Goodall 1971). Similarly, anecdotal accounts of rhesus macaques report that a severely distressed infant will often cause other infants to approach, embrace, mount, or even pile on top of the victim; the distress seems to spread to the other infants who then seek contact to soothe their own arousal (de Waal 1996). This type of emotional contagion is also the first stage of empathic responding in humans, exemplified in experiments where infants in a nursery cry in response to other infants' cries (Sagi & Hoffman 1976; Simner 1971) and year-old children seek comfort after witnessing the injury of another (Hoffman 1990; Zahn-Waxler et al. 1992a).

There are a few main reasons not to reject the continuity of these phenomena. First, the behavioral repertoires of mammals are superficially very similar. However, behaviors of different species may appear similar, or achieve the same function, but may not share the same mechanism ("analogy" in evolutionary biology). This is especially likely for species that diverged hundreds of millions of years ago, such as vertebrates and invertebrates. Cases that rely on innate releasing stimuli, or rule-based behavior would not be related to empathy, while those that share the perception-action mechanism would. For example, fish schools could rely on a general rule where each individual maintains an equal distance to all neighboring individuals. If one individual detects a predator and tries to move quickly away, it would create mass violations to the rule and adjustments. This would have the overall appearance of group alarm, but would not be an example of empathic processing. This exemplifies the need to understand mechanism in order to categorize behavior.

Should we expect the mechanisms to be the same? Information processing, brain structure, and brain design are greatly conserved across species (Finlay & Darlington 1995; Krubitzer 1995). Moreover, there is direct behavioral, physiological, and neurological evidence for perception-action processes in monkeys, chimpanzees, and humans (reviewed in sect. 3). Finally, although there are surely differences in the cognitive capabilities across species (discussed in sect. 3), or in the phenomenology of empathy, perception-action processes are not generally accessible to conscious awareness. Therefore, the basic structures, mechanism, and application to social behavior are likely to be shared at least across group-living mammals.

### *2.2. Perception-action processes facilitate the mother-offspring bond*

The parent-child relationship both relies upon and is necessary to develop the ability of individuals to be affected by the emotional state of others (as noted by others, including Darwin 1998/1872; McDougall 1908/1923; Plutchik 1987). Infants are emotionally affected by the state of their mothers and mothers are emotionally affected by the state of their offspring.

**2.2.1. Effects of the mother on the infant.** Continuous and coordinated emotional and physical contact between the mother and infant are thought to organize the emotion regulation abilities of the infant, which determine the emotional competence of the individual (e.g., Brazelton et al. 1974; Deboer & Boxer 1979; Gable & Isabella 1992; Levine 1990; Stern 1974; 1977).

On a neurophysiological level, maternally-separated rat pups show reduced levels of growth hormone (GH) and a peripheral biochemical block between GH and the enzymatic activity required for cell protein synthesis. This can be reversed with appropriate stimulation. After 24 hours of separation, the sleep of these rat pups is also disturbed, due to the lack of entraining interactions with the mother (Hofer 1995; 1999). Separation causes arousal and the release of stress hormones in attached primate infants and mothers (Levine 1990). Rhesus macaques raised without their mother lack the normal, adaptive relationship between behavior and neurochemistry in response to stress (Kraemer & Clarke 1996). In humans, infants of depressed mothers have reduced left hemisphere activation (Jones et al. 1998) and lack the normal increase in vagal tone between 3 and 6 months that is correlated with vocalizations and optimal neurological functioning (Field et al. 1995).

Behavioral development has also been shown to rely on the mother-infant relationship. Isolate monkeys are impaired at sending and receiving emotional expressions to typically-developing conspecifics (Miller et al. 1967), a task easily done by normally-developing individuals (Miller et al. 1962; 1963). The expressive impairments of the isolate animals has been compared to that of humans with autism, who are also impaired at the communication of affect (e.g., Bemporad 1987; Harlow & Harlow 1966; Miller et al. 1967). Infants of depressed mothers are impaired at matching happy facial and vocal expressions (Lundy et al. 1997) and show less orientation and fewer facial expressions in response to modeled happy and surprise expressions (Lundy et al. 1996).

We argue that the PAM subserves the ability of infants to perceive and learn from the expressions of the caregiver. The actions and expressions of the mother are mapped onto existing representations of the infant and generate actions and expressions in response. This facilitates not only the infant's ability to understand the behavior of the mother, but also facilitates coordinated activity in the dyad, necessary for the development of emotion regulation.

Infants and their caretakers are thought to use their emotional expressions to reinforce positive affect, transform negative affect, and provide breaks when arousal becomes too high (Malatesta & Haviland 1982; Tronick 1989). Such responsiveness is thought to organize behavior (Campos et al. 1983) and create a sense of security and efficacy (e.g., Bell & Ainsworth 1972). The coordinated activity between caregiver and infant seems required for emotional regulation and control (Field 1994), which are in turn required for empathic competence throughout life (Ungerer 1990). A lack of coordinated activity may contribute to behavioral problems associated with an inability to assess and control emotions, such as tantrums, poor impulse control, and risk-taking (Tronick 1989).

In humans, fear and personal distress lead to self-directed efforts and, thus, are prohibitive of empathy, sympathy, and perspective taking (Eisenberg et al. 1994). Emotion regulation problems are correlated with personal distress and a lack of helping in preschoolers, older children, college undergraduates, and the elderly (Doherty 1997; Eisenberg et al. 1994; 1996; Eisenberg & Okun 1996, respectively). Similarly, although albino rats press a bar to eliminate the distress of a hoisted animal, they do not press a bar to eliminate the distress of a conspecific being shocked. The latter situation is interpreted as being too stressful for the subjects, precluding an empathic response (Rice 1964). Thus, without emotional linkage, or the interactions necessary to develop its capacities, infants cannot learn to regulate their emotions and the development of more advanced forms of empathy are compromised.

Emotional linkage can also teach offspring about their environment. If an infant is aroused by the display of emotion in the parent (especially fear or distress), then the infant can use the mother's reaction as an unconditioned stimulus to learn about danger. For example, if an infant monkey is aroused by the arousal of a parent in the presence of a snake, it can learn to fear snakes without the need for a more costly direct experience (Mineka & Cook 1988; 1993; Mineka et al. 1984). Typically-developing 12-month-old children socially reference the mother in the face of ambiguity (Feinman 1982; Klinnert et al. 1983). When presented with a loud toy in the lab, children this age approach the toy if the mother smiles but approach the mother if she expresses fear. When infants approach a visual cliff, social referencing to the mother determines whether or not the infant will cross (Sorce et al. 1985). These infants display negative affect after referencing a mother with a fearful expression (Klinnert et al. 1983; Sorce et al. 1985). The mother's emotion is adaptively perceived and incorporated into the offspring's actions without necessitating the same level of response (as in alarm) or direct experience (as required by conditioning). Social referencing studies have found negative emotions to affect the behavior of infants much more than positive ones. This is in accordance with findings from other fields, and with the importance of alarm and distress contagion on reproductive success.

**2.2.2. Effects of the infant on the mother.** It is also adaptive for the parent to be affected by the emotional state of the infant. In the ethological literature, Eibl-Eibesfeldt (1971/1974) postulates that the evolution of parental care in birds and mammals created not only actions by the parent to care for offspring, but also concurrent actions by the offspring to request care. Interactional views of development similarly postulate that the infant directs the mother's behavior as much as the mother directs the infant's (Bell 1968; 1971; Brazelton et al. 1974; Osofsky 1971; Wiesenfeld & Klorman 1978; Yarrow et al. 1971). Smiling and crying by the infant are thought to modify the affective and behavioral responses of their caregivers. Such behaviors signal the infant's state, providing the impetus for attention and action (Acebo & Thoman 1995; Bowlby 1958; 1969). Illustrating the importance of infant-to-mother communication, a deaf female chimpanzee at a zoo lost a succession of infants despite intense positive interest because she did not correct positional problems (such as sitting on the infant, or holding it the wrong way) in response to soft distress calls (de Waal 1982). What is the mechanism for such interpersonal communication?

Crying and smiling can induce autonomic arousal in the caregiver that simultaneously acts as an unconditioned stimulus to motivate a response and as the precursor stimulation for the response (Wiesenfeld & Klorman 1978). When rat pups are separated, they produce ultrasonic vocalizations that instigate the mother to search for, retrieve, and return the pups to the nest (Smotherman et al. 1978). Crying in human infants elicits high levels of maternal attention in postnatal weeks with high, continued levels of maternal stimulation (Acebo & Thoman 1992). High levels of crying associated with colic cause distress in parents (e.g., Liebman 1981; Meyer & Thaler 1971; Rowell 1978). Mothers are physiologically aroused when witnessing their own infant crying; they show an increase in heart rate and large skin conductance responses. The crying of a strange infant elicits the standard orienting response (Wiesenfeld & Klorman 1978).

Emotional contagion proximately guides the parent-offspring relationship, increasing the success of both individuals. If a similar emotion is elicited in the subject as in the object, then tailored care is much more likely. Proper care increases viability of the offspring and, thus, the reproductive success of the parent. Fulfilling the needs of the offspring also assuages the arousal of the caregiver and offsets the unwanted attention from group members and predators caused by an individual displaying distress.

Although emotional displays can coordinate, regulate, and guide the parent-child relationship, care is often provided in the absence of such releasers. What is the mechanism for these acts of helping? The association between a context and its outcome is facilitated by emotional arousal (e.g., Corodimas & LeDoux 1995). Therefore, contagious distress from offspring to parent can act as an unconditioned stimulus, motivating the parent to act before a stressful display erupts. For example, captive and wild ungulate species approach their calves for nursing before a request is emitted (Murdock et al. 1983). Through empathy, the parent can also provide care when conditioned associations to personal experience dictate it necessary. The parents (indirectly) and the offspring (directly) benefit because the offspring's needs are satisfied without the cost of unwanted attention and a stressful display.

Emotional displays can continue to indicate the needs of altricial offspring into adolescence. Distress vocalizations that include sounds of crying and whining may signal appeasement and recruit help. Temper tantrums, an extreme example, are used by offspring to direct the behavior of the caregiver after their needs diverge (Einon & Potegal 1994; Trivers 1974). Tantrums that include "screaming, crouching, hurling self on ground, running and occasionally attacking the mother" are common in young humans and chimpanzees (Einon & Potegal 1994). The temper tantrum endangers reproductive success by causing respiratory distress, damage to the vocal folds, and involving self-inflicted injury (Einon & Potegal 1994; Potegal & Davidson 1997), but it can be a successful technique because the parent is averse to the loud display of anger (Potegal & Davidson 1997).

The preceding evidence suggests that the emotional linkage between parent and offspring has a profound effect on reproductive success. It provides an unconditioned access to the infant's emotional state, and thus the need as well as the motivation to help. It conditions offspring to know when and how to request care and conditions parents to know when and how to provide care. Thus, the direct emotional link between individuals is highly adaptive for group-living individuals, especially those that provide extended care. This direct link also provides the basis for empathy and helping outside of these contexts.

Phenomena that increase the reproductive success of relatives are the purview of inclusive fitness. However, inclusive fitness models would argue that the PAM evolved to indirectly increase the reproductive success of mothers through offspring. According to our model, the PAM evolved because it is adaptive for basic responses to the environment, and for group living. Subsequently, the mechanism was exapted in altricial species to improve care of offspring, and to develop emotion regulation and synchrony; which in turn are necessary for the proper development of empathy, cognitive empathy, and helping behavior.

### 2.3. Perception-action effects outside the mother-offspring bond

Empathy may have a phylogenetic and ontogenetic basis in the emotional linkage between parent and offspring, but empathy is exercised across the lifespan in many mammals. How is empathy extended from these rudimentary forms of emotional linkage?

Empathy in alarm and parent-offspring situations was described as resulting from innate releasing stimuli. High pitched sounds that resemble alarm calls or screams induce fast action in situations of immediate physical danger, while sounds that resemble crying induce action for less immediate needs like food, comfort, and warmth. These same stimuli can be used to elicit empathy and help from nonoffspring. A distressed chimpanzee, for example, who has just lost a major battle will "pout, whimper, yelp, beg with outstretched hand, or impatiently shake both hands" in order to solicit the consolatory contact of others (de Waal & Aureli 1996). Eibl-Eibesfeldt (1971/1974) argues that the infantile releasers of caregiving are used throughout adult life, such as the use of a high-pitched voice or "baby names" between lovers.

Why is it beneficial to extend innate releasing mechanisms and care-giving beyond the parent-child relationship? Because releasers elicit distress in the receiver through the PAM, they can initiate the actions of potential allies and terminate the actions of predators and conspecific attackers. It is mistaken to argue whether help is given for the benefit of the object or to terminate the object's aversive distress signal or the subject's personal distress. Aversive signals evolved because, by definition, others want them terminated. The comparative evidence below attests to the success of these signals in soliciting help from conspecifics (for a detailed review of the comparative data, see Preston & de Waal 2002).

Given a perception-action view of empathy, these processes extend to the prediction and response to allies as well as competitors. The PAM can produce appropriate helping behaviors, as well as effective punishments. In both cases, the subject accesses the object's state and generates an appropriate response. Associated representations of the object and situation will determine whether the desired outcome is to produce or alleviate distress. The generation of the state in the subject can be bottom-up or top-down. And both could occur simply with learned, conditioned responses that prove effective in producing the desired outcome. However, there is a difference between the normal phenomenon where the subject creates distress in the object for self-defense, or to secure resources (like Machiavellian intelligence; Byrne & Whiten 1988), and the abnormal phenomenon where the subject seeks to produce or witness high levels of distress in noninterrelated objects (like psychopathy). The latter case is an impairment in the perception-action circuit for emotional states, addressed in section 3.4.5, "Evidence from disorders of empathy."

In summary, combining an ultimate and a proximate description of empathy greatly changes the argument for adaptation, allows one to link different levels of empathy, and exhibits the inherent relationship among these levels. Data is presented in the following section to support the proximate model.

## 3. The proximate bases of empathy

> *The fact was overlooked that, in order to express it, the body must in the last analysis become the thought or intention that it signifies for us.*
>
> Merleau-Ponty, *Phenomenology of Perception* (1962/1970, p. 197).

The "Perception-Action Hypothesis" (a term from motor behavior) is grounded in the theoretical idea, adopted by many fields over time, that perception and action share a common code of representation in the brain (reviewed by Allport 1987; Prinz 1987; 1992; 1997; Rizzolatti & Arbib 1998). According to the perception-action hypothesis, perception of a behavior in another automatically activates one's own representations for the behavior, and output from this shared representation automatically proceeds to motor areas of the brain where responses are prepared and executed. This organization makes sense if perceptual systems evolved to provide accurate information about the environment to appropriately plan and guide movements (Prinz 1992). These common codes are not restricted to physical movements, they include abstract, symbolic representations (Decety et al. 1997; Jeannerod 1994; Prinz 1997).

### 3.1. Existing theories

Previous theoretical accounts of empathy have implicated a perception-action model to varying degrees (Adolphs 1999; Boodin 1921; Brothers 1990; Levenson & Reuf 1992; Lipps 1903; McDougall 1908/1923; Meltzoff & Moore 1997). Lipps' (1903) theory was an early proponent of the perception-action model in motor behavior and he explicitly applied the theory to empathic processes. Similarly, McDougall stated, "sympathy is founded upon a special adaptation of the receptive side of each of the principal instinctive dispositions, an adaptation that renders each instinct capable of being excited on the perception of the bodily expressions of the excitement of the same instinct in other persons" (1908/1923, p. 95).

In more recent history, Brothers (1990) suggested that understanding the emotion of others entails to some degree experiencing the emotion observed. This hypothesis was certainly correct, though it was not linked to the experimental empathy literature, and at the time had little backing from physiological and neurological evidence. Gallup also suggested that information about the self is used to model the states of others. His "introspective" model seems implicitly more cognitive than the PAM since he did not see the object's state as being mapped automatically onto the subject's representations, and reserved the process for the few species that exhibit theory of mind (Gallup 1998b). Less directly implicating perception-action processes, Levenson and Reuf (1992) suggested that the heart-rate concordance between subjects in affect communication paradigms could be the basis for empathy. This agrees with the PAM since similar states are induced in the subject and object, but does not include central nervous system components.

Based on extensive research, Meltzoff and colleagues propose the Active Intermodal Mapping Hypothesis (AIM). The AIM is proposed to explain early facial imitation, and lay the groundwork for empathy (Meltzoff & Moore 1977; 1983; 1994). According to the AIM, the object's expression is perceived and compared to the subject's own current expression (from proprioceptive feedback) in a supramodal representational space. The subject's efferent copy is compared to the object's afferent copy in this space, equivalences are detected and reduced, and imitation results (Meltzoff & Moore 1997). According to a perception-action view the perception of the object's expression *automatically* activates a similar motor expression in the subject (in contrast to AIM), but through a representation (in agreement with AIM). This expression could in turn be compared through feedback to the representation, and the difference between copies could be detected and reduced (in agreement with AIM).

Simulation theory has also been proposed to be a mechanism for empathy, where the subject understands the mental and emotional state of the object by simulating the object's state internally (Carruthers & Smith 1996; Davies & Stone 1995a; 1995b). Generally, the perception-action mechanism and simulation theory are not in conflict. Some descriptions of the simulation process seem more explicit and cognitive than a perception-action model would suggest, but most postulate implicit as well as explicit processes.

In the literature, simulation theory stands in contradistinction to the theory-theory, which postulates that individuals understand the world through theories that they develop (Gopnik 1993; Gopnik & Wellman 1992). With the PAM, the two theories are compatible; simulation theory is a description at a level between metaphor and mechanism that is interested in how the state of the object is imparted to the subject while theory-theory is a description at the level of metaphor that is interested in the ways that these perceptions change during development (see Schulkin 2000, for a comparison of the two theories with respect to mirror neurons).

The discovery of mirror neurons (di Pelligrino et al. 1992) prompted a series of papers extending the possible function of these cells from the coding of simple motor acts, to the coding of other's mental states and these cells were suggested to provide evidence for the simulation theory of empathy (Adolphs 1999; Adolphs et al. 2000; Gallese & Goldman 1998; Iacoboni et al. 1999; Ruby & Decety 2001; Williams et al., 2001; Wolf et al. 2001; literature reviewed by Motluck 2001). While mirror neurons alone cannot produce empathy at any level, they do provide concrete cellular evidence for the shared representations of perception and action that were postulated by Lipps (1903) and Merleau-Ponty (1962/1970) and behaviorally demonstrated by Prinz and colleagues (Prinz 1997).

Given the history of a perception-action theory of empathy that extends back at least to the beginning of the last century, with small upsurgences along the way, the model seems to have had intuitive appeal to researchers looking for simple, mechanistic ways to instantiate empathy. The theory has not yet enjoyed mass acceptance, however, for many reasons. The behaviorist and cognitive revolutions directed theory away from the level of mechanism. In addition, folk psychology generally regards empathy as a phenomenon reserved for humans. Given a lack of knowledge of the mechanism, these approaches are appropriate. Now, data in humans, nonhuman primates, and rodents support the perception-action model for motor and emotional behavior, and suggest that at least across these species, the mechanisms for processing emotional stimuli are similar. These data are reviewed in section 3.4.

### 3.2. Motor evidence for the PAM

Many experiments in cognitive psychology support the direct link between perception and action. The development of cognitive neuroscience tools including brain imaging, single cell recording, electroencephalograms (EEG), transcranial magnetic stimulation (TMS), and patient studies, generated a spate of experiments testing the Perception-Action Model (PAM).

Evidence suggests that sensory inputs are automatically processed to a response phase. In a response-competition paradigm where human subjects have to choose an action based on the features of the stimulus on each trial, event-related potentials (ERP) measures suggest that partially analyzed sensory information is passed to the response phase even though the perceptual analysis is not complete (e.g., Hommel 1997; reviewed in Hillyard 1993). The results were replicated using single-unit recordings in the macaque monkey (Miller et al. 1992). Reaction-time (RT) data with a similar paradigm confirm the covert preparation of responses (Craighero et al. 1998). Similarly, when subjects have to perform two stimulus-response tasks simultaneously, the response to the second stimulus seems to be prepared before the response to the first is completed (Hommel 1998).

Premotor neurons are thought to retrieve the appropriate motor acts in response to sensory stimuli. Particular neurons in the rostral-most part of the premotor area (F5) are active during goal-directed hand movements such as reaching and grasping. A class of these cells fire when a monkey observes others making these actions (di Pellegrino et al. 1992; Jeannerod et al. 1995). These "mirror neurons" are thought to represent goal-directed actions, allowing individuals to understand and imitate the actions of others (Rizzolatti & Arbib 1998). In a brain-imaging study using Positron Emission Tomography (PET), observing an action with the intent to imitate it activated the areas used in planning and performing the actions (bilateral dorsolateral prefrontal cortex and pre-supplementary motor area) (Decety et al. 1997). In an fMRI study, the left inferior frontal cortex and the rostral-most part of the right superior parietal lobule were activated when subjects observed a finger movement and when initiating the same movement under different conditions. Further, activation was highest when the subject made the movement in response to observing the movement in another (i.e., the area was activated by the observation in addition to the movement). The results are interpreted by Iacobani and colleagues as support for the common code or "direct matching" hypotheses of perception and action. Taken with the F5 data (above), they suggest that the left frontal areas code the goal of movements and are necessary to understand the meaning of one's action. The right parietal area would then code the precise movements involved and would be necessary for memorizing or repeating actions (Iacoboni et al. 1999).

These shared representations for perception and action are also activated when a movement is imagined (Jeannerod 1995; 1996; Jeannerod & Frak 1999). Response times (RTs) for imagining walking in a three-dimensional environment follow Fitts' Law, increasing with increasing distances and difficulty (Decety & Jeannerod 1995). In addition, much evidence supports a common representation for mental and manual rotation. RTs for imagining and performing a rotation movement are virtually identical (Wohlschläger & Wohlschläger 1998). Further, task interference and facilitation in the rotation task occur only at a high level of motor processing (increasingly involving planned execution of action) (Wohlschläger & Wohlschläger 1998). When given the choice of two stimuli to rotate, the majority of subjects choose the object corresponding to their preferred hand (Cook et al. 1994). RTs for a left-right hand orientation judgment are similar for doing and imagining the movement (Parsons 1994). Further, in a PET brain-imaging study, premotor, somatosensory, and cerebellar regions were activated when subjects imagined moving their hands (Parsons et al. 1995).

There are differences in the activation between observation and imagination. In one experiment that used grasping movements as stimuli, observation of grasping movements activated the superior temporal sulcus, the inferior parietal lobule, and the inferior frontal gyrus, while grasp imagination activated Broca's area (area 44), caudal inferior parietal cortex (area 40), rostral SMA proper, and dorsal PMC (all in the left hemisphere only), and the middle frontal cortex. Cerebellum was also differentially activated by the two conditions (Grafton et al. 1996). The researchers concluded that grasp observation areas contribute to the recognition of movements while the grasp imagination areas contribute to the actual production of grasping movements (Grafton et al. 1996).

Beyond perception or imagination of the action *per se,* these motor representations seem to be activated when people perceive or think about objects that have movements associated with them. For example, naming and observing common tools activates the left premotor cortex (Grafton et al. 1997), an area involved with the planning of movements in response to stimuli, where learned motor sequences might be stored. Therefore, even relatively abstract cognitive affordances of objects may be partially coded with respect to their appropriate motor acts, or at least activate the representation of the appropriate motor responses.

Taken together, actions that are self-generated, perceived in another, imagined, or even suggested by an object seem to activate shared representations. These shared representations may be at the abstract level of meaning, but they are linked downstream with areas responsible for the performance of the action. Activation is thought to spread from the representation of the meaning to that of the performance if there is no inhibition, but the extent to which motor sequences are activated depends on the mode of input, salience of and attention to the stimulus, and extent of inhibitory control (addressed further below).

The following section will address the extent to which this data can be applied to a proximate mechanism of empathy. The major findings in the empathy literature are recontextualized in light of the PAM so that a coherent model can be created that incorporates prior theories and empirical findings with the ultimate model and this emerging Zeitgeist in cognitive neuroscience.

### 3.3. The neuroanatomy of empathy

Based on the literature reviewed in the mechanism section, one might conclude that mirror neurons in premotor or parietal areas are where shared representations are stored, regardless of the type of stimuli. However, natural complex emotional situations require the activation of many complex factors, including episodic memories, autonomic sensation, and emotional valence. Because shared representations are networks of neurons that are interconnected, there is no one place in the brain where they exist. Below, a sketch is provided of some of the neural structures required for complex empathic processes (see Adolphs 1999, Schulkin 2000 for detailed reviews on the functional neuroanatomy of social cognition).

Premotor areas are necessary for planning, sequencing, and executing motor acts. As described above, the left frontal operculum of the premotor cortex (Broca's area 44) and the right anterior parietal cortex (PE/PC) contain mirror neurons activated by self and other movements, which are thought necessary to understand and imitate the actions of others. The right parietal operculum contains cells that receive direct kinesthetic, sensory feedback; thus, it is likely that this area codes for the precise movements involved in an action (Iacoboni et al. 1999), which can also be used as a template of the outcome of a motor act during active imitation. Since movements include emotional body postures and facial expressions, these cells would be activated by the perception of the object's emotional state. Generation of facial expressions occurs from brain stem nuclei projections to the facial nerve. Insular cortex (especially the dysgranular intermediate zone) is also situated between the premotor cortex and the limbic system. So, if the mirror neurons represent emotional behavior, then the insula may relay information from the premotor mirror neurons to the amygdala (see Augustine 1996).

Long-term memories of objects, places, and people are stored in the temporal lobe. The fusiform "face" area of the temporal lobe seems particularly specialized for processing face and eye gaze information. Somatosensory-related areas are activated for sensations in the self and when observing another's state. These "representations" of information change with experience, accounting for the major effects on past experience, similarity, and familiarity in the empathy literature (see sect. 4).

The amygdala helps to potentiate memory consolidation processes in the hippocampus (McGaugh & Cahill 1997), and may directly mediate memories of some fear-related stimuli (LeDoux 1993). There are direct connections from the amygdala to the brain stem areas that control autonomic states and indirect connections through the hypothalamus. The former connections are more likely to be involved with the perception of emotional information, especially for fear and distress, because they code for learned emotional associations, while the latter maintain homeostasis on a moment-to-moment basis. Cortical projections are also thought to be able to affect autonomic states, but these pathways are not well known (Burt 1993).

Similar to LeDoux's two systems for processing emotional stimuli (LeDoux 1996/1998), empathy processes likely contain fast reflexive sub-cortical processes (directly from sensory cortices to thalamus to amygdala to response) and slower cortical processes (from thalamus to cortex to amygdala to response). These roughly map onto contagious and cognitive forms of empathy, respectively.

The limbic circuit projects primarily to the cingulate and orbitofrontal cortices, which are known to be involved with the perception and regulation of emotion. Prefrontal size correlates with emotional regulation skills in development and phylogeny, thus, the prefrontal cortex is thought necessary for the ability to control the extent of personal distress and remain focused on the object. Dorsolateral and ventromedial prefrontal regions are necessary for the maintenance of information in working memory, the former even more for the manipulation of this information. They are thus implicated in cognitive empathy processes where the state of the object must be held in mind and alternative interpretations considered by activating somatosensory, limbic, and response areas. The ventromedial prefrontal cortex is additionally thought to be necessary for combining immediate goals with long-term goals to determine an adaptive response, thus it is likely involved in cost/benefit analyses for when to engage the empathy system and when to help.

The cerebellum (which is necessary for the prediction and planning of attentional shifts) feeds heavily to the frontal lobes, where the frontal eye fields control eye movements. The cerebellum is important for learning and executing attentional shifts that maximize the amount of information obtained from a given scene (e.g., the object's state), as well as for learning how to avoid attending to emotional stimuli that would be unnecessarily arousing.

The fact that the left hemisphere is most often affected in the former motor studies while the right hemisphere is selectively implicated in emotion processing is not problematic for the PAM. If it is a general principle of the nervous system that perception activates response, then the particular hemisphere involved depends on the stimuli. Broadly speaking, the left hemisphere (in right-lateralized subjects) processes detailed information while the right hemisphere is selective for more holistic information (reviewed by Liotti & Tucker 1995). Related to the PAM, the left prefrontal area is more active in response to semantic cues, the right when responses must be generated from memory, and both when the task requires generating voluntary or imagined actions (e.g., Adolphs et al. 2000; Decety et al. 1997). Related to emotional processing, the right hemisphere may process all emotional stimuli (Gur et al. 1994; Lane et al. 1999; Schwartz et al. 1975), or the right hemisphere may subserve fearful or negative emotions while the left subserves positive (e.g., Canli et al. 1998; Davidson & Ehrlichman 1980). Supporting the lateralization of emotions in our closest relative, chimpanzees shown positive, negative, and neutral videos, showed increased brain temperatures in the right hemisphere to the negative videos depicting severe aggression (Parr & Hopkins 2000). Future research specifically aimed at delineating the perception-action circuit for empathy and emotion processing can confirm hemispheric specializations.

Data suggest that all of these areas are activated when observing or experiencing an emotional state, as well as when imagining such a state; damage to any of them will impair some aspect of the phenomenon. The effects of the damage will crucially depend on the interaction of the time the damage was incurred and the location. Damage to areas necessary for the learning of information are more devastating early on, while damage to areas where the memories are stored are more devastating later.

### 3.4. Emotional evidence for the PAM

**3.4.1. Animal behavioral evidence.** As discussed in the introduction, albino rats pressed a bar to terminate the distress of an object suspended by a hoist (Rice & Gainer 1962). This "altruism effect" could not be replicated with a paradigm that used looped recordings of rat squeaks as the stimulus (Lavery & Foley 1963). Alternatively, rats decrease bar pressing for an object that is being shocked (Church 1959; Rice 1964). A decrease in bar pressing by the subject is an indication of fear (cf. Estes & Skinner 1941). According to a perception-action theory of empathy, the subject is distressed because the state of the object is imparted to him directly. Consistent with Church's conditioning model, prior experience with shock facilitates and augments the natural distress response. These effects were replicated with pigeons (Watanabe & Ono 1986).

In experimental paradigms, rhesus monkey subjects also pressed a bar to avoid witnessing the shock of a conspecific object. Subject-object pairs were conditioned to expect a shock to the object after illumination of the compartment.

In these cases, the object "leap[t] and [ran] around whenever its compartment was illuminated." Seventy-three percent of the time, the subject pressed the bar to this agitation alone, displaying "piloerection, urination, defecation and excited behavior" (Mirsky et al. 1958, p. 437). After the subjects' response was extinguished, it could be reinstated using pictures of monkeys, but not using the shock of a live albino rat or the thrashing of a monkey-like puppet (Miller et al. 1959a). The response to pictures was less strong and clear than to the live animals, but the response was stronger to pictures of familiar monkeys than unfamiliar ones (Miller et al. 1959a). These results replicate those from rats and pigeons. After learning the consequences of shock, the monkeys were aroused by the sight of a conspecific in distress, acted to eliminate the suffering of the stimulus animal, but were not responsive to artificial or unfamiliar stimuli.

The chain-pulling experiment in the introduction more directly indicates an "altruistic" effect, as monkeys refrained from rewarded actions, even starving themselves, when it caused another monkey to receive a shock (Wechkin et al. 1964). Again, subjects who had previously experienced shock or were familiar with the object were more likely to sacrifice food rewards (Masserman et al. 1964). Chimpanzees also show emotional contagion-like responses to the displays of conspecifics. In one experiment, subjects were shown three types of videos, depicting positive, negative, and neutral stimuli (play, severe aggression, and scenery, respectively). The subjects responded to the aggression tapes with "piloerection, pant-hoots, and bluff-displays," to the positive play videos with "play faces, body gestures and solicitations to the video monitor that indicated an initiation of play," and to the control tapes with "strong visual orientation . . . but no indication of social arousal." (Parr & Hopkins 2000). In a similar experiment, peripheral skin temperature decreased (indicating greater negative arousal) when subjects viewed videos of conspecifics injected with needles or videos of needles themselves, but not videos of a conspecific chasing the veterinarian (Parr 2001). These subjects correctly matched the video with a picture of an emotional expression in a chimpanzee that had the same valence (Fig. 3).

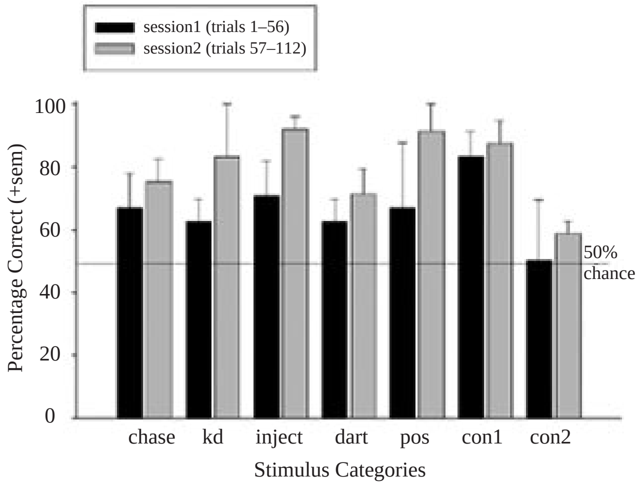


Figure 3. Mean performance on matching-to-meaning trials on the first and second testing sessions (Parr, in press).

**3.4.2. Human developmental evidence.** Infant nonhuman and human primates are known to respond to the distress of others with distress (e.g., de Waal 1989; Sagi & Hoffman 1976). Further, newborn human infants are predisposed to mimic the facial expressions of others (Field et al. 1982; 1985; Meltzoff & Moore 1977; Stern 1977). Human newborns can imitate fear, sadness, and surprise (Field et al. 1982), again indicating the importance of communicating distress.

In preschool observations of 25–41 month-olds, sustained play occurred when the bout was initiated with imitation. In a study with toddlers (21–30 months) and preschoolers (31–64 months), toddlers that were friends (as compared to acquaintances) had greater concordance in the amount of time spent in directing and following/imitating behaviors, parallel play, and requesting. Connecting behavior to physiology, the friend dyads also had a greater concordance in baseline heart rate and cortisol measures. Therefore, similarity even on a physiological level seems to predict friendships characterized by imitative or reciprocal behavior (Goldstein et al. 1989).

The infant data suggests that the link between perception and action is strongest initially, and refined through experience. Thus, while perception automatically proceeds to action in infants, this progression weakens with age and experience. In an imitation task with human infants of different ages, there was an overall decrease from two to three and from four to six months in perception-action processes, assessed through multiple measures such as: attention of the infants to the object, general expressiveness of the infants, correspondence between the infants' expression and the object's expression, ability to predict the object's expression from that of the subject (Field et al. 1986). Indicating that imitation is still prominent in subsequent months, children 10- to 14-months old respond to the distress of others with distress expressions that imitate the object (Zahn-Waxler et al. 1977 in Thompson 1987). The researchers suggested that these children were "trying on" the expressions to understand them. Einon and Potegal (1994) note that the open display of emotions in 2-year-olds "would be considered pathological in an adult" (p. 189). They cannot explain in principle why the intensity of emotions should be so strong in children, especially with family members, but postulate that tantrums play a role in learning to control and confine expressions.

The perception-action link can explain the strength of expression and imitation in children if, initially, processing automatically proceeds from perception to activation of the representation to response. In development and phylogeny, tonic inhibition of activated motor representations can prevent perceived actions from generating overt responses. Thus, while the cries of an infant object cause an infant subject to cry (Sagi & Hoffman 1976), the same is not necessarily true even in early childhood. Patients with prefrontal lesions exhibit compulsive imitation of gestures and complex actions in the laboratory (L'hermitte et al. 1986), supporting the idea that responses are always prepared or primed, but prefrontal cortex inhibits the response. Display rules may also play a role in learned inhibition of expressions (Cole 1986; Ekman et al. 1969).

The ability to distinguish self from other would also explain a developmental decrease in expression and imitation. The proliferation of experience with self-generated motion and causal agency (e.g., Johnson 1987) creates response circuits that are dedicated to, or primed for self-action. For example, activity in the right parietal lobule seems to represent reafferent activation from motor action. Thus, activity in this area could distinguish activity from observing an act in another from self-generated activity. This mechanism is suggested for distinguishing self from other in imitation (Georgieff & Jeannerod 1998; Iacoboni et al. 1999). Applied to empathy, with an understanding of the way representations change with experience, this mechanism parsimoniously explains differences between and within individuals in the level of empathy expressed, since development of self-other differentiation is highly correlated with the development of empathy (see Hoffman 1978a; Meltzoff 1993; Meltzoff & Moore 1993), and both are correlated with development of the prefrontal cortex.

**3.4.3. Human behavioral evidence.** Most behavioral research with humans focuses on the way that representations change with experience. These data are addressed below in section 4 – "Representation and cognition." Data in humans also implicate a "direct matching" between subject and object. In a six-condition experiment, subjects attend either to an object in need or the potential helper, when help is given or not, and appreciation is shown or not. The subjects felt the emotion they imagined the attended character to be feeling, and the quality of the emotion determined the likelihood of helping. For example, if help is not given in the scenario and subjects were attending to the object, they report sadness and anger. If help is given, subjects attending to the object or the helper report elation (Aderman & Berkowitz 1969). In another study, 2-year-olds are more aggressive towards peers after observing a simulated conflict between adults (Cummings et al. 1985). The perceptions and responses of the subjects were primed by the observation of aggressive encounters. Such responses can be inhibited or overridden by prosocial responses towards others, but this requires learning.

These effects have profound practical importance, since the spread of emotion from one individual to another may be a source of error in social interactions. When the subject perceives the negative state of the object, it primes the subject's own negative state, which is often falsely appraised as "the object is mad at me" or "I am mad at the object." The subject is then negative towards the object and vice versa, resulting in an unpleasant interaction or a fight even though the object's original state was unrelated to the subject. Similarly, in parent-child interactions, the distress of the child may distress the parents, causing inappropriate parenting and possibly physical abuse. These effects underscore the fact that the outcome of empathic processes is not always positive.

**3.4.4. Physiological and neurological evidence.** Humans experience the same physiological changes participating in a conversation and watching it later from video (Gottman & Levenson 1985). Macaques have the same heart rate response experiencing distress or perceiving expressions of distress in others (Miller et al. 1966). The successful communication of affect in monkey and human subjects requires an equivalent heart rate in receiver and sender (Miller et al. 1967; Levenson & Reuf 1992, respectively). This "physiological linkage" has been speculated to be the physiological substrate for empathy (Levenson & Reuf 1992).

People exposed to pictures of emotional facial expressions spontaneously activate the valence-appropriate muscles, measured with EMG (Dimberg 1982; 1990). Pictures of happy faces elicit *zygomatic major* muscle activity and angry faces elicit *corrugator supercilii* activity (Dimberg & Thunberg 1998), even when the pictures are processed outside of awareness (Dimberg et al. 2000). Moreover, subjects in a similar experiment reported feeling an emotional reaction, consistent with the emotion displayed and the muscles activated (Lundqvist & Dimberg 1995).

Damage to the right somatosensory-related cortices (S-I, S-II, anterior supramarginal gyrus, insula) impairs the ability to recognize basic emotions and make intensity judgments from photographs (Adolphs et al. 1997; 2000). In addition, damage to the somatosensory-related cortices impairs emotional concept retrieval. Adolphs and colleagues interpret these results as evidence for a cortical role in emotion recognition. Upon perceiving the facial expression of the object, the subject automatically retrieves visual and somatic information that can be used to understand the state of the other, or constructs a somatosensory representation on-line to simulate the state of the target (Gallese & Goldman 1998; Goldman 1992; Rizzolatti et al. 1996).

Evidence for perception-action processes also exists at the cellular level. During a single-cell recording experiment in the anterior cingulate cortex, a variety of painful and innocuous stimuli were administered to awake human patients. One neuron responded selectively to the anticipation and delivery of noxious mechanical stimulation (pinching, pinpricks), as well as to observation of the experimenter receiving pinpricks. In general, cells in this area code selectively for stimulus recognition properties as well as affective properties of certain painful stimuli (Hutchison et al. 1999).

**3.4.5. Evidence from disorders of empathy.** A general "empathy disorder" has been suggested to be a characteristic component of many other disorders including autism, sociopathy, prefrontal damage, fronto-temporal dementia, and even anorexia nervosa. Empathy disorders are characterized by impairments in the conception of mental states, expression of emotions, and verbalization of feeling states due to dysfunction in the brain areas that subserve empathy (see Gillberg 1992). The diffuse nature of the PAM circuit explains how many different disorders can result in empathy impairments. Extensive reviews of empathy disorders already exist (e.g., Baron-Cohen et al. 1994; Cohen & Volkmar 1997; Gillberg 1992; 1999; Prior 1988; Sigman & Ruskin 1999); thus, only data that shed particular light on the mechanism of empathy are addressed.

Supporting the importance of the mother-infant relationship for perception-action processes, dyads of depressed mothers and their infants spend a smaller proportion of time matching behavior states than nondepressed dyads (Field et al. 1990). The behavior states and heart rates of the depressed mothers and their infants also cohere less (Field et al. 1989). The fact that depressed dyads match negative behavior states more often than positive (Field et al. 1990) reveals that they are capable of matching behavioral states through the PAM. However, the depressed mothers seem to model positive expressions less; this would impair the ability of the infants to represent positive states, which in turn accounts for impairments in attention, recognition, and imitation of such states. Further, the depressed mothers may spend less time imitating the expressions of the child, which would impair modeling, imitation, and general emotion regulation abilities of the child.

By contrast, a disruption in the perception-action link in psychopathic or sociopathic individuals (the terms have been used interchangeably) would account for the characteristic lack of normal autonomic responses to the distress cues of another, the social isolation, and the apparent disregard for the emotional and physical state of others (Aniskiewicz 1979; Blair et al. 1997; House & Milligan 1976). Moral reasoning is also impaired in sociopathic children, even controlling for cognitive development, IQ, or social class (Blair 1995; 1997; Blair et al. 1997; Campagna & Harter 1975). Without the ability to be aroused by the distress of others, these individuals cannot understand and learn about the state of others through their own substrates. Providing a sense of continuity, psychopathy also appears to be a relevant dimension for personality in animals, namely, chimpanzees and dogs (Lilienfeld et al. 1999).

Focal prefrontal cortex damage and closed-head injury in adults result in changes in empathy (reviewed by Eslinger 1998). Patients with early-onset damage to the prefrontal cortex have a syndrome resembling psychopathy, with little or no empathy or remorse, a paucity of lasting social relationships, significant impairments on moral reasoning despite normal performance on intellectual tasks, and a deficient increase skin conductance response to risk in a gambling task (Anderson et al. 1999). One of the two subjects with early prefrontal damage was a mother marked by "dangerous insensitivity to the infants needs" (Anderson et al. 1999, p. 1032). The authors propose a mechanism for the disorder whereby brain damage prevents patients from developing knowledge of the emotional aspects required for navigating and understanding social situations.

Empathy impairments in sociopathy and autism are also thought to be partially due to a disruption in the prefrontal system because both involve deficiencies on tasks requiring inhibition, planning, and attention (Campagna & Harter 1975; Dawson 1996; Gillberg 1999). However, because expression, imitation, and recognition of expressions and gestures are impaired in individuals with autism, it is likely that the disorder is characterized by an impairment early on in the perception-action pathway (see also Williams et al. 2001).

Deficits in autism exist on the same processes required for development of empathy in typically-developing individuals. Infants with autism lack the coordination of activity with their caregiver suggested to regulate and organize emotions (e.g., Brazelton et al. 1974; Deboer 1979; Gable & Isabella 1992; Levine 1990; Stern 1974; 1977). They are less likely than normal children to smile in response to smiles from their mother and less likely to combine eye contact with smiles (Dawson et al. 1990; Kasari et al. 1990). Twenty-month-old infants do not attempt to engage the attention of an adult in response to an ambiguous object or situation, do not respond with affect and attention to the live distress of an adult, and are impaired at imitation (Charman et al. 1997). Later in childhood, similar tasks also show a diminished response to the object's distress (Dawson et al. 1990; Kasari et al. 1990; Loveland & Tunali 1991; Sigman et al. 1992). Older children with autism do not use joint attention or gestures to share mental experiences with others (Baron-Cohen 1989; 1995; Kasari et al. 1990; Mundy et al. 1986; Sigman et al. 1986), though they can direct their own and the attention of others to obtain and convey information (Charman et al. 1997; for a review see Mundy et al. 1994). Children with autism do not report feeling the same emotion as a protagonist on a videotape (Yirmiya et al. 1992). Skin conductance measures of autistic and normal children show higher responses to color slides of distress and threatening objects than to neutral stimuli, and some autistic subjects spontaneously report an aversive response to distress slides, but the autistic children had significantly lower responses to threatening objects than normals (Blair 1999).

The spontaneous expressions of individuals with autism are more neutral and idiosyncratic than comparison subjects, described as including "bizarre," "mechanical," or "incongruous" aspects (Loveland et al. 1994; Ricks 1979; Yirmiya et al. 1989). They display less positive affect than comparison individuals, especially the vicarious form (Dawson et al. 1990). They have difficulty recognizing emotional expression in the body (Hobson 1993; Hobson et al. 1989), and the face (Bormann-Kischkel et al. 1995; Capps et al. 1992; Hobson et al. 1989; Macdonald et al. 1989; Tantam 1989, but see Ozonoff et al. 1990 and Prior et al. 1990). There are also impairments on matching different but corresponding aspects of emotional expression such as facial expression and vocal affect (Hobson 1986a; 1986b; Hobson et al. 1988; 1989; Loveland et al. 1995). Some believe, however, that their deficit is restricted to complex emotions such as surprise and embarrassment (Baron-Cohen 1994; Bormann-Kischkel et al. 1995; Capps et al. 1992). Children with autism also show impairments imitating body movements (particularly unfamiliar ones), actions on objects, and gestures (particularly facial) (Curcio 1978; DeMyer et al. 1972; Jones & Prior 1985; Ohta 1987). However, basic-level gestural and procedural imitation may be intact in school-age children with autism (Charman & Baron-Cohen 1994; Morgan et al. 1989).

A high-functioning autistic adult reports that although he has difficulty understanding or participating in social interactions, he puts great effort towards such interactions and as a result has formed meaningful relationships (Cesaroni & Garber 1991). Indeed, the data suggest that individuals with autism have emotional reactions to their environment and the people in them, but the quality of their experience is different. Individuals with autism have been responsive and playful in some laboratory interactions, show positive and negative emotions like comparison groups, and form attachment relationships (for a review see Capps & Sigman 1996). They show autonomic reactions to the distress of others, but may be less likely to attend to this distress and/or have a matching physiological response, reducing the possibility of an accurate behavioral response.

Theories about the neurological nature of the disorder implicate the cerebello-frontal pathway. Twelve out of twelve cerebellum samples from individuals with autism showed decreased Purkinje cell counts in the vermis and hemispheres of the cerebellum. On average, cells in the cerebellum were reduced by 30–50%, in one case 95%. Imaging data shows that individuals with autism have smaller cerebellums than typically-developing individuals, evident from before the first year and persisting throughout life. As further evidence, this decrease in cerebellar size from MRI analysis is correlated with the degree of slowed orienting in children with autism (Harris et al. 1999).

The cerebellum is thought to be important in motor and cognitive tasks that require subjects to coordinate physical and mental activities with external stimuli, including social and emotional processes (see Courchesne 1997). It is required for stimulus-driven motor behavior and feeds heavily to the frontal cortex. Thus, autism may result from an abnormality that precludes forming the normal links between perception and action, perhaps at the level of orienting attention to the relevant stimuli. Given the importance of orienting and joint attention processes in emotional development, individuals with autism are doubly impaired because the inability to gather information from the environment compromises their ability to learn shared affect and to develop emotion regulation, both of which are necessary for empathy and theory of mind.

The role of attention in empathy is supported by behavioral data from individuals with autism. These subjects perform better on tasks in the laboratory than in more naturalistic settings, possibly because there are fewer distractions in the laboratory and response time is not limited (Capps & Sigman 1996; Gillberg 1999). Children with autism are only impaired on social perception tasks when there is more than one cue, suggesting that their impairment on orienting, disengaging, and selecting targets for attention underlies the general social deficits (Gillberg 1999). In cognitive tasks, children with autism tend to focus on local-level, isolated stimuli, rather than global-level, contextualized stimuli; normally developing children and developmentally-delayed children without autism tend towards the reverse (Frith 1989).

In conclusion, the varied types of empathy disorders support the idea that empathy is a neurologically-distributed process. Empathy disorders are most severe in individuals who have problems from infancy. The specific impairments of individuals with empathy disorders support the need for an innate orientation towards socio-emotional stimuli. Without that, emotional development in general will be impaired, precluding empathy. For proper development, social-emotion interest must also be met with behavioral responsiveness and coordination by the caregiver. Many PAM-related processes seem to rely on this unfolding of events, including lower level behavioral processes like imitation, expression production, and expression recognition.

## 4. Representation and cognition

### *4.1. Representation as a common denominator*

As mentioned in the introduction, the most robust effects in empathy experiments can broadly be categorized as effects of familiarity/similarity, past experience, learning (explicit and implicit), and cue salience. The former three effects can be explained by the PAM because they inherently rely on representations; the last because it differentially activates representations.

**4.1.1. Representations change with experience.** The effects of familiarity, similarity, past experience, and learning are often addressed as separate variables due to the slightly different emphasis of each discipline. Learning, for example, is more relevant to developmental studies, because these studies focus on the role of rearing on individual differences. Past experience is more applicable to animal studies because of its role in determining a subject's response to an unconditioned stimulus. However, all of these effects result from the ability of the nervous system to create and refine representations through experience.

In his famous essay, "What is it like to be a bat?", Nagel postulates that the "objective ascription of experience is possible only for someone sufficiently similar to the object of ascription to be able to adopt his point of view . . . the more different from oneself the other experiencer is, the less success one can expect with this enterprise" (Nagel 1974, p. 442). Similarly, Titchener thought that through empathy, one could understand individuals of intellectual and moral similarity (Titchener 1915, in Wispé 1987). Hume (1888/1990) noted that it is easier to sympathize with someone if you have something in common with that person. According to Freud, "everything that establishes significant points in common between people arouses such fellow feelings, such identifications" (Freud 1950, p. 83). These theorists all touch on the extent to which familiarity and similarity facilitate empathy and perspective taking.

The greater the familiarity or similarity, the richer the subject's representation of the object. A rich representation involves more associations, and thus, creates a more complex, elaborated, and accurate pattern of activity in the subject; this pattern is encoded with reference both to personal experience and experience with the object. For example, when one perceives the distress of a loved one, the subject's own representation of distress will be activated by the facial, body, and vocal expressions of distress in the object. Importantly, the representation of the loved one will also be activated. These representations have been created over many, many interactions, across many situations, and thus, include associations to previous instances of distress in the object, the object's attitude towards the situation, the long-term consequences the distress will have on the object, and so on. Thus, the distress of the subject will be greater upon perceiving distress in a familiar or similar individual because the ability to elaborate on the distress is greater.

The most robust findings across all species studied are for familiarity or similarity of the subject with the object and previous experience with the distress situation (Table 1). For example, from 9–12 months, children prefer to play with children of the same age and sex (Smith 1988). In an experiment with preadolescent boys, subjects imitated the actions of a model when playing a war strategy game more when manipulated to feel similar to the model (Rosekrans 1967). Experiments with 6- and 7-year-old children show that there is more empathy for an object that is the same sex of the subject (Feshbach & Roe 1968). In experiments with adults, human subjects who witness the shock of a conspecific offer to take the shocks for the object if their similarity is manipulated with demographic descriptions. If they do not feel similar, they only offer to take the shocks if they have to watch the object receive the remaining shocks (e.g., Batson et al. 1981; Toi & Batson 1982). The same interaction occurred with an attribution paradigm (Batson et al. 1981). In another paradigm, male subjects presented with an object that won money or was shocked showed more of a physiological response, identified with the object more, reported more distress to the shock and helped more when they were made to feel similar (Krebs 1975). In addition, because of the perception-action link, familiarity will cause the emotional expressions of the subject and object to converge (Anderson, 2001). This results in a more ready mapping of perception to action, and better understanding.

The richness of the representation also entails that the subject's ability to perceive the state of the object will be less affected by noise in the signal. The subject will recognize the object from further away, in less clear conditions, and with a shorter exposure time than an acquaintance. Applied to empathy, the subject will perceive the state of the object more quickly, from more subtle cues, and in more ambiguous situations. Although, given longer to decide, a subject can apply conscious cognitive processes to interpret the state of an unfamiliar object.

At the most basic level, the PAM requires the subject and object be at least familiar or similar enough to allow for direct perception. The prototype theory of categorization (e.g., Rosch 1973; 1988; Rosch & Mervis 1975) predicts that the strength of the activation of a representation is proportional to the degree of overlap between the input and the representation (McClelland & Rumelhart 1985). Thus, the sight of a primate moving a forelimb would more strongly activate a human's representation than the sight of a rodent. In turn, a rodent would activate the representation more than a reptile. The morphology and biomechanics of the movement overlap more in the former cases and thus activate the representation more strongly.

The extent to which animals empathize with members of their own and other species can be attributed to such differences in morphology and biomechanics (as also noted by Hume 1888/1990). The pervasive tendency for humans to anthropomorphize and personify exemplifies the perception-action process, but the extent to which one identifies with these objects is proportional to the extent of overlap. Monkeys experimentally conditioned to react to an object's distress did not respond to the shock of an albino rat or to the simulated distress of a monkey-like puppet (Miller et al. 1959a). Much comparative data notes the need for stimuli to be naturalistic or multi-modal to evoke a response (e.g., Lavery & Foley 1963; Miller et al. 1959; Partan & Marler 1999; Preston & Jacobs, 2001). Similarly, increased experience is thought necessary for empathy towards differently-abled objects. For example, through learning, nonhuman primates show increased tolerance toward handicapped individuals. Two chimpanzee juveniles housed with an injured female were anecdotally described as they "scrupulously avoid disturbing [the female] . . . now and then one or the other would go to her and touch her gently or caress her" (Yerkes & Yerkes 1929, p. 297). Even aggressive macaque species treat handicapped individuals with more tolerance than typically-developing individuals (de Waal et al. 1996). Experience can refine the subject's representation, promoting tolerance and help that is tailored to the object's needs.

Familiarity can supplant absolute similarity, perhaps especially when emotional attachment is involved (which is also when a response is more necessary). In home tests of empathy with children, the family pet often responded with consolation to the adult feigning distress (Zahn-Waxler et al. 1984). Lucy, a chimpanzee raised by a human family is anecdotally described as exhibiting efforts to break up conflicts, running to comfort the wife when ill, exhibiting "protectiveness toward her, bringing her food, sharing her own food, or . . . attempting to comfort by stroking and grooming her" (Temerlin 1975, p. 165). There are also anecdotal reports of apes helping unfamiliar birds and humans, sometimes even incurring great risk to do so (e.g., de Waal 1997b; O'Connell 1995).

Effects of similarity and familiarity explain why empathy in some models requires state matching (e.g., Feshbach & Roe 1968) or accuracy (e.g., Levenson & Reuf 1992). The more similar or familiar the subject and object, the more their representations will be similar, which in turn produces more state-matching, better accuracy, and less "projection." Although state matching is correlated with accuracy and appropriate helping behaviors, a strict requirement is not warranted. There is never absolute state matching, some factors prevent accuracy and helping even when there is state matching, and one can be accurate or helpful without state matching through purely cognitive processes.

The role of representations can also eliminate the need to distinguish empathy from "projection." In the former case the subject feels the state of the object, in the latter the subject assumes that his or her own state is that of the object. Existing representations shape the subject's perception as much as perceptions shape representations. Thus, Hume (1888/1990) noted, "There is a very remarkable inclination in human nature, to bestow on external objects the same emotions, which it observes in itself; and to find every where those ideas, which are most present to it" (p. 224). Similarly, a high-functioning autistic adult challenged current theories of empathy, concluding that empathy is only less likely between himself and others because his projections do not match their perceptions and vice versa (Cesaroni & Garber 1991). According to this man with autism: "It is . . . much easier to empathize with someone whose ways of experiencing the world are similar to one's own than to understand someone whose perceptions are very different" (p. 311). Human interpretations of animal behavior are also criticized for resulting from projection more than perception (see Mitchell et al. 1997). Projection is thought to be inconsistent with empathy, because the mapping goes from subject to object rather than object to subject (Eisenberg & Strayer 1987).

With a perception-action model of empathy, there is no empathy that is *not* projection, since you always use your own representations to understand the state of another. The degree to which it is empathy rather than projection depends purely on the extent to which the subject's representations are similar to those of the object, or include information about the object, which in turn determine accuracy.

Past experience effects can also be explained by the same principles as familiarity/similarity. If a subject needs to access representations of a particular internal state to understand the object's situation, then one would expect more empathizing for situations or states that the subject has experienced. For example, in the comparative empathy experiments, previous experience with shock greatly facilitated empathic responding. Subjects who were shocked previously would have mapped the perception of a conspecific in a familiar situation onto their own representation of pain reactions, activating the associated distress. After experiencing shock, subjects had richer representations of this event and their representations were directly associated with autonomic consequences. These mechanisms would hold throughout the life span. Thus, a correlation should exist between the scope of the subject's life experience and the scope of situations in which the subject responds appropriately (as in Hoffman 1990). Beyond effects of experience, advanced cognitive capabilities of adult humans would facilitate cognitive perspective taking that is not stimulus driven.

The "affective congruency effect" indicates that being in a similar state to another facilitates attention, processing, and memory. Subjects respond more quickly to targets that are affectively congruent with the priming stimuli. Congruous states may be more easily processed due to priming and spread of activation (e.g., see Bower et al. 1981; Singer & Salovey 1988; Spizzichino & Bonaiuto 1990) or due to the response interference that primes create for distractors (Wentura 1999). Either way, affective congruence predicts that individuals who are primed for the situation or emotion of the object will be more aroused, will engage in more perspective taking, and will exhibit more empathy than a nonprimed subject.

**4.1.2. Representations and cue salience.** The refinement of representations through experience was able to parsimoniously explain three of the four major effects in the empathy literature. The final effect, cue salience, is related because of its ability to increase the likelihood and extent to which a representation is activated. The more salient an event, the more likely it will be attended to (Colby & Goldberg 1999; Taylor & Stein 1999), providing the opportunity for empathy. Generally, stimuli that are perceptually loud or include releasing stimuli (like crying or screaming) will be most salient, but the perception-action model predicts that attention is focused towards features that require response and prediction.

Attention and imitation are also correlated because the former activates perception-action circuits more. In infants, attention towards and imitation of a model both decrease between 2 and 6 months (Field et al. 1986). When observed actions are particularly salient, a brief, truncated version of the movement is produced (personal communication from L. Fadiga, in Rizzolatti & Arbib 1998), called an "ideo-motor action" (cf. Carpenter 1874; Eisenberg & Strayer 1987; James 1890; Lotze 1852; Prinz 1987). Thus, attention may reduce learned inhibition, allowing a reduced version of the movement to "leak out." In this way, the PAM can replace cognitive perspective-taking explanations for such effects, parsimoniously linking the mechanism for these effects with infant imitation, emotional contagion, empathy, and helping.

The mediating role of attention on empathy could be tested with negative priming paradigms whereby reaction times assay the extent of inhibition (response times to previously-inhibited locations are much longer) (Tipper 1985; Tipper & Cranston 1985). It should take longer to identify previously seen items that inhibit empathic attention (like a homeless beggar), than neutral stimuli or releasing stimuli (like a child or a puppy).

**4.1.3. Representation and other theories.** A behaviorist or a purely perception-action perspective might not want to include representations in the description. But, the clarification of the term "representation" in Table 3 should largely assuage this disagreement. Our use of representations does not eliminate the importance of conditioned associations or responses for empathy. Firstly, individuals can be "empathic" in the folk psychological sense by learning how to associate certain behavioral cues with the correct response for the situation. Objects that are sufficiently different from the subject would require this type of processing in order to be accurate. Data also suggest that individuals with autism or psychopathy may use such alternative strategies to compensate for an impairment in empathy. More importantly, to the extent that conditioned and unconditioned stimuli can be seen as dynamic and multi-dimensional, rather than fixed and singular, a conditioning view is completely compatible with a perception-action view.

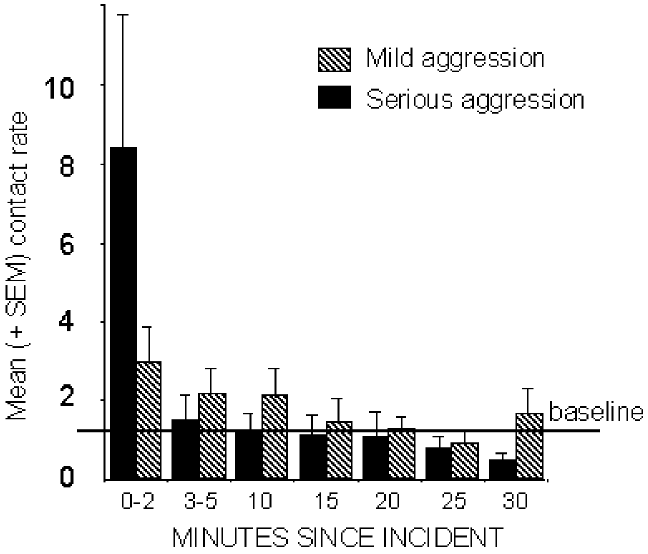
Because of the importance of representations in a PAM of empathy, there is a strong overlap with the Somatic Marker Hypothesis of emotion (Damasio 1994) and with Damasio's views on the neurobiology of emotion and feeling (Damasio 1999; Damasio et al. 2000). Both models postulate that perception activates one's stored representations and that these representations are linked to one's associated feeling states (Damasio calls these re-activated representations "images").

The importance of representations also makes our theory similar to appraisal models of emotion processing (see Omdahl 1995). In appraisal models of emotion, emotions are generated when the subject consciously or unconsciously evaluates or appraises the event. According to Roseman and Smith (2001), "the different emotions manifest in characteristic facial expressions and action tendencies are produced by differing evaluations of events." Further, "*each distinct emotion is elicited by a distinctive pattern of appraisal*" (their emphasis). If one assumes that the manifest responses to emotions are produced as in the Perception-Action Model, and if one assumes that a "pattern of appraisal" is equivalent to patterns of activation in the network, then there is no conflict between appraisal model of emotion, and the Perception-Action model of empathy.

### *4.2. Incorporating cognitive empathy into the model*

Some theories or forms of empathy are more actively cognitive, or more controlled processes than the ones discussed thus far. With cognitive empathy, the subject is thought to use perspective-taking processes to imagine or project into the place of the object. Cognitive empathy appears to emerge developmentally and phylogenetically with other "markers of mind" (Gallup 1979; 1992; Povinelli et al. 1994; Premack & Woodruff 1978), including perspective taking (PT), mirror self-recognition (MSR), deception, and tool-use. The behavioral complexity and flexibility of these behaviors is greatly increased in humans and apes relative to other primates and most mammals. Only humans after certain ages and the great apes have been cited as passing tests for the markers of mind and evincing higher than first order intentionality (cf. Dennett 1988; for a review see Byrne & Whiten 1988; O'Connell 1995; Tomasello & Call 1997). In addition, there is anecdotal evidence of helping behavior in dolphins (de Waal 1996), the only nonprimate mammal that passes MSR tests (Reiss & Marino 2001).

Comparative evidence of cognitive empathy per se focuses on apes, using extensive data on consolation behavior. Consolation involves contact initiation by a previously uninvolved bystander who is assumed to be less distressed, and directs consolatory efforts to the victim (first defined as such by de Waal & van Roosmalen 1979). It has not been found in monkey species despite intensive efforts to find it (de Waal & Aureli 1996). Far from anecdotal reports, conclusions are based on analyses of hundreds of post-conflict observations that compare third-party contact tendencies with baseline rates (de Waal & van Roosmalen 1979; de



Waal & Aureli 1996; Fig. 4). One can postulate that the consoling individual has become distressed from the sight of the victim and seeks comfort for his or her own feelings. While some level of distress in the subject is inherent in our model, the consoler often does not show overt signs of distress, and may wait until after the most intense display to approach (de Waal & Aureli 1996; Fig. 5).

An anecdotal report of cognitive empathy: Kuni, a bonobo female at the Twycross Zoo in England, once captured a starling. She took the bird outside and set it onto its feet, the right way up, where it stayed shaking. When the bird didn't move, Kuni threw it a little, but it just fluttered. Kuni then picked up the starling, climbed to the highest point of the highest tree, and carefully unfolded the bird's wings, one wing in each hand, before throwing it into the air. When the bird still remained in the enclosure, Kuni guarded it for a long time against a curious juvenile (de Waal 1997b, p. 156).

The tailored helping of Kuni or of Binti Jua, an 8-year-old female western lowland gorilla who rescued a 3-year-old boy at the Brookfield Zoo (de Waal 1997a), are also well-known examples of tailored helping that indicate cognitive empathy in apes. Anecdotal accounts are subject to bias, but a metaanalysis of over 2,000 anecdotal reports of nonhuman primate empathy revealed three types of empathy in chimpanzees: emotional, concordance (like cognitive empathy), and extended (tailored helping) (O'Connell 1995). Understanding excitement, grief/sadness/frustration, and fear of the subject were extremely common, with most outcomes resulting in the subject comforting the object of distress. Chimpanzees comprehend the emotions, attitude, and situation of another and even endangered their lives to save others in danger. An adult male chimpanzee died trying to rescue an infant who had fallen over the electric fence into a moat. Monkey displays of empathy, by contrast, were restricted to mediation of fights, adoption of orphans, and reactions to illness and wounding.

Thus, cognitive empathy appears to be differentially available across species and partially distinct from the more automatic and emotional forms of empathy discussed above. Heretofore, it has been unclear how exactly more cognitive forms of empathy are related to more automatic forms. Some have argued that these processes are linked to automatic and emotional forms of empathy because they are themselves the products of simple social facilitation and/or conditioning (Galef 1992; Heyes 1993a; 1993b; Tomasello & Call 1997). According to the PAM, these processes were augmented by prefrontal capacities to increase the flexibility and control. "Markers of mind" and cognitive empathy are associated with a larger proportional prefrontal region. The protracted development of Hominoid species increases the extent of learning before adulthood and is speculated to result in the disproportionate increase in the prefrontal cortex (Finlay & Darlington 1995; Finlay et al. 1998). Prefrontal functions facilitate cognitive empathy through increased inhibition, increased working memory, and an increased ability to assess short- and long-term goals before responding (for reviews see Fuster 1997; Shiamamura 1996; Thierry et al. 1994).

The following developmental and phylogenetic sequence is proposed. Early on, automatic processes cause the state of the object to elicit a similar or relevant state in the subject. This limits empathic processes to ones like social facilitation, alarm, and emotional contagion because the subject cannot distinguish personal distress from the object's distress, and has less control over emotional reac-

Figure 5. A juvenile chimpanzee comforts a distressed adult.

tivity. Longer life spans increase the base of knowledge of individuals and situations, allowing individuals to better predict and understand the situations that cause distress in particular people, and what helps to assuage the distress. Altricial development increases the period of dependence, giving individuals more time to learn (neuronally and subjectively) how to distinguish distress directly caused by personal insult from distress caused indirectly by insult to the object. Activation patterns in response to perception of the object's state differ in some respects from those arising from one's own state. Perception of the object's movements may activate the subject's premotor areas, but without peripheral somatosensory cues and efferent motor feedback. Even shared representations are more intensely activated in self-experience than in observation or imagination. Overall, the pattern of activation is different for experiences that originated in the object from ones that originated in the subject.

Extended prenatal and perinatal development disproportionately expands prefrontal cortex, increasing working memory, planning, and inhibition. With working memory, individuals can hold information in mind and manipulate this information to predict, compare possible outcomes, and decide on an appropriate course of action. Working memory also increases imaginative processes that allow individuals to evoke empathic processes in the absence of the object. With increased inhibition, the subject can avoid becoming contagiously distressed from the object. The subject can inhibit the processes that normally augment personal distress such as attention to the distress, expression of the distress, and elaboration on the distress.

Higher cognitive faculties can also augment helping behaviors through explicit teaching. In human children, direct instruction, reasoning, discipline, and reinforcement of helping are necessary for prosocial competence (Eisenberg et al. 1983; Radke-Yarrow 1983; Ungerer 1990; Zahn-Waxler et al. 1979; 1984). These explicit factors can either push a below-threshold state of empathy into an act of helping or subvert empathy altogether when it is required by social rules, but not naturally evoked.

Taken together, an extended life history, altricial development, and the increase in prefrontal functions can account for increases in the effectiveness of empathy by helping the subject to focus on the object, even in it's absence, remain emotionally distinct from the object, and determine the best course of action for the object's needs.

## 5. Final comments

The complex social world of primates requires the central nervous system to perceive the facial expressions, body postures, gestures, and voices of conspecifics accurately and quickly in order to generate a response (Brothers 1990; Byrne & Whiten 1988). Parsimoniously, the same nervous system link between perception and action that helps us to navigate the physical environment helps us navigate the social environment. The perception-action link allows for facile motor skill acquisition as well as facile social interaction, as we perceive external conditions and incorporate them into our current plan of action. In this way, the proximate model is intricately linked with the ultimate model. While natural selection acts on phenotypes, these phenotypes reflect the underlying physiology. Thus, the general design of the nervous system, created through millions of years of evolution, should be considered a factor in the evolution of emotional processes like empathy and overt behaviors like helping. In this way, the proximate and ultimate levels of analysis are intimately related.

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# Open Peer Commentary

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## Hyperbolic discounting lets empathy be a motivated process

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**Abstract:** The Perception-Action Model (PAM) is a cogent theory of how organisms get information about others' experiences. However, such a stimulus-driven mechanism does not handle well the complex choices that humans face about how to respond to this information. Hyperbolic reward discounting permits a reward-driven mechanism for both how aversive empathic experiences can compete for attention and how pleasurable empathic experiences are constrained.

Preston & de Waal (P&deW) present a plausible case that empathy entails modeling of an object's experience, that this modeling is highly prepared by mirror neurons and distributed networks subtending perception and action, and that empathic skills are selected for in a species because of their social consequences. Less adequate is the proximate mechanism they propose: that "*attended perception of the object's state automatically activates*" representations, and that this activation "*automatically primes or generates the associated autonomic and somatic responses, unless inhibited*" (target article, sect. 1.1.3, emphasis in the original). In this account, empathy is not a motivated process, but the reflexive consequence of perception. Reward-based processes weigh in only in modifying what the individual attends to, and which empathic reflexes she will attempt to inhibit.

But reflexive empathy does not account for the range of empathic experience. Accepting for the moment that the empathic response is controlled by attention, "whether or not a subject perceives the state of the object" does *not* depend "crucially on their interdependence or interrelationship" (sect. 1.1.3). A person may relate only superficially to family members while empathizing intensely with pets, chance acquaintances, people in the news, and wholly fictional characters. Empathic experience is not just aversive ("All forms of empathy involve some level of . . . personal distress," target article, sect. 1.1.3) and thus subject only to variable inhibition; it may be satisfying and subject to cultivation. Furthermore, people cultivate not only pleasant relationships but also those that provoke anger and even terror (with characters in horror films) and grief (in tear-jerkers). Finally, appreciation of an object's state may occasion not just a copy of that state, but a wholly different state that nevertheless depends on that appreciation. The authors note but do not deal with the case where a "subject seeks to produce or witness high levels of distress" (sect. 1.3). They call this case abnormal, but an empathic appreciation of an object's distress is the point not only of sadism but also of minor forms of gloating and retribution in everyday life. The relatives of murder victims who are regularly reported as saying that painless execution is "too good" for the murderer are not necessarily psychopaths. Taken as a whole, empathic experience presents a complex menu of choices; the many opportunities to seek or avoid empathic experiences are probably the greatest incentives that influence any nonautistic people who are not on the edge of starvation.

In a cosmopolitan society suitable objects of empathy are available *ad lib.* The selection of what kind of empathy, if any, actually occurs will depend not on what objects are perceived, but on what obliges a subject to tolerate aversive empathy and what constrains a subject's generation of pleasurable empathy. Commonsense answers are ready at hand: Duty aside, people are drawn into getting involved, even with strangers, when their plight makes too vivid a story to ignore. Conversely, people cannot share the joys of an endless succession of objects because that very freedom would reduce the experience to the level of daydreams. The PAM does not exactly contradict these intuitions – it contemplates a decrease in the "automaticity" of the empathic process with frontal lobe development and experience – but its stimulus-driven structure keeps motivation at the periphery of any discussion of mechanisms.

Since empathy has both plasticity and the stimulus-driven quality described in the PAM, it is natural to ask whether empathically based emotions are *emitted* as motivated behaviors or *elicited* as unmotivated responses to perceptions. The demonstration that reward value is inversely proportional to reward delay (Kirby 1997; Mazur 2001; Myerson & Green 1995) provides a means of accounting for both properties within the framework of motivated behavior. Hyperbolic discounting predicts that many smaller, or briefer, but earlier rewards will be temporarily preferred to larger but later ones when they are imminent, and that long range stability of choice is not spontaneous but depends on making choices in whole categories rather than singly; both effects have been observed (Ainslie & Herrnstein 1981; Ainslie & Monterosso, in press; Kirby & Guastello 2001). The temporary preference phenomenon suggests a way that aversive empathic experiences (as well as aversive emotions generally) can compete with pleasurable experiences in an open market, thus eliminating the necessity for considering them reflexive. The irresistible quality of aversive experiences may be produced by intense but brief reward that lures freely directed attention, but is followed, possibly cyclically, by much longer periods of blocked reward, for a net loss (Ainslie 2001, pp. 51–61, 173). This is to hypothesize that aversive emotions follow the same pattern as addictive binges – strong attraction that is hard to resist up close, but avoided at a distance – only with a much shorter time course. Such a dissociation of immediate and overall values could produce not only strong negative and strong positive emotions, but also those like anger and nostalgia, which can be compelling but are sometimes experienced as positive and sometimes as negative, depending on context. The initial excitation of mirror neurons would thus generate an offer that would be acted on in an individual's marketplace of motivations, rather than being just a step in a stimulus-reflex arc.

Hyperbolic discounting also provides an explanation for why positive empathy produced *ad lib.* will lose its value. If a process rewards increasingly as consumption is delayed – for instance, if an emotion is more intense insofar as its realization is preceded by a period of suspense – then an individual will prefer a smaller yet immediate satisfaction to greater, deferred satisfaction when the smaller satisfaction is imminently available, but not at some remove (Ainslie 2001, pp. 164–71). That is, an organism that emits emotions *ad lib.* will tend to waste its appetite for them. Such spontaneous emotional behavior will tend to be replaced by emotions cued by adequately rare, externally determined occasions. Since the behavior of another individual is varied and not entirely predictable, an empathic attachment entails limitations on occasions for positive empathy, thereby providing a means for emotional pacing and, thus, richer rewards. The prepared mechanism of the PAM model suggests why the particular targets chosen for such attachments will tend to be those in close proximity. However, other solutions such as those discussed above (e.g., pets and fictional characters) are not uncommon; empathic attachments to more distant objects can be selected if these attachments pace reward effectively.

The predictions of hyperbolic discounting theory strongly support the PAM's conclusions that "there is no empathy that is not projection," but suggest that this projection is a reward-dependent process constrained by the properties of temporary preferences (see Ainslie 2001, pp. 181–89).

## The role of empathy in the formation and maintenance of social bonds

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**Abstract:** A primary function of empathy is to help individuals form and maintain social bonds. Empathy should thus occur only when individuals seek to solidify social bonds, and not in response to any opportunity to process others' emotions. Empathy should also involve only certain types of emotion – specifically, emotions that facilitate social bonds – and not any and all types of emotion.

Empathy has long mystified social theorists, resisting simple description and explanation. In the target article, Preston & de Waal (P&deW) take on a difficult task – to provide structure and organization to the empathy literature, a literature rife with contradicting terms, definitions, theoretical accounts, and levels of explanation. Perhaps more impressive, their account of the perception-action mechanism is parsimonious yet powerful, providing a compelling explanation of the evolutionary origins of empathy, and its more rudimentary and complex forms.

However, while arguing that empathy meets certain demands of group living, the authors are relatively vague in discussing exactly what empathy does for social relationships, in particular relationships outside the mother-infant bond. Perhaps more important, the authors say little about the boundary conditions in which empathy will occur and when it will not. In a more general sense, the target article seemed to address the bases of perception-action processes rather than the bases of empathy.

***The functions of empathy.*** Social animals achieve the goals of survival and reproduction in the context of relationships. Thus, forming and maintaining strong social bonds throughout the lifespan is critical to attaining these fundamental goals. The primary function of empathy is to help individuals form and maintain lasting social bonds. While the authors recognize the role of empathy in the mother-infant bond, they fail to address the importance of empathy in building relationships throughout life.

Empathy strengthens social bonds in at least three ways. First, empathy coordinates the actions of individuals in rapid, automatic fashion, which allows them to respond more effectively as a collective to potential opportunities or threats (Anderson et al. 2001; Hatfield et al. 1994; Keltner & Haidt 2001).

Second, empathy helps solve the problem of understanding others' thoughts and intentions. When two individuals feel similar emotions they are better able to understand each other, to take each other's perspective, and thus are more likely to accurately perceive each other's perceptions, intentions, and motivations

(Keltner & Kring 1999; Levenson & Ruef 1994). This increases the predictability of others' behavior, a foundation of cooperative bonds (Anderson et al. 2001; Axelrod 1985; Frank 1988).

Finally, empathy signals solidarity. When individuals feel similar emotions, they communicate to each other that they share a common stance and shared interests (LaFrance & Ickes 1981). Because it is more difficult to feign emotions than it is to deceive with words (Ekman 1993), empathy can be construed as a "true test" of individuals' solidarity with each other. Individuals can be more confident of their bond when others share their emotions than when others communicate their solidarity verbally.

***The moderators of empathy.*** We have reasoned that empathy promotes the formation and maintenance of social bonds. This argument implies that empathy should occur only when individuals want to have a social bond with another individual. In contrast, P&deW assert that empathy is likely to occur when individuals have a rich enough representation of another individual to feel empathic (i.e., when the emotion is salient, when they are familiar with the target, or when they have personal experience with the situation). Therefore, their argument implies that empathy occurs at any and all times individuals are able to be empathic. We argue empathy is more likely to occur when individuals are motivated to be empathic.

Thus, asymmetries in the inclination to connect with another should predict asymmetries in empathic response. Individuals should be more likely to be empathic toward friends than enemies, even if they have rich representations of both targets. Also, as individuals are typically more motivated to connect with powerful others, we expect individuals to be empathic toward powerful individuals more than powerless individuals, even if they are equally able to be empathic toward both (Anderson et al. 2001).

***The forms of empathy.*** The emotions of others do not always evoke an empathic response. Sometimes they elicit a complementary response, as when anger evokes fear. Even the same emotion can produce different reactions at different times. For example, embarrassment sometimes evokes empathic embarrassment, and other times it evokes forgiveness (Keltner et al. 1997). P&deW recognize the distinction between empathic and complementary reactions, yet they do not explain when each type of reaction is more likely.

Consistent with our assertion that the primary function of empathy is to strengthen social bonds, we expect empathic responses to be more likely when they would help individuals solidify social bonds. For example, if feeling a similar emotion would communicate solidarity (as when individuals empathically feel sadness), then empathy should be likely to occur. However, if feeling a similar emotion would not necessarily communicate solidarity (if an individual were to feel similarly guilty), empathy should be less likely. On a related note, the likelihood of empathy can sometimes depend on the target of the emotion. Individuals should be more likely to empathically feel anger if anger is directed at a third party, for example, than if anger is directed at them. Why? Mutual anger felt toward a third person strengthens their bond, in that it synchronizes their thoughts and actions against the third party.

***Differentiating perception-action processes from empathy.*** It is important to emphasize the distinction between perception-action processes and empathic processes. Although the perception-action mechanism might be an evolutionary and ontogenetic precursor to empathy, the two processes are not isomorphic. Thus, while the ultimate bases of perception-action are relatively basic as the authors claim, the ultimate bases of empathy are not. Similarly, while the proximal bases of perception-action seem simple enough, the proximal bases of empathy are likely more complex and nuanced.

## Emotion-specific clues to the neural substrate of empathy

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**Abstract:** Research only alluded to by Preston & de Waal (P&deW) indicates the disproportionate involvement of some brain regions in the perception and experience of certain emotions. This suggests that the neural substrate of primitive emotional contagion has some emotion-specific aspects, even if cognitively sophisticated forms of empathy do not. Goals for future research include determining the ways in which empathy is emotion-specific and dependent on overt or covert perception.

What role do the emotion perception mechanisms play in emotion induction and experience? While a detailed picture has yet to emerge, some significant signposts can be seen. Here are four of them. (1) The neural substrates of emotion perception and emotional experience are not highly localized. Each of these capacities involves complex patterns of activation and deactivation across a number of different cortical and subcortical regions (e.g., Adolphs 2002; Damasio et al. 2000; Davidson & Irwin 1999; Panksepp 1998). (2) Specific regions often contribute both to the perception and to the experience of emotions, such as the somatosensory cortices (Adolphs et al. 2000; Damasio et al. 2000). (3) There is some degree of emotion specificity in the neural substrates of these capacities: the patterns of activation and deactivation vary with each emotion, and certain regions contribute more to the perception and experience of particular emotions or classes of emotion than to others. (4) In addition to more cognitively sophisticated routes to empathy, there is a process of "primitive emotional contagion," as suggested by Preston & de Waal (P&deW) and others (e.g., Hatfield et al. 1992; Wild et al. 2001). This is a means by which one can catch the emotion of another by virtue of one's perception of that person's expression, and is likely to be biologically "hard-wired."

Point (3) highlights a lacuna in P&deW's otherwise comprehensive survey of the literature relevant to the proximate basis of empathy. My task here is to help fill that gap.

Our capacity for perceiving distinct types of emotional expression in the face was, until recently, assumed by many investigators to be subserved by a unitary set of processes, instantiated by a unitary set of neural structures (e.g., Bruce & Young 1986; Young et al. 1993). Recent neuropsychological and neurophysiological studies have overturned this assumption. The relevant findings show that distinct neural structures are disproportionately involved in the perception of fear and anger, on the one hand, and the perception of disgust, on the other (see Calder et al. 2001, for a review). Patients with bilateral amygdala damage have particular difficulty recognizing fearful and sometimes angry facial expressions, but have little difficulty recognizing other emotions expressed in the face, including disgust, happiness, sadness, and surprise (e.g., Adolphs et al. 1999; Broks et al. 1998; Calder et al. 1996). People with damage in the region of the basal ganglia and insula, in contrast, have difficulty recognizing facial expressions of disgust, but are not nearly so impaired at recognizing other facial expressions, including fear and anger (e.g., Calder et al. 2000; Sprengelmeyer et al. 1996; 1997). This double dissociation is supported by neurophysiological evidence, mostly from functional brain imaging. The amygdala is the most active structure when normal subjects view expressions of fear, but when they view expressions of disgust, structures in the area of the basal ganglia and anterior insula are more active (e.g., Morris et al. 1996; Phillips et al. 1997; Sprengelmeyer et al. 1997). There are also indications that the scope of these emotion perception mechanisms is not restricted to facial expressions – vocal and body posture expressions are also implicated (e.g., Calder et al. 2000; Scott et al. 1997; Sprengelmeyer et al. 1996; 1999). But it is still an open question as to how multimodal these systems are (e.g., Adolphs & Tranel 1999).

Testing using self-assessed emotion questionnaires (e.g., Calder et al. 2000; Sprengelmeyer et al. 1997) reveals that patients with emotion-specific recognition deficits also appear to have a corresponding circumscribed deficit in their phenomenal experience of the same emotions they have great trouble recognizing in others. (Yet their verbal understanding of what it means, or used to mean, to be frightened or disgusted seems relatively unimpaired.) This is not surprising, given that other work has shown how the amygdala, basal ganglia, and insula are heavily implicated in the experience of various emotions, including fear, anger, and disgust (see Damasio et al. 2000; Davidson & Irwin 1999; Panksepp 1998, for reviews). So these structures do not relay perceptual information to separate mechanisms underlying emotional experience; like the somatosensory cortices, they are directly involved in both our perceiving and experiencing emotions. But if Adolphs (1999) is right, then the role of the somatosensory cortices in empathy is more cognitively sophisticated than the role of these other structures. Adolphs' suggestion is that somatosensory cortices are directly involved in our capacity to understand the perceived emotional states of others by mentally simulating those states. One need not actually experience the emotion one is simulating, however, for simulation can be taken off-line, thus allowing room for different emotional responses. So it makes sense that the empathy functions of somatosensory cortices appear not to be emotion-specific. But there is another, simpler form of empathy that involves experiencing only the perceived emotion. It is at least plausible that the neural substrate of this primitive emotional contagion has emotion-specific aspects, and the research reviewed above provides some motivation for examining this possibility in more detail.

Suppose you were to lose the ability to perceive a certain primitively contagious emotion. Presumably, you would as a consequence become immune to experiencing that emotion by virtue of perceiving it. But what if you could still recognize that emotion covertly, despite your loss of overt recognition? While we do not yet know for sure whether covert recognition of a particular emotion in the absence of its overt recognition is possible, there are nevertheless some tantalizing pointers worthy of further investigation. Covert recognition of facial identity has been demonstrated in prosopagnosia, that is, in the absence of overt face recognition, using various behavioral and physiological techniques (see Young 1998, for a review). One of these measures is the skin conductance response (SCR), and aversively conditioned masked facial expressions can elicit changes in SCR without being consciously perceived (e.g., Esteves et al. 1994). It is also possible to measure neural responses to subliminal presentations of emotional expressions: for example, masked fearful and angry expressions increase, and happy expressions decrease, amygdalar activity (Morris et al. 1998; Whalen et al. 1998). Moreover, merely viewing images of facial expressions elicits emotion-specific facial EMG responses (Dimberg 1982; Lundqvist & Dimberg 1995), even when the faces are presented subliminally (Dimberg et al. 2000), and voluntary facial action generates emotion-specific autonomic activity, including changes in SCR (Levenson et al. 1990). Might, then, patients who are impaired in recognizing particular emotions nevertheless show the signature patterns of facial EMG and autonomic responses to those emotions, thus indicating a degree of both covert recognition and covert contagion?

# Empathy as a special case of emotional mediation of social behavior

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**Abstract:** Empathy can be viewed as an intervening variable to explain complex webs of causation between multiple factors and the resulting responses. The mediating role of emotion, implicit in the concept of an intervening variable, can be at the basis of the flexibility of empathic responses. Knowledge of the underlying neurophysiological mechanisms is needed for empathy to be considered as a biologically functional intervening variable.

Preston & de Waal (P&deW) present a great example of how proximate and ultimate explanations can be combined for better understanding of phenomena that have, thus far, been tackled from many different perspectives with much disagreement. Although we may not agree on all the issues raised in the target article (see below), we praise the authors for the successful enterprise, especially for elucidating the neurophysiological mechanisms for empathy.

P&deW present empathy as a process linking the perception of the object's emotional state with the subject's somatic and autonomic responses via the activation of the subject's corresponding representations. In this respect, empathy can be viewed as an *intervening variable.* An intervening variable is a construct used to explain complex webs of causation. The causal linkage between a multiplicity of independent variables and the many dependent variables they may influence can be explained most economically by positing a central intervening variable. For example, many aspects of drinking behavior (e.g., effort to obtain drink, amount drunk, tolerance of impurities) can be caused by many factors (e.g., time since last drink, salt load); in this case "thirst" can be used as the intervening variable (Miller 1959). The usefulness of the construct is that we can infer an individual's state of thirst from observable features and, having done so, we can predict how the individual will behave in a variety of contexts. This approach to identifying phenomena, which are not directly observable, has been used to explain phenomena ranging from thirst (Miller 1959) and dominance (Hinde & Datta 1981), to mental states (Call 2001; Whiten 1996) and emotions (Aureli & Smucny 2000; Aureli & Whiten, in press; Hinde 1972).

Economical explanations of events, although elegant, may not reflect reality if they are too simplistic. Biological solutions do not emerge exnovo as the most parsimonious possibilities, but develop from preexisting structures and therefore are constrained by their evolutionary past. We have recently argued that biologically relevant explanations of emotions as intervening variables should aim to incorporate information about the underlying neurophysiological processes (Aureli & Schaffner 2002; Aureli & Whiten, in press; cf. Zupanc & Lamprecht 2000). We suggested an integrated view of emotion as a biologically functional intervening variable based on a neurophysiological foundation. P&deW presented an excellent example by providing plenty of evidence for the neurophysiological basis of empathy.

One of the main functions of emotions is the modulation of the motivation to act (LeDoux 1996/1998; Rolls 1990). The intrinsic plasticity makes emotions suitable candidates to mediate the behavioral flexibility typical of humans and other animals. This can be achieved by considering the mediating role of emotion implicit in the concept of intervening variable. There has been growing attention to the mediating role of emotions in the human literature (Frijda 1994; Panksepp 1989; Rolls 1995), which is paralleled by similar perspectives in animal research (Aureli & Smucny 2000;

Crook 1989; Lott 1991; Owren & Rendall 1997). The emotional experience of an individual is certainly affected by the frequency and quality of previous experiences with the physical and social environment. Emotional states may express a critical integration of the information contained in previous experiences, so that emotional differences can be at the core of the observed variation in behavioral responses. Emotion leads the individual to take a particular motivational stance, which channels its further behavior. In other words, a certain emotional state constrains decision making for an appropriate period of time (Aureli & Whiten, in press). Empathy can be considered as a special case of emotional mediation because the emotional change guiding the subject's behavioral response is triggered by the perception of the object's emotional state.

P&deW emphasized that the Perception-Action Model predicts that the more interrelated the subject and the object, the more their similar representations will be activated, and the easier the subject will produce appropriate responses. This view explains how the degree of familiarity between individuals influences empathic responses in humans and other animals. We believe that this effect is similar to the proposed role of emotion in mediating differential interaction between individuals depending on the quality of their social relationships, of which familiarity is an aspect (Aureli & Schaffner 2002). We argued that for the variation in relationship quality to lead to flexibility in the frequency and quality of interaction with different group members and with the same individual over time, individuals need to be able to assess relationship quality. Such an assessment requires bookkeeping of the various interactions, computation of their relative frequencies, and conversion of their quality and information associated with them into common currencies. Emotional mediation is a possible mechanism for such an assessment because emotion elicited when interacting with a partner would be based on the emotional experience related to previous interactions with the same partner (similar to P&deW's stored representations and Damasio's [1994; 1996] somatic markers). Emotion would then offer an integrated summary of previous interactions, and emotional mediation could therefore fulfil the requirements and provide the individual with a timely assessment to guide his or her social decision (Aureli & Schaffner, 2002).

Familiarity, and more in general relationship quality, is certainly an independent variable that would affect empathy viewed as an intervening variable. Similarly, factors, such as age, sex, personality, experience, strength of the perceptual signal, and distraction, can all play a role in affecting empathy and the subsequent responses (as reported by P&deW). Their relative roles, as independent variables, can be easily integrated if empathy is viewed as a biologically functional intervening variable (cf. Aureli & Whiten, in press). The Perception-Action Model provides the neurophysiological basis for how such integration can be achieved.

While we are impressed about the range of studies reviewed in the article, we are puzzled about the inclusion of a couple of examples. The increase in heart rate of rhesus macaques when approached by dominant individuals is difficult to interpret as evidence for empathy; it likely reflects an emotional response to prepare the individual for action in a potentially risky situation (Aureli et al. 1999). Similarly, it is unlikely that reconciliation between former opponents is an empathic response to the distress of the partner; rather, it is an act to restore social relationships based on anxiety experienced by the actor (Aureli 1997). There is also a suggestion that behaviors to warn group members of danger have an empathic component. Emotion can mediate the warning behavior, but it is unclear how it is a case of empathy.

Apart from these small problems of interpretation, the article by P&deW shows an important direction for research on empathy in humans and other animals. It should stimulate work on various empathic behaviors, combining ultimate and proximate explanations.

## Reflexive empathy: On predicting more than has ever been observed

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**Abstract:** A model positing that perception of another's affective state automatically generates matching emotional and instrumental responses predicts more than has ever been observed. Reflexive empathicness would produce emotional exhaustion, inhibitory strain, and debilitate everyday functioning. Self-regulation of empathic responses involves, not only reactive inhibition, but agentic proactive control. Pervasive inhumanities involve selective disengagement of empathic restraints through dissociative psychosocial mechanisms.

The article by Preston & de Waal (P&deW) is an ambitious feat of synthesis encompassing diverse theories of empathy and manifestations of empathicness across individuals, species, stages of development, and situational circumstances. In their view, their perception-action model can fully integrate this entire theoretical and empirical diversity. As the authors amply document, organisms have the capacity to react to another's emotional state. However, they do not come equipped with ready-made emotional and instrumental responses activated reflexively by evolved brain design. This capacity must be cultivated experientially. Once developed, empathic proneness remains subject to modification by experience. Moreover, in the case of humans, empathic responsiveness is extensively under cognitive control.

The capacity for vicarious arousal plays a vital role in empathic responsiveness. Learning experiences largely determine whether observers will be roused or unmoved by the emotional expressions of others. The research by Church (1959) underscores the importance of correlative experiences in vicarious arousal. Cries of pain by a conspecific evoke strong emotional arousal in animals who had suffered pain together; weak arousal in animals who had undergone equally painful experiences but never correlatively; and leave unmoved animals who had never been subjected to painful treatment. Monkeys reared in total isolation during their infancy remain unresponsive, behaviorally and physiologically, to the facial expressions of emotion by other monkeys (Miller et al. 1967). There is little in the preceding findings to support the view that perception of the emotional state of another automatically activates a shared emotional state in observers.

Correlative experience plays a central role in creating not only empathetic responsiveness, but counter-empathy as well (Englis et al. 1982). Past conjoint experiences in which modeled pleasure signaled reward for oneself and modeled distress signaled personal pain heighten observers' empathetic reactions to the model's emotional expression alone. Observers who had undergone discrepant experiences (e.g., when a model's joy brings suffering to oneself) respond indifferently or counter-empathetically to the model's joy and suffering (Englis et al. 1982). Vicarious activation relies heavily on a cognitive conveyance. Thus, when observers are merely led to expect cooperative interactions, the joy and distress of a cooperative model elicit similar reactions from observers. By contrast, displays of joy by an alleged competitive model distress observers and displays of distress calm them (Lanzetta & Englis 1989).

Similarly, observers respond empathetically to the emotional experiences of models simply depicted as in-group members, and counter-empathetically to those portrayed as out-group members, in the absence of having shared any experiences with them (McHugo et al. 1982). If a sense of mutuality has been created, so that the joys and distresses of an outgroup member foretell similar experiences for the observers, correlative outcomes transforms disempathy to empathy.

To underscore the continuity of empathy across species, P&deW minimize the power of the human advanced capacity for symbolization in the regulation of empathicness. Because a functional consciousness is not a hallmark of lower species, it too gets short shrift in the perception-action model of empathy. According to P&deW, cognitive capacities may augment empathicness but the governing processes do not require conscious awareness. As already noted, thought processes play a regulatory role in both empathic and counter-empathic reactions to the emotional states of others. In social cognitive theory (Bandura 1986; 1992) vicarious arousal operates mainly through an intervening self-arousal process. Because of their capacity for emotional self-arousal, people can cognitively generate emotional reactions to cues that are only suggestive of a model's emotional arousal; their emotional reactions to the same expressive cues can vary markedly depending on what they believe about the situational causes of the model's reactions; and they can neutralize the impact of human distress by mobilizing calming trains of thought.

Cognitive self-arousal can take two forms: personalizing the experiences of another or taking the perspective of another. Evidence suggests that personalizing modeled experiences is more vicariously arousing than perspective-taking. Observers react more emotionally to the sight of a person in pain if, at the time, they imagine how they themselves would feel than if they imagine how the other person feels (Stotland 1969). Studies of the development of empathetic understanding in young children corroborate the importance of personalization over perspective taking (Hughes et al. 1981).

A major problem with an automatically activating empathic mechanism of the sort proposed in the perception-action model is that it predicts vastly more than has ever been observed. Moreover, it would exact too heavy an emotional toll to be adaptive. In their daily transactions, people are repeatedly exposed to others in distress, pain, apprehension, frustration, anger, and despondency. If perception of the affective states of others automatically generated matching emotions in observers, they would not only be continually burdened with emotional exhaustion but unable to conduct their daily affairs. Indeed, in many service professions, where each day brings endless lines of distressed people, if service providers fully experienced the agonies suffered by their clients, their viscera could not withstand the wear and tear for long. Those who cannot regulate their empathic arousal fall victim to emotional burnout (Bandura 1997; Maslach & Jackson 1982). Adaptive functioning requires effective self-regulation of empathic reactivity. Even informal observation of human transactions would reveal that people are hardly consumed by empathicness. All too often they act indifferently or callously to the suffering of others.

P&deW include an inhibitory function in their model. However, describing the neural mechanics of inhibition at the prefrontal and spinal cord locus does not explain how people come to regulate their empathicness. There is a difference between reactive inhibition at the neuronal level and proactive control at the psychosocial level.

In the conceptual scheme proposed by P&deW, empathy does not involve a conscious agent. The evolved perception-action mechanism does the empathic work automatically. In fact, people regulate their everyday emotional life by developing strategies for managing vicarious arousers, especially the aversive forms. This is graphically revealed in microanalysis of coping strategies in vicarious emotional learning through the painful experiences of models (Bandura & Rosenthal 1966). Observers under high epinephrine-induced arousal resorted to a variety of maneuvers to keep the model's pain out of sight and out of mind. By these cognitive and attentional means, they insulated themselves from the modeled distress and learned little from the model's aversive experiences.

P&deW comment on empathy impairments in sociopathy and autism in terms of dysfunctions in prefrontal systems. Deficient empathicness is a pervasive phenomenon rather than confined to pathologic types, as evident in the widespread inhumanities that people perpetrate on each other. Otherwise considerate people selectively disengage empathic restraints and moral self-sanctions in executing destructive activities in the name of religious doctrines, righteous ideologies, and nationalistic imperatives. The conversion of socialized people into fierce fighters is achieved, not by altering their personality structures, aggressive drives, moral standards, or neural structures. Rather, it is accomplished by cognitively reconstruing injurious conduct so that it can be done free from the restraint of empathy and self-censure. The psychosocial mechanisms of empathic disengagement enable people to do extraordinarily cruel things (Bandura 1999). The prevalent failures in empathic control stem from ideology rather than impaired biology.

## Developmental processes in empathy

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**Abstract:** In recent years, explanations of primate cognition highlighted clever arguments, rather than different ability. In the target article, definitions unify, explanations rely on basic nervous system functioning, theory is built on data that fit, and the emphasis is on evolutionary continuities. This commentary describes complexities inherent in the development of empathy that are not accounted for in Preston & de Waal's theory.

Preston & de Waal (P&deW) have written an important and timely article proposing mechanisms to explain the evolution of empathy. It is exciting to have theories put forward that emphasize evolutionary continuity, especially in positive emotions (e.g., Panksepp 2000b). In recent years, explanations of primate abilities have had a tendency to highlight "clever philosophical arguments" (as noted by Maestripieri 2001, p. 453) rather than to elucidate the topic of study. It is refreshing to find the argument that the most basic of empathetic abilities, such as emotional contagion or neonatal imitation, are affordances inherent in nervous system functioning with no need to add cognitive "frills" to the explanation. However, the impression should not be created that simple functioning of the nervous system is sufficient to explain the development of empathy. There are complexities in the developmental process that are not adequately explained by the theory.

It is vital to acknowledge that developmental changes occur as an interaction of the influences of biology and environment with the changing organism. These interactional and developmental changes begin very early in life. Differences observed when individuals are raised in different environments (e.g., cultural differences, ethnic group differences, family differences), are just the tip of the iceberg. The very early, and subtle, nature of social-emotional learning is exemplified by Coles et al. (1999). Eight-week-old infants, exposed prenatally to drugs (uniquely accounting for 3% of the variance) and postnatally to parenting instability (uniquely accounting for 14% of the variance), exhibited heart rate (HR) acceleration (a stress reaction) in interaction with a social partner, whereas those not exposed exhibited a HR deceleration (an alert orientation). These early physiological reactions of stress and attention were not evident in behaviour and were in response only to social, not inanimate stimuli. By 4 months, human infants show preferences for interacting with the imperfect contingencies of their mother compared with the perfect contingencies of a trained examiner (Bigelow 1998). The power of these early interactive preferences in setting the stage for future social and emotional interactions has not yet been fully explored. The simple assertion by P&deW that empathy is biologically based does not fully capture the process of development. Moreover, their discussions of maternal influences in infant emotion regulation do not contribute substantially to a better understanding of the mechanism underlying these developmental processes.

The complexity inherent in developmental processes is not limited to human infants. Chimpanzees also exhibit clear indications of changes as a result of interaction with the environment, and this occurs from very early in life. Some chimpanzee newborns imitate facial and vocal actions (Bard & Russell 1999), exhibit different "temperaments" as a consequence of being raised in differentially responsive environments (Bard & Gardner 1996), and very young chimpanzees learn conventionalised communicative signals through interaction with social partners (Bard 1996). In fact, in the first month of life, chimpanzees' ability to regulate their behavioural state is greatly influenced by their social environment. Counterintuitively, it was chimpanzees raised by their biological mothers, rather than nursery-reared chimpanzees, that were less able to maintain a calm behavioural state as measured during a 20-minute standardized laboratory assessment (albeit there are demonstrably greater benefits to mother-rearing versus nursery-rearing in the long term; see Bard et al. 2001).

P&deW broaden the term "empathy" to include a range of behaviours from emotional contagion, through cognitive empathy, to prosocial behaviours. There is a degree of complexity inherent in the process of learning prosocial communicative signals which is not adequately addressed in their model. Young chimpanzees learn comforting behaviours, such as grooming. Additionally, they learn the behaviours that signal to others that they are willing to engage in grooming (a concentrated gaze directed toward a particular patch of skin, with hands ready, whilst emitting grooming vocalizations). They learn the behaviours that signal that they wish others to engage in grooming (a body part placed in front of the groomer-to-be, with loud scratches around the to-be-groomed spot of skin). Additionally, they learn when to initiate and receive grooming, and with whom. As a result of a behavioural intervention project, it was clear that this task is not accomplished easily when chimpanzees were reared in peer (i.e., same-age) groups, because some rules of grooming require rank-related evaluations, for instance. In the responsive care nursery, chimpanzees engaged in grooming behaviours with others when they were approximately 23 weeks of age (Veira & Bard 1994), earlier than when this behaviour occurred in mother-raised infants in the lab (Bard 1996) or in the wild (Goodall 1986b). It was important for the groomer to learn the consequences of grooming, namely, that the groomed individual typically becomes very relaxed. Chimpanzees, from 2 through 5 years of age, were still learning when to initiate grooming and how to use grooming to change the emotional state of others. During tests of social referencing (Russell et al. 1996), one young chimpanzee hugged, kissed, and groomed his favourite caregiver when she displayed fear at a novel toy. This infant chimpanzee did not exhibit any fear, recognised the fear displayed in the caregiver, and exhibited an empathetic response, at the age of 17 months. Clearly, the response is a product of this chimpanzee's individual temperament and emotional relationship with the caregiver. Is this instance of empathy dismissable because the caregiver is human, or empathy a characteristic of the individual (whether human or chimpanzee)?

P&deW have provided an excellent model that unifies the diverse definitions of empathy currently in use, and provides a mechanism to explain, at the proximate and ultimate evolutionary levels, why empathy exists. The risk of a unified, simple, and straightforward theory, however, is that one might interpret all processes as simple. Prosocial behaviours develop, for example, as a result of complex biological and psychological processes involving emotion, emotional regulation, and cognitive abilities that are continuously interactive between the individual and the social environment. This article encourages and stimulates thought. Can definitions of empathy be expanded further? Could empathy encompass any manipulations of emotional state, for example, from being content to angry, or from being nondistressed to happy?

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## Empathy: Common sense, science sense, wolves, and well-being

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**Abstract:** Empathy is likely more widely distributed among animals than many researchers realize or perhaps are willing to admit. Studies of social carnivores, other group-living animals, and communication via different modalities will help us learn more about the evolutionary roots and behavioral, sensory, and cognitive underpinnings of empathy, including what it means to have a sense of self. There are also important implications for debates about animal well-being.

Preston & de Waal's (P&deW's) comprehensive essay is a welcome addition to the literature for it assumes that at least some nonhuman animal beings (hereafter, animals) can be empathic creatures, whereas many discussions of animal empathy question whether empathy exists in any animals other than human beings. The PAM model explains much that has been observed in captive and free-ranging animals, and is a valuable contribution in and of itself. The authors' reliance on both anecdotes and hard data is also refreshing. Studies of animal cognition and animal emotions require us to use data ranging from single-subject stories to detailed empirical and experimental information and encourage us to reconcile common sense with science sense. There are many ways of "knowing." These studies also require us to be *biocentrically anthropomorphic* (Bekoff 2000a; 2000c; 2002). Using anthropomorphic language does not force us to discount the animals' point of view. Anthropomorphism allows other animals' behavior and emotions to be discussed in a way that is intelligible to humans and it is highly unlikely that emotions and empathy are merely by-products of humans' anthropomorphic tendencies (Bekoff 2002).

Discussions of empathy necessarily include consideration of the notions of self-awareness (also referred to as self-recognition and self-consciousness). Mirrors have been used to study these phenomena. While it is not known if animals know *who* they are, a limited number of individuals, especially chimpanzees and other great apes, have been shown to use their mirror image to groom parts of their bodies that they cannot see – their teeth and their backs – without a mirror. A few chimpanzees, but surely not all who have been tested, also look into a mirror and touch a spot that was placed on their foreheads when they were sedated and unaware that the spot was placed there (Shumaker & Swartz 2002). Some dolphins also respond to a spot on their foreheads as if they know the spot is on themselves (Reiss & Marino 2001).

The "red spot" technique was first used more than three decades ago by Gordon Gallup (1970) and widely ever since. Some researchers argue that the self-directed behavior involved in touching the spot indicates that chimpanzees might not only have a sense of their own bodies, but also know "this is me"; that is, they are self-aware and can infer the states of minds of others and model the experience of others (Gallup 1998). Whether this rich explanation for self-directed behaviors is warranted remains an open question (Bekoff 2002). My and others' caution about what self-directed responses indicate should *not* be taken to mean that some animals do not know who they are. Rather, our hesitancy stresses that we really do not know very much about animal self-awareness, nor about its taxonomic distribution. A single technique based solely on visual cues such as the mirror test is not the only valid test of self-awareness. If animals fail this test it does not mean that they cannot have a sense of self (Bekoff 2002; Fox 1982; Mitchell 2002; Shumaker & Swartz 2002). Likewise, passing this test does not necessarily mean that an individual knows who she is.

Studies of social carnivores and other group-living animals will be helpful in investigations of empathy. Fascination with self-consciousness has largely been stimulated by work on mirror self-recognition in primates, but we need more research on other animals for whom the red spot experiments are not appropriate, for species in which touching the forehead is not a natural act and in which other senses may be involved in differentiating self from others.

As a working hypothesis and to broaden the array of animals in which self-awareness is investigated, I suggest that self-awareness might be found in such highly social animals as gray wolves (*Canis lupus*), carnivores who live in packs in which coordination and efficiency in communicating among individuals is essential for activities such as playing, hunting, rearing young, defending and sharing food, and defending territory boundaries. It would be highly inefficient for an individual to have to guess all of the time what others are feeling (or thinking). Understanding the psychological states of others would allow for accurate and flexible predictions of their behavior (Tomasello & Call 1997). Empathy could evolve in wolves and other animals by individuals knowing that they are not another individual, that their body is not that of another, in the absence of self-awareness. While individuals surely need to know that they are not another individual, this does not mean they need to be self-aware in the rich sense that most humans are self-aware. Rather, it is necessary and sufficient that they only have a sense of their own bodies and body-awareness (Bekoff 2002).

Consider gray wolves. For a long time researchers thought pack size in wolves was regulated by available food resources. However, long-term research by Mech (1970) showed that pack size in wolves was regulated by *social*, not food-related, factors. Mech discovered that the number of wolves who could live together in a coordinated pack was governed by the number of wolves with whom individuals could closely bond ("social attraction factor") balanced against the number of individuals from whom an individual could tolerate competition ("social competition factor"). Codes of conduct and packs broke down when there were too many wolves. Whether or not the dissolution of packs was due to individuals being unable to empathize with a sufficient number of other individuals so as to retain necessary reciprocal social bonds remains unknown, but this would be a valuable topic for future research in wolves and other social animals.

Recent research by Gallese and his colleagues (Gallese et al. 2002) on mirror neurons suggests a neurobiological basis for sharing emotions and empathy. Decety and Ruby, using PET scans have shown that empathy seems to be hard-wired in the human brain (see Glausiusz 2001). These data suggest that humans come to understand other individuals' behavior by imagining the latter performing the behavior and then mentally projecting themselves into the same situation. Whether or not this is the case for animals remains to be seen. Similar noninvasive and ethically sound techniques will prove useful in learning about the evolution of empathy across different species.

It also is essential to expand studies of empathy to include investigations of the role of sensory modalities other than vision, and of how cues from different modalities might interact with one another. Perhaps a sense of self relies on composite signals that result from an integration of stimuli from different modalities. Suffice it to say, individuals of numerous animals rely more heavily on auditory and olfactory stimuli than on visual input, and sounds and odors might also carry much information about one's self and also others' intentions and perhaps feelings. The mirror test concerns only visual cues, mirror-like images are absent in most field situations, and out of sight does not necessarily mean out of mind.

If animals, including those that are routinely used for research, education, amusement, food, and clothing, are aware of the emotional states of others (as suggested by P&deW and others; see Bekoff 2002), there are serious implications for considerations of their well-being. An additional dimension of awareness must be taken into account because individuals not only enjoy and suffer their own but also others' feelings (Bekoff 2001; 2002). Considerations of empathy compound an already challenging and contentious debate about the humane treatment of animals, whether in captivity or in nature (Bekoff 2000b; 2002).

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# Empathy: A unitary circuit or a set of dissociable neuro-cognitive systems?

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**Abstract:** We question whether empathy is mediated by a unitary circuit. We argue that recent neuroimaging data indicate dissociable neural responses for different facial expressions as well as for representing others' mental states (Theory of Mind, TOM). We also argue that the general empathy disorder considered characteristic of autism and psychopathy is not general but specific for each disorder.

The target article is an interesting attempt to develop a unitary model of empathy, indeed even a unitary model of social cognition, around mirror neurons and perception action processes. It joins other unitary accounts of empathy and social cognition such as those of Adolphs (1999), Brothers (1990), and Feshbach (1975). However, it goes some way beyond these positions by attempting to provide explanations at both the cognitive and anatomical levels (as well as providing some evolutionary speculations).

Yet there is a difficulty. The model, following tradition, fundamentally assumes that there is a single, unitary empathy system. However, we would argue that there is a growing body of work which suggests that there are dissociable neuro-cognitive systems involved in empathy. To be fair, the authors do assume some dissociable components to their model. Thus, for example, there are "fast reflexive sub-cortical processes (directly from sensory cortices to thalamus to amygdala to response) and slower cortical processes (from thalamus to cortex to amygdala to response)" which "roughly map onto contagious and cognitive forms of empathy, respectively" (target article, sect. 3.3.). However, these are dissociable systems that operate on a unitary data base of expressions; that is, all expressions are mediated by these sub-cortical and cortical processes. Yet, the neuro-imaging data on the processing of the facial expressions of others challenges this position. Thus, for example, there have been a series of imaging studies investigating the neural response to fearful and angry expressions. Fearful expressions consistently elicit a neural response in the amygdala and rarely elicit a neural response in the orbitofrontal cortex (e.g., Morris et al. 1996). In contrast, angry faces do not elicit a neural response in the amygdala but consistently elicit a neural response in the orbitofrontal cortex (e.g., Blair et al. 1999). This may be related to the differential roles of these expressions. Thus, fearful expressions may act as unconditioned aversive stimuli to encourage conspecifics to avoid the object/action that elicited the expression. In contrast, angry expressions appear to be social signals to encourage response reversal. In other words, the "empathic" response can be specific at both the neural and cognitive levels.

Moreover, it is worth considering the considerable neuro-imaging data on Theory of Mind, or "cognitive empathy"; that is, the ability to represent the mental states of others. A series of studies, using a wide variety of methodologies, have consistently identified an integrated set of neural systems including medial frontal cortex, superior temporal sulcus, and temporal pole (see, for a review, Frith & Frith 1999). Theory of Mind may recruit mirror neurons but the process leads to a representation of another's mental state that can then be used to guide decision-making. This is a qualitatively different type of functioning from the basic associations that are formed as a response to the expressions of other individuals.

The unitary, as opposed to multiple, system's positions on empathy/social cognition give rise to different interpretations of evidence generated from the disorders of empathy. The unitary position suggests, as the authors note, that "the diffuse nature of the PAM circuit explains how many different disorders can result in empathy impairments" (target article, sect. 3.4.5). Thus, the PAM circuit position assumes that there are qualitative similarities between the different disorders of empathy. In contrast, a multiple systems viewpoint is likely to assume that there are qualitative differences between different disorders of empathy. We argue that the data support the latter position. To take the data on autism and psychopathy, the authors suggest that autism is characterized by an impairment early on in the perception-action pathway. This should give rise to difficulties in the representation of the mental states of others as in processing the expressions of others. There is considerable data suggesting a Theory of Mind impairment in this population (Frith & Frith 1999).

However, the data indicating impairment in the processing of others' expressions in the autistic population is mixed at best. Indeed, more recent studies that have controlled appropriately for verbal IQ, have found no evidence of impairment, at least for the six basic expressions (e.g., Adolphs et al. 2001). In contrast, psychopathic individuals have no difficulty representing the mental state of others (Blair et al. 1996). Yet they show very great difficulty indeed in processing the emotional signals of others, particularly fearfulness and sadness (Stevens et al. 2001). It is unclear how the unitary PAM circuit position would account for these types of data.

In conclusion, we appreciate the authors' attempt to develop a model of empathy at both the cognitive and neural levels. We would only suggest that perhaps it is now time to consider that there can be no unitary, single circuit model of empathy. Instead, dissociable systems for social cognition must be considered.

## Peers, cooperative play, and the development of empathy in children

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**Abstract:** Cooperative peer play emerges in the second year of life. How applicable is Preston & de Waal's (P&deW's) model to the empathic processes in cooperative play? Empathic responses during peer play are more general than they propose, and more dependent on mental state understanding. Moreover, peer play forces children to reason about others' feelings, possibly serving as a unique mechanism for empathy development.

In the second year of life, human infants become true social partners with one another for the first time. Between 18 and 24 months of age, children begin to engage in unique, nonritualized, cooperative interactions with peers (agemates), and this development appears to be universal (Brownell & Carriger 1990; Eckerman et al. 1989; Eckerman & Whitehead 1999). Thenceforth, peer play and interaction become progressively more central as a context for socialization. It can be argued, in fact, that children's peer play enables and drives enculturation as much as does adult-child interaction (Tomasello et al. 1993).

Although peer play occurs in many species, among human children peers not only accommodate their behavior to one another dynamically and share emotion expression and behavior during play, but they also share one another's goals, desires, and beliefs. Thus, one characteristic feature of the peer play that emerges in the second year of life is its fundamentally cooperative nature. Cooperative play, in turn, is permitted by the child's emerging ability to infer others' intentions, feelings, and thoughts, and to accommodate play to a peer's mental states as well as to a peer's overt behavior (Brownell 1986; Brownell & Carriger 1991; Smiley 2001).

Emotion infuses children's social play with peers, and empathic concern for others constitutes "the underpinnings of compassion and connection in social relations" (Zahn-Waxler et al. 1992b, p. 1083). However, empathy with others' distress is but one aspect of this complex socioemotional landscape. A wide variety of emotions are shared in children's social play with one another. Emotional contagion and vicarious experiences of interest, joy, glee, pride, shame, guilt, and envy can be observed during dyadic interactions as well as at the group level. Thus, empathic arousal during young children's play is more general than Preston & de Waal (P&deW) propose in their PAM model of empathy, which focuses largely on contagious processes associated with fear or distress responses. A model explaining the development of empathy must account for how children come to experience positive emotions vicariously as well as fear and distress, and secondary emotions such as pride and guilt as well as primary emotions.

At the same time, empathic arousal via vicarious processes is too narrow a mechanism to encompass and explain the emotional communication and understanding that underlie the development of both peer social play and empathy past infancy. Consider the following scenarios. A preschooler watches her little brother crying in frustration as he tries repeatedly to set his truck on the shelf and the truck repeatedly rolls off. Later, she watches the same younger brother laughing gleefully as his truck rolls off the shelf each time he sets it there. A toddler in a playgroup watches as a peer has a temper tantrum after an adult has taken away the peer's toy. Later he watches the same peer weeping sadly after another child has grabbed her toy. In these common, everyday events, children must read well beyond other children's emotion behavior to understand and respond appropriately both to their intentions or desires and to the emotions that follow from the other's success or failure in fulfilling those desires (Meltzoff et al. 1999). Participation in cooperative play depends on these abilities, and it is not coincidental that the first instances of empathy emerge at the same age as the first instances of cooperative play (Zahn-Waxler et al. 1982).

These complex emotional scenarios are different from expressions of pain or fear in response to an identifiable object or observable event in a given setting. One of the hallmarks of human emotional response is that emotions can be generated by unobservable mental states, including beliefs, desires, attitudes, memories, and their interaction with one another as well as with the external world. Thus, to empathize with and respond appropriately to others' emotions requires the child to infer these mental states based on understanding how they are induced and how they relate to one another and to behavior (Eisenberg et al. 1997; Feshbach 1978; Hoffman 1984). And it is precisely these kinds of events and circumstances that pervade and define the daily social experiences of young children in play settings with peers.

By the middle of the second year, children respond with sympathetic concern rather than personal distress to simple pain and distress expressions in others (Zahn-Waxler et al. 1992a), and this occurs in tandem with the initial development of cooperative peer play (Brownell & Carriger 1990; Eckerman et al. 1989). But not until 3 years of age or older do children respond appropriately to more complex emotional events such as those described above, presumably because it is only then that they understand the intentions or desires that produce emotional responses in others. It is also during the third year that children first begin to mark linguistically and to take into account behaviorally their peers prior intentions during play (Smiley 2001).

By the later preschool years, children can infer their peers' emotional states from knowing about the particular events that another experiences, from the contexts in which the events occur, and from knowledge of an individual's history and preferences (Eisenberg et al. 1997). These inferential abilities become critical for empathic arousal and empathic responses, including prosocial behavior, in part because external behavioral cues become less reliable as indices of another's emotional state (Saarni et al. 1998). Human children learn to blunt, mask, exaggerate, or otherwise alter expressive behavior to coincide with cultural display rules. Thus, the cognitive contributions to development of empathy in human children are as important as are the emotional and behavioral components.

As developmental psychologists, we wish to explain the age-related changes in children's understanding of and behavioral responses to these kinds of emotional events. Although empathic arousal must enter into peer play, and empathic concern must play a role in governing children's responses to one another during play, such processes must themselves be subordinated to still more complex processes of interpersonal reasoning that include inferences about the very feelings that define and constitute peer play. Thus, one key question for understanding the development of empathy in humans is how the ability to infer emotional states develops and how children come to discover the causal links among external events, mental states, and emotion behavior. Can a perception-action model, even one enriched by recognizing cortical processes and mechanisms, address the developing social understanding and reasoning about mental states that ultimately must enter into description and explanation of human empathy and its development?

Correspondingly, we must ask whether the social mechanisms residing within mother-child interaction, as proposed by P&deW to explain the development of empathy, are the same ones that reside within peer play. Preschool children talk about shared emotions, intentions, and inner states with friends and peers more than they do with siblings or parents, and this especially occurs during cooperative play (Dunn 1999). Similarly, 2-year-olds announce their own mental states more often to peers during play than they do when playing with mothers. By the preschool years, children direct helping and other altruistic behavior more to peers than to adults (Zahn-Waxler et al. 1982).

Furthermore, peer play forces children to behave altruistically and to take account of one another's feelings, whether real or imagined. Peers share play materials based on inferred emotions in others and they collaborate in thematic play based on inferred desires and intentions of others. They also participate in the altered realities of joint pretend play, which includes sharing altered emotional realities such as pretending to be afraid of the jointly imagined tiger, to be distressed by the jointly imagined pain of its teeth, and to be overjoyed by the jointly imagined superhero's rescue. How do the normative changes in peer play, and the unique demands and collaborations of peer play, contribute to normative changes in emotion behavior, emotion reasoning, and empathy past infancy?

One measure of the utility of P&deW's model is how applicable it is to the multiple social contexts in which emotion communication processes are paramount and empathic processes are central. Cooperative play among young human peers is one such context. It is the development of children's emotional responses, including empathic experiences and behavior, in these complex emotional ecologies that we seek to understand.

## Understanding the imitation deficit in autism may lead to a more specific model of autism as an empathy disorder

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**http://www.ich.ucl.ac.uk/ich/html/academicunits/behav_brain_sci/b_b_s_unit.html**

**Abstract:** Preston & de Waal are understandably cautious in applying their model to autism. They emphasise multiple cognitive impairments in autism, including prefrontal-executive, cerebellar-attention, and amygdala-emotion recognition deficits. Further empirical examination of imitation ability in autism may reveal deficits in the neural and cognitive basis of perception-action mapping that have a specific relation to the empathic deficit.

The elegant model that Preston & de Waal (P&deW) develop has potential to help us understand the empathic deficit that characterises individuals with autism. From early in infancy, individuals with autism are impaired in their empathic response to signals of emotional distress (Charman et al. 1997; Sigman et al. 1992). This impoverished empathic response entails reduced orientation to (and perhaps recognition of) the distress display, reduced matching of facial affect, and reduced prosocial "empathic" responding to the model (Bacon et al. 1998; Charman et al. 1997; Sigman et al. 1992). What remains unclear in terms of P&deW's account is at what level the basic impairment lies: at the proximal level of perception-action matching (PAM), or at the ultimate level that is mediated by cognitive or representational maturity and by experience?

P&deW somewhat hedge their bets between these two alternatives, developing an account that includes impairments both at the perception-action pathway and at the cognitive, prefrontally-mediated level. Such caution is appropriate as autism is a heterogeneous, multi-determined neurodevelopmental condition, which is unlikely to be the result of a single neural deficit, even given the developmental downstream effects of early damage to the developing brain (Bishop 1997; Karmiloff-Smith 1997). However, in exercising such caution in the application of their model to autism, P&deW may deflect attention from the very promise that their account holds. Whilst impairments in other neurally-mediated cognitive abilities are present in autism, they are not as pervasive as P&deW indicate. In terms of prefrontal, or executive, function, inhibition processes appear to be relatively intact (at least when not combined with a prepotent stimulus), in contrast to impairments in flexibility, set-shifting, and planning (Ozonoff & Jensen 1999). Similarly, whilst some aspects of cerebellar-attention processing appear to be impaired (Courchesne 1997), perhaps particularly when related to social objects (Swettenham et al. 1998), other aspects appear to be intact (Minshew et al. 1999). Amygdala dysfunction is also present in autism, although how this relates to the pattern of intact and impaired face-processing and emotion-recognition deficits remains to be determined (Baron-Cohen et al. 2000). How each of these cognitive deficits interact with each other, and with any deficit in PAM, over the course of development is unknown. The empirical task of delineating differential trajectories between related social cognitive abilities that emerge on-line and appear to be interdependent in development has been a challenge in the study of typical development, let alone in atypical populations (Charman et al. 2000).

Further delineation of the imitation deficit in autism may help reveal the nature of the deficits in affect- and action-mapping in autism that underlie the ultimate empathic impairments seen in the disorder. Imitation abilities are impaired in infants and young children with autism (Charman et al. 1997), although basic imitative abilities emerge with maturation (Charman & Baron-Cohen 1994). What is less clear is at what level this impairment occurs. There is some evidence that imitation of gestures (and perhaps in particular gestures with a meaningful communicative content) may be more impaired than imitation of actions on objects (Smith & Bryson 1994). Further, imitation of sequences of actions is more impaired than imitation of single gestures (Rogers et al. 1996), and even when actions are reproduced, the degree to which the "style" of the modelled actions are reproduced is diminished (Hobson & Lee 1999). Matching of emotional expressions is also impaired in autism (Hobson 1986a; 1986b; Loveland et al. 1995). However, it cannot yet be determined how these deficits fit into the proximal PAM account that P&deW outline.

A fundamental deficit in perception of the object-state would clearly impair imitation, and this may operate at the level of both the affective state and motor-positional state of the object. However, so too would an inability to proprioceptively map these onto one's own (affect or motor-positional) state. Further, a fundamental lack of a "like me" identification (Hobson 1993) would impair both these processes and any hardwired tendency to respond to the percept and proprioceptive match. Williams et al. (2001) have raised the intriguing possibility that the function of mirror neurons (Rizzolatti et al. 1996) may be impaired in autism. Future behavioural and functional imaging studies will determine whether this thesis is correct. The developmental consequences of such a deficit would be far-reaching. Existing accounts suggest the potential cascade that may follow such a deficit. Some emphasise the role of affective identification (Hobson 1993), others the role of physical identification (Meltzoff & Gopnik 1993), and others still the combined role of physical and affective processes in the development of intersubjectivity (Rogers & Pennington 1991; Stern 1985).

One limitation of the study of imitation in autism to date has been reliance on paradigms that do not allow us to clearly separate the role of motor-perceptual influences from affective-intentional influences. Such a "fine cuts" approach has been pursued more diligently in the comparative literature. In the normative developmental literature such approaches are now being adopted, and these may allow us to disentangle the perceptual and representational contributions to the imitation of affect, gestures, and actions on objects (Charman & Huang 2002; Heyes 2001; Want & Harris 2002). In time, further evidence will emerge that may allow a more precise application of the P&deW model to autism. An impairment very close to the proximal level of PAM might underlie the impoverished empathic response of individuals with autism to distress displays. Alternatively, an impairment further towards the ultimate level, consequent upon impairments in cognitive and representational abilities and experience, may emerge from such studies.

## A complete theory of empathy must consider stage changes

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**Abstract:** A sequential, hierarchical stage model of empathy can account for a comprehensive range of empathic behaviors. We provide an illustrative table, "Stages of Empathy," to demonstrate how increasingly complex empathic behaviors emerge at each stage, beginning with the infant's "automatic empathy" and ending with the advanced adult's "coconstruction of empathetic reality."

The Perception-Action Model (PAM), even with "additional cognitive capacities" to explain empathic behaviors, cannot account for stages of empathy. The model is useful and necessary but not sufficient. Although aspects of empathy follow an "automatic" process, we assert there is a long development of stage-like changes in empathic action in humans, and perhaps to some extent in great apes. This development results in the adult's very complex empathic stages of action. We argue that the Model of Hierarchical Complexity (MHC) (Commons et al. 1998) provides a coherent account of these developmental changes (see Dawson 2002 for a discussion of its validity and reliability). The increases in the hierarchical complexity of empathic actions are due to a dialectical process of transition from one stage to the next (Commons & Richards 2002; Wolfsont 2002).

We have constructed a table of stages of empathy to underscore the hierarchically sequential stage changes (also see Fischer 1980). The table shows that at each stage there is a new, more abstract "layer" of actions added that organizes the previous component actions. Such ordered changes can be described by using the MHC because of this model's universality. It posits mathematical definitions of "ideal" actions that define stages and a dialectical process of actions that define transitions between stages (Commons & Richards 2002). The model has been applied to a variety of domains in psychology including attachment (Commons 1991), social perspective-taking (Commons & Rodriguez 1990; 1993), and evaluative reasoning (Dawson 1998).

**Stages of empathy**

| **Stages** | **Empathetic Affect and Action** |
|---|---|
| **Sensory and motor actions** (Simple reflexes and conditioning) | Reflex reactions occur including comfort to distress and comforting stimuli, elicited smiles (Field 1989). Reflexive imitative tongue protrusion; mouth opening (Meltzoff & Moore 1977). Shows emotional contagion: Cries and keeps crying when hears other infants' cries (Hoffman 1978b). |
| **Circular sensori-motor actions** (Instrumental and social referencing) | Coordinates perceiving the parent's emotion cues and its own behavior. Behavior is adjusted in situations (e.g., watch for adults' facial expressions when meeting a stranger [Boccia & Campos 1989]). Turns away (avoidance), suppresses an ongoing activity, or gets more involved with an alternative activity from others' aversive emotions. |
| **Sensory-motor** (Physical consoling) | Couples motor action with emotional action, matching intensity of expressions when imitating. Recognizes disparities in across persons. Displays consoling type (or empathic) responses when someone else is upset. These responses involve only the infant's own body. Pats another person, hugs them, or looks concerned. Infants compare emotional responses to caretaker; defer to caretaker's response to determine their response to stranger. |
| **Nominal** (Multireferential or Deferred) | Names and associates feelings (e.g., happy, sad) with familiar entities, events, or representations (e.g., pictures). Infant responds with a distressed look to an adult who looks sad, then offers the adult infant's beloved doll; child runs to fetch his own mother to comfort a crying friend (Hoffman 1978b). Emotionally reacts to the distress and anger of other family members (Zahn-Waxler et al. 1979). |
| **Sentential** (Egocentric helping) | Simple sequences of empathic interactions limited to egocentric helping (e.g., console crying infant). Talks about cause and effect, reflects on cause, actor, action and outcome, hiding, reparation. Guilt is assuaged by reparations or is evaded (Kuczynski et al. 1987; Zahn-Waxler & Kochanska 1988). There is play-acting or pretense (e.g., acting hurt). |
| **Pre-operational** (Storied empathy) | Empathize with a character in a story. Confuses real and imaginary. May act on mistaken beliefs. Acculturation determines whether the context requires empathy (e.g., it is all right to kill fish, but not dogs). Narrative form integrates situations and context, and less salient cues, to infer whether an emotion indicates suffering or something else. |

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|---|---|
| **Primary**<br>(Personal empathy) | Matches feelings towards the sufferer to sufferer's reality. Feelings belong more to oneself than to the other person's feelings aroused in a situation. Also can empathize with another's situation. But cannot coordinate the two. Projects self into other's situation if familiar or perceptible but not into other's perspective if it is not familiar. Empathy consists of "Me too-isms." |
| **Concrete**<br>(Interpersonal inclusion) | Describes feelings as inferred directly from expressions and linked to a situation. Feelings include understanding the other's motives in terms of one's own motives in a similar situation. They include statements of preferences of others as well as stated values of things and acts. One not only understands how the other person feels, but relates those feelings to the ones oneself has had during similar experiences. There is coordination between how they feel now and how they have felt in the same concrete situation and what did help them feel better. |
| **Abstract**<br>(Normative personal sympathy) | Identifies degrees of feelings and suffering along a continuum as states or moods inside the person and expressions on the outside. Feelings and expressions may conflict (Selman 1980). Generalizes feelings and situations but does not logically link generalizations. Sees feelings as normative. "This is how people feel in a situation like this." Nonsystematically tries various things to help. |
| **Formal**<br>(Ideal sympathy) | Links suffering, moods, expressions, and situational variables. Asks about how people feel in a given situation. Aware that feeling states influence immediate perspectives or perceptions. Imagines self in other's position and situation, when these are unfamiliar or abstract. May sympathize with abstract persons and situations (e.g., idealistically sympathizes with individual foreign enemies). |
| **Systematic**<br>(Interpersonal reflection) | Organizes feelings and expressions into systems in each person. Sees self as impartial, though caring, reflector of other's states and perspective. Empathic responses moderated by standing in the hierarchy of the sufferer. |
| **Metasystematic**<br>(Universal principles) | Coordinates and subordinates congruently expressed emotions, taking into account that some systems of emotions conflict with other systems (e.g., social and individual caring emotions; personal survival emotions; justice emotions). Recognizes they could be anyone else and in their universal situations. Acts on universal principles of caring and suffering. |
| **Paradigmatic**<br>(Collaborative co-construction and transformation of reality) | Sees that caring, justice, and survival systems cannot be integrated entirely. Sees failure to find universal principles for empathy. Knowledge about others as regards preference and feelings needs direct representation by the person. |

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## Deconstructing empathy

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**Abstract:** Under Preston & de Waal's proposed model, empathy might be regarded as everything that determines the quality of a social relationship. Although the authors provide a useful heuristic for understanding relationships, clinical research efforts with a somewhat narrower focus have provided some additional insights into this topic, which might lead to testable hypotheses regarding the neurobiology of empathy.

In Preston & de Waal's (P&deW's) model, empathy is viewed as a hierarchy of capacities that originally evolved from the need for social animals to respond accurately and quickly to complex stimuli. The emergence of perception-action organization – believed to be a distinguishing characteristic of social animals – was subsequently superimposed (evolutionarily) by modulatory mechanisms that incorporated internal representations of prior experience (which enhanced the computational efficiency of the system), as well as higher order cognitive processes. At the core of the authors' hypotheses, the seemingly divergent entities of empathy (in which the subject feels the state of the object) and projection (in which the subject assumes that his or her own state is that of the object) are actually seen as complementary epiphenomena of the mediation of perception-activation processes by internal representations of prior experience. In elaborating their model, the term empathy encompasses phenomena as disparate as the reaction to a gory movie and the reaction to a tragic one, incorporates a range of emotional responses from "contagion" to altruism, involves unconscious processes, cognition and "meaning" (in an existential sense), is influenced by genetic and environmental factors, and includes both automatic responses and imaginative processes "that allow individuals to evoke empathic processes in the absence of the object" (target article, sect. 4.2).

This broad range speaks to the comprehensiveness of their approach, but also threatens to make empathy so unwieldy a construct that it is difficult to test. Under the proposed model, empathy might be regarded as everything that determines the quality of a social relationship. Although the authors provide a useful heuristic for understanding relationships, clinical research efforts that have had a somewhat narrower focus have provided some additional insights into this topic which might lead to testable hypotheses regarding the neurobiology of empathy.

The authors' own examples of autism and antisocial personality disorder (ASPD) illustrate distinct naturalistic deficits in the apparatus for empathy, but there are obvious differences in the *quality* of empathic deficiency between these two conditions which are not entirely explained by the model. Fully autistic children appear to lack the neuro-developmental capacity for joint attention, yet may be exquisitely sensitive to seemingly trivial socio-environmental cues, to which they stereotypically respond. Sociopathic individuals exhibit low levels of arousal and are unmotivated by interpersonal contingencies, but may become incensed by perceived insults from others. These observations suggest that awareness of social cues, the capacity to appropriately interpret those cues, the ability to respond competently, and the inherent motivation to respond may represent distinct variables in whatever system or systems contribute to what is subsumed under the term "empathy." It is also worth keeping in mind that there are pronounced, universally-observed gender differences in the prevalence of both autism and ASPD; such differences suggest sex-specific pathways that would deserve incorporation into any biologic model of empathy. Furthermore, recent research has suggested that both of these disorders have polygenic determinants and may represent extremes of continua of social deficiency that exist in the general population (Constantino & Todd 2000; Slutske et al. 1998). If so, it will be important to understand whether milder social deficits that have been preserved over the course of evolution might confer specific advantages to some individuals. Any of the above considerations could lead to revisions to the notion of empathy evolving as a singular, highly adaptive capacity.

ASPD can also be compared with other types of personality disorder, all of which are quintessential disorders of human relationship-relevant capacities, and are characterized by varying degrees of deficiency in empathy. Cloninger and colleagues (Cloninger 1987; Cloninger & Svrakic 1997) have shown that among subjects with personality disorders (including ASPD), an individual's specific diagnosis is best predicted by his or her configuration with respect to three highly heritable stimulus-response tendencies: behavioral activation (measured by novelty seeking), behavioral inhibition (measured by harm avoidance), and reward dependence. These tendencies, which seem highly relevant to the perception-activation model, are not, however, what determines whether an individual will have a personality disorder; rather, they predict which of the various personality disorders an affected individual will have (pronounced variations in these stimulus-response characteristics are also observed in normal [empathic] individuals without personality disorder). Rather, presence or absence of personality disorder are strongly predicted by indices of characterologic maturation: self-directedness and cooperativeness, both of which depend on self-object differentiation. In other words, in Cloninger's empirically-derived model, the proximate determinants of empathic deficiency are actually higher-order cognitive functions; variations in stimulus-response characteristics result only in syndromal variations among these primary disorders of interpersonal function.

Direct attempts to characterize internal mental representations of attachment relationships (Main et al. 1985; van Ijzendoorn 1995) have indicated that such representations are measurable and that in patients with personality disorder, they are generally disorganized or incoherent. Attachment research has supported many aspects of P&deW's model in that, the way in which early attachment relationships are incorporated into an internal working model predicts important aspects of interpersonal function over the life course, including child rearing behavior. Further research specifically exploring the genetic, environmental, and neurobiologic determinants of mental representations of attachment may provide important insights into the biology of empathy.

Finally, Karasu (1992) has contrasted "understanding" with "empathy" by highlighting the distinction between two ways of responding to a suffering patient: in the first (understanding), the therapist states, "You must be feeling sad"; in the second (empathy), the therapist states, "How sad." The first may constitute what P&deW refer to as a "cognitive form of empathy." But it is not clear that they have left enough room in their model to differentiate the first condition from the second condition, in which empathy seems to transcend cognition, rather than the other way around. Conscious decisions to engage or disengage the latter (altruistic) capacity might constitute an important component of what is considered to be free will (since doing so ostensibly represents a departure from what is reflexively self-preserving). The sense of meaning that an individual derives from making such decisions may, as the authors suggest, in turn exert substantial influences on subsequent empathic behavior.

## Too early for a neuropsychology of empathy

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**Abstract:** To date, a wide range of interdisciplinary scholarship has done little to clarify either the why or the how of empathy. Preston & de Waal (P&deW) attempt to remedy this, although it remains unclear whether empathy consists of two discrete processes, or whether a perceptual and motor component are joined in some sort of behavioral inevitability. Although it is appealing to offer a *neuroanatomy of empathy,* the present level of neuropsychology may not support such reductionism.

It's hard not to sing the praises of empathy, whatever it is. You don't need an iron-clad definition to appreciate empathy. We pretty much agree that the word denotes a good thing: empathy is the stuff of group cohesion, and may be the reason we attract, or are attracted to, one person over another. Unfortunately, you do need a solid definition if you're going to study empathy, and it's here that the gaps and inconsistencies in our understanding loom large.

Plainly, empathy is relevant to a host of topics studied by psychology; they include observational learning, sociopathy, altruism, social facilitation, deception, vicarious learning, and autism. In addition to attracting all kinds of psychologists who rarely speak to each other professionally, empathy has also been studied by philosophers, theologians, and ethologists. This alone should tell you there is trouble brewing.

P&deW readily acknowledge the conceptual mess that swirls around empathy. It's probably what drove them to write their article. It is thus fair to ask how so many people with such disparate interests and training all find this common topic worth their attention? One possibility is that empathy is not a single topic; it is simply an umbrella term masquerading as a discrete topic. Of course, it remains possible that empathy really is a single entity that happens to hold interdisciplinary relevance. But how many subjects do you know that can be studied equally well using questionnaires, field studies, and MRIs?

I don't believe that the "riddle of empathy" (to use Allport's phrase) will be solved by some grand interdisciplinary synthesis and neither, as far as I can tell, do P&deW. What seems more likely is that empathy has been the beneficiary of some very good press and some very bad scholarship. The "good press" stems from the fact that the trait is largely regarded as a good, even ideal thing. Unlike other aspects of human nature (e.g., jealousy, rage), empathy is almost universally regarded in positive terms. People with "it" (whatever it is) are viewed as being better human beings: we aspire to be more like them; we choose them for friends and lovers. Therapists with "it" are presumed to be better at their craft than less empathic therapists. Indeed, Rogerian therapists are explicitly *trained* to create more of it.

The "bad scholarship" stems from the fact that workers have often free-associated to "empathy," seizing on those aspects of the term that most engaged them, and then bringing the peculiar skills and vocabularies of their discipline to the task. Good luck integrating that body of literature! A second factor compromising our ability to investigate empathy is the high regard with which it is held. It is difficult to be analytical about the roots of any behavior or phenotype that seems to provide such obvious interpersonal benefits. Note how few papers there are on why it is better to be good looking, healthy, and rich.

P&deW have attempted to find a way through this conceptual quagmire. Their approach offers hope that we may yet understand the *why* of empathy (i.e., an evolutionary account) as well as the *how* (a physiological mechanism underlying empathy). Regarding the *why,* P&deW note that "Ultimate accounts are notorious for being cursory and speculative" (target article, sect. 2.) They are right. Certainly, some evolutionary psychologists have had too easy a time explaining why empathy would fare well under selection pressure. Glib accounts, often extrapolated from today's world, suggest that empathic skills offer an advantage in (1) attracting mates (what woman wouldn't want an empathic man by her side?), and (2) child rearing (what kid wouldn't thrive under the auspices of an empathic parent?). But do these facile judgments tell us anything about the selective advantage empathy provided in the ancestral environment? To their credit, P&deW look beyond our species in attempting to answer the question of why empathy might offer a reproductive advantage. Fortunately, nobody has yet suggested an inter-species account of empathy which argues that empathic men were more successful hunters because they better *listened* to their prey, thus increasing their efficiency and providing more resources for their mates and offspring. Presumably, if no such evidence exists, one could argue that prey animals used such empathic listening to avoid detection by human predators.

There is an inconsistency in this target article. On one hand, the Perception-Action model is essentially a dualist position. The authors do well to remind us that there are two distinct stages to empathy – one perceptual/cognitive, and one behavioral. This is all the more important because folk psychology does what it can to blur this distinction. The term "empathy" is used in everyday language to describe both the mental side (the *theory of mind* part of empathy) as well as the behaviors that follow from such understanding. Note that these behaviors are only considered empathic as long as they are compassionate. If the resultant behavior is exploitative, the term "deception" is applied. In that sense, deception is the evil twin of empathy – both stem from a sensitive reading of another person, but differ in the use to which that information is put.

On the other hand, the physiological account offered by P&deW – with its emphasis on mirror neurons in the prefrontal cortex – suggests such a degree of behavioral inevitability that empathy might as well be a single process, embracing both the perception and the action. Once those perceptions occur and the relevant motor centers light up, only a fool would bet against the appropriate behavioral output. The phrase "automatically primes and generates" (sect. 1.1.3) embodies this confusion. To prime and to generate suggest different levels of behavioral determinism. Using an analogy from Learning Theory, it is the difference between a Pavlovian CS (which *elicits* the response) and an operant $S^D$ (which sets the occasion for a response to be emitted). P&deW need to clarify the degree of behavioral determinism suggested by their account.

Although it is deeply appealing to refer to "the neuroanatomy of empathy" as a way to deepen our understanding, it is wise to remind ourselves that the comforts of reductionism come at a price. Neuropsychology is in its relative infancy. It is quite possible that our present level of sophistication may represent as big a jungle as the confusion surrounding empathy.

## Distinctions among various modes of empathy-related reactions: A matter of importance in humans

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**Abstract:** Preston & de Waal minimized differences among constructs such as empathy, sympathy, and personal distress. However, such distinctions have been shown to relate differently to altruistic behavior. Moreover, although the authors discussed the role of regulation in empathy, they did not consider the possibility that sometimes empathy is not well-regulated and likely leads to personal distress rather than sympathy.

Preston & de Waal's (P&deW's) article provides a very interesting and useful interdisciplinary integration of theory and empirical literature on empathy. Although I agree with many of their points, I disagree with their tendency to dismiss the importance of the distinctions among personal distress, sympathy, and empathy, and their tendency to assume that empathy will be related to prosocial rather than self-focused behavior.

P&deW state that "It is mistaken to argue whether help is given for the benefit of the object or to terminate the object's aversive distress signal or the subject's personal distress" (sect. 2.3). There is much evidence contradicting this statement in research that differentiates between two emotion-based reactions that often may stem from empathy (Eisenberg et al. 1991) – *sympathy* (an emotional response stemming from the apprehension or comprehension of another's emotional state or condition, which is not the same as what the other person is feeling or is expected to feel but consists of feelings of sorrow or concern for the other; called "empathy" by Batson 1991); and *personal distress* (a self-focused, aversive affective reaction to the apprehension of another's emotion, e.g., discomfort, anxiety). Specifically, in situations in which it is easy to avoid contact with a needy other and minimize the likelihood of a benefactor receiving social approval or concrete rewards for helping, children's and adults' sympathy has been positively related to prosocial behavior, whereas their levels of personal distress have been unrelated or negatively related (Batson 1991; Eisenberg & Fabes 1998). Thus, there seems to be fundamental differences between the motives and behaviors associated with sympathy and with personal distress, although P&deW argue that the distinctions among definitions in their Table 2 "have been overemphasized to the point of distraction" (sect. 1.1.2).

Moreover, sympathy and personal distress are differentially related to regulatory capacities. P&deW noted the role of the prefrontal cortex in regulation: "prefrontal size correlates with emotional regulation skills in development and phylogeny, thus, the prefrontal cortex is thought necessary for the ability to control the extent of personal distress and remain focused on the object" (sect. 3.3). Related to this point, the effortful control processes associated with the middle of the frontal lobe of the cortex (e.g., the abilities to effortfully shift or focus attention and inhibit behavior as needed) have increasingly been viewed as contributing to socioemotional and moral development, including empathy-related responding (Eisenberg 2000; Kochanska et al. 2000; Rothbart et al. 1994). For example, my colleagues and I (Eisenberg & Fabes 1999; Eisenberg et al. 1994) have argued that effortful, voluntary regulation is associated with sympathy rather than personal distress, and that empathic overarousal in situations involving negative emotion results in an aversive emotional state, which leads to a self-focus (i.e., personal distress). If individuals cannot maintain their emotional reactions to others' emotions within a tolerable range of arousal, they would be expected to focus on their own emotional needs. Conversely, individuals who can maintain their vicariously induced emotional arousal at a moderate level, which is arousing but not aversive, were hypothesized to experience sympathy (Eisenberg et al. 1994). If these propositions are true, individual differences in effortful emotion-related regulation would be expected to be linked to differences in dispositional sympathy and personal distress.

Consistent with the view that personal distress involves overarousal, we have found that children's and adults' heart rate and skin conductance tend to be higher in experimental situations likely to induce personal distress (in comparison with control or sympathy-inducing contexts; see Eisenberg & Fabes 1999, for a review). In addition, my colleagues and I (also see Rothbart et al. 1994) have found different relations between effortful regulation and sympathy versus personal distress. In adults, we have found positive relations between measures of effortful control and sympathy (Eisenberg & Okun 1996), although sometimes only after controlling for individual differences in negative emotional intensity (see Eisenberg et al. 1994; Okun et al. 2000). In contrast, self-reported dispositional personal distress has been related to low levels of both self-reported regulation and friends' reports of students' coping (Eisenberg et al. 1994; Okun et al. 2000). In addition, children's effortful control has been positively related to their dispositional sympathy at several ages and across time (Eisenberg et al. 1996; 1998; Murphy et al. 1999). Although findings for situational measures of sympathy are less clear (see Eisenberg & Fabes 1999), in general the data support a positive relation between sympathy and regulatory capacities, and an inverse relation between personal distress and regulation. Such findings are consistent with P&deW's contention that regulatory processes play a central role in empathic processes; however, they also illustrate the need to clearly differentiate among empathy, sympathy, and personal distress (unless one equates empathy and sympathy, which does not seem to be the case in Table 2). Indeed, it is unlikely that all the types of responding that P&deW have included in their construct of empathy are associated with high effortful regulation.

In summary, although P&deW are probably correct in many of their assumptions about the origins of empathy, it is important to consider the differences between relatively rudimentary forms of empathy (defined as an affective response that stems from the apprehension or comprehension of another's emotional state or condition, and which is similar to what the other person is feeling or would be expected to feel), and sympathy or personal distress, which probably often stem from empathy (see Eisenberg et al. 1991).When studying beings such as humans who sometimes can regulate and modulate empathic arousal, the distinctions among empathy, sympathy, and personal distress should not be ignored.

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## Emotional and cognitive processing in empathy and moral behavior

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**Abstract:** Within the perception-action framework, the underlying mechanisms of empathy and its related processes of moral behavior need to be investigated. fMRI studies have shown different frontal cortex activation patterns during automatic processing and judgment tasks when stimuli have moral content. Clinical neuropsychological studies reveal different patterns of empathic alterations after dorsolateral versus orbital frontal cortex damage, related to deficient cognitive and emotional processing. These processing streams represent different neural levels and mechanisms underlying empathy.

Preston & de Waal's (P&deW's) effort to make order out of the chaos that surrounds the concept of empathy is a laudable one. It is in line with the pressing clinical and scientific needs for a deeper understanding of the cerebral mechanisms that govern empathy and how they fail in psychopathy, traumatic brain injury, schizophrenia, Alzheimer's disease, and related disorders.

The authors propose to apply the perception-action model as a fundamental empirical framework for the study of empathy. Furthermore, they emphasize empathy as a process rather than a response, allowing for numerous and diverse subordinate mechanisms such as emotional contagion, sympathy, and so on. In this sense, the study of empathy and related emotional, cognitive, and physiological processes can be aligned with scientific approaches that have been fruitful in other domains of human adaptation such as language, visuospatial memory, and executive functions. The larger issues they allude to as the "ultimate bases of empathy" have important implications not just for the reproductive success and adaptive fitness of a species, but also for many other human social and cultural phenomena, from family structures to legal-political systems that govern masses of people. Though we agree that a unified working definition of empathy is needed, structuring the concept of empathy as "perception-action" does not explain the multidimensional features of empathy nor its mechanisms. However, the perception-action analysis of empathy follows parallel developments in related fields. Further specification can come from two approaches: fMRI studies and clinical neuropsychological studies.

***fMRI studies.*** Moral judgment is a higher order type of social decision-making that draws heavily on cognitive and emotional empathic processes. Accordingly, moral actions in the real world are not simply a "cold" product of scholarly reflections, but result from the covert interaction of social decision-making and deeply rooted emotional dispositions, which are themselves strongly biased by individual empathic tendencies (Rozin et al. 1999). As suggested by P&deW, social stimuli can elicit spontaneous brain responses in areas mediating emotional and decision-making processes. We recently completed a functional magnetic resonance imaging study of normal volunteers viewing pictures of emotionally charged scenes with and without moral content, as well as emotionally neutral pictures (all stimuli independently rated and validated). By design, no responses were required of subjects, so as to capture spontaneous, automatic processing. Results demonstrated that viewing moral and nonmoral visual stimuli activated a common network of brain areas that included the amygdala, insula, thalamus, and upper brain stem. Importantly, the medial orbitofrontal cortex, medial frontal gyrus, and posterior superior temporal sulcus were additionally recruited during spontaneous processing of moral stimuli, unrelated to emotional valence and arousal. We interpret these findings as evidence that one of the roles of the medial orbitofrontal and medial frontal cortical regions involves the quick, automatic detection of salient social-emotional stimuli and events, in conjunction with corollary effects in the superior temporal, limbic, and other subcortical structures (Moll et al., 2001). Such a mechanism essentially permits a more comprehensive perceptual apparatus than flight or fight detection. It also extends the type of rapid, automatic processing associated with the amygdala to related regions that have cortical learning and memory capacities. Its activation can prepare diverse cognitive processing systems for detailed perceptual analysis, decision-making, and action. The automatic nature of the processing suggests it is a pervasive feature of social-emotional perception-action mechanisms.

A different pattern results when normal individuals are specifically asked to judge sentences with explicit moral content (e.g., "we break the law when necessary") versus factual statements devoid of moral connotations (e.g., "stones are lighter than water"). Subjects were instructed to silently judge each sentence as right or wrong without previous knowledge that the experiment had anything to do with morality. After the scanning session, each participant rated the degree of moral content and the quality and emotional valence of each sentence on Likert-like scales. In comparison to factual judgments, moral judgments strongly activated the frontopolar cortex (FPC) and the medial frontal gyrus (MFG) (see Fig. 1). The right anterior temporal cortex, lenticular nucleus, and cerebellum were also significantly activated but differently from the FPC and MFG. These brain regions were strongly influenced by emotional experience, as revealed by covariance analysis using hemodynamic modeling within an event-related fMRI approach.

This task required more explicit reasoning and judgment and showed a different pattern of brain activation than when automatic responses are monitored (i.e., more polar frontal and less orbitofrontal). Together with other studies (e.g., Baron-Cohen et al. 1999; Jarvie 1954), the findings suggest that there are multiple levels of neural activation, particularly within prefrontal regions, for social events that engage empathic mechanisms through automatic emotional and acquired cognitive processes.

***Clinical neuropsychological studies.*** Complex social actions requiring moral evaluations, empathy, theory of mind, and stable

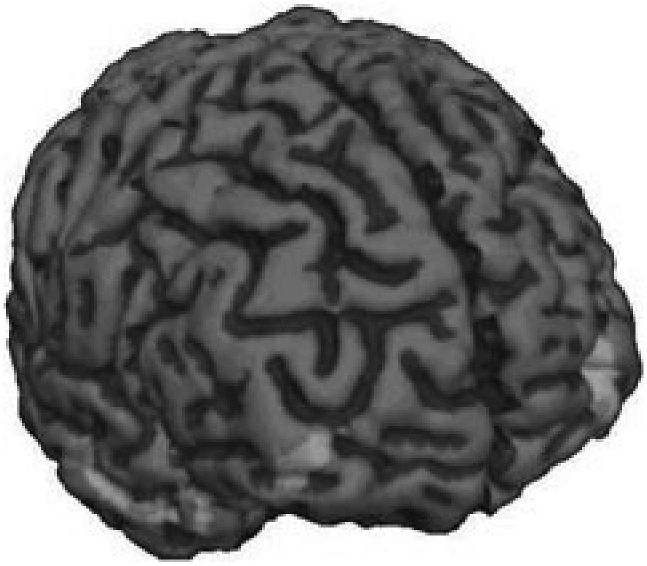

Figure 1 (Eslinger et al.). Results of fMRI study of normal volunteers making explicit moral judgments, showing activation primarily of frontopolar cortex, medial frontal gyrus and related regions

social bonds have been traditionally conceived to rely on two main streams of processing (Eslinger 1998): one more cognitively oriented and dependent on the dorsolateral prefrontal cortex, and the other more emotion-oriented and mediated by anterior temporal, limbic, and orbitomedial frontal cortical systems. In a neuropsychological study of humans with acquired lesions of the frontal lobe (Grattan et al. 1994), comparisons between quantitative measures of cognitive flexibility and empathy indicated that left and right dorsolateral frontal lesions caused deficits in both cognitive flexibility and empathy (with correlations ranging as high as $r = .81$). In contrast, orbitofrontal lesions profoundly affected empathy but did not alter cognitive flexibility, suggesting different mechanisms of pathophysiology for empathic change that may have its basis in deficient automatic tagging of salient stimuli or evocation of autonomic-visceral states. The latter pattern has also been reported in patients with lesions of the insula and deep white matter of the frontal lobe, likely disconnecting orbitofrontal, amygdala, and insula interconnections. Despite the lack of automatic emotional responsiveness, these individuals can be trained to use cognitive mechanisms for recognition of salient facial, vocal, and body expressions, and for the verbal expression of their concern. Thus, frontal regulation of social conduct favors the view that the prefrontal cortex may need further functional fractionation, with polar, orbital, medial, dorsolateral, and deep white matter sectors mediating distinct, but complementary roles in the emotional-cognitive regulation of social behavior. In our experience, early damage to polar, mesial, and dorsolateral regions disrupts the developmental acquisition of automatic and learned empathy, moral judgment, and interpersonal conduct (e.g., Eslinger et al. 1992; 1997).

The cerebral correlates of specific dimensions of moral and empathic behaviors need further study (Grattan & Eslinger 1989). P&deW's article offers a solid conceptual frame against which specific hypotheses and models can be put to empirical testing in normal individuals, as well as in patients with a variety of neuropsychiatric disorders which express themselves as disorders of empathy, social, and moral behavior.

## The mirror matching system: A shared manifold for intersubjectivity

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**Abstract:** Empathy is the phenomenal experience of mirroring ourselves into others. It can be explained in terms of simulations of actions, sensations, and emotions which constitute a shared manifold for intersubjectivity. Simulation, in turn, can be sustained at the subpersonal level by a series of neural mirror matching systems.

The article by Preston & de Waal (P&deW) has the merit of raising the issue on how different and multifarious social behaviors such as emotional contagion, helping behaviors, imitation, and cognitive empathy may be reconciled within a unified explanatory framework. Their proposal is that empathy can constitute such a framework, provided that it is "construed broadly to include all processes that rely on the perception-action mechanism" (see target article, sect. 1.1.3, Fig. 1 caption).

Unfortunately, the discussion of these interesting issues is, in our view, most of the time too vague, and sometimes even confounding, so that it is difficult to draw any firm conclusion on the validity of the proposed model.

The definition of empathy given by P&deW seems to oscillate between a "superordinate category" of behaviors, and a process underpinning the same different types of behavior. They introduce the Perception-Action Model (PAM), which is presented as a "superordinate class," capable of including and subsuming different types of behaviors and effects, among which empathy is also listed (see their Fig. 1). This makes it almost impossible to understand whether in the authors' view empathy and PAM are the same thing or not. Furthermore, the term PAM is used interchangeably to denote either a model (as the acronym seems to suggest) or a basic (neurophysiological?) level of description. Such a use of the term makes several statements hard to understand. How can a model possibly *interact* with specific brain functions? (e.g., see the Abstract where it is stated that: "The interaction between the PAM [Perception Action Model] and prefrontal functioning can also explain different levels of empathy.") Models should *explain,* or *interpret* functions, not interact with them.

The broad and general sense attributed by P&deW to the term empathy fails to provide a coherent picture of the mechanism that is at the basis of their model. There is confusion here – if not even a category mistake – about the chosen *level of explanation.*

In our opinion, the term "empathy" makes sense only if used to denote a phenomenological level of description: the one responsible for the sense of similarity that we experience anytime we confront ourselves with other human beings, and sometimes even with animals. Empathy is deeply grounded in the experience of our lived-body, and it is this experience that enables us to directly recognize others, not as bodies endowed with a mind, but as *persons* like us. Actions, sensations, and emotions experienced by others become meaningful to us because we can *share* them with others. How can such a sharing of experiences be possible? We need to introduce a second level of description, one pertaining to the functional mechanism that enables such an experience to occur. This functional mechanism may be constituted by *simulation.* Simulation mechanisms are a possible way for a given organism to control and model its performances. By modeling a given process, our brain provides a *simulated representation* of the same process that can be used to produce it, on the one hand, and to decode it when performed by someone else, on the other. We suggest that these "as if" simulation mechanisms may subsume a wide range of processes as diverse as action perception and imitation (as simulation of the observed action; see Gallese 2000a; 2000b; 2001; see also Rizzolatti et al. 2001), emotion perception (as simulation of the perceived emotion; see Adolphs 1999; Adolphs et al. 2000;

Gallese 2001), and mindreading. Simulation theory in fact holds that we understand others' thoughts by *pretending* to be in their "mental shoes," and by using our own mind/body as a model for the minds of others (Gallese & Goldman 1998; Goldman 1989; Gordon 1986; Harris 1989).

Is there a further level of description that can provide a common and coherent explanatory frame for all these different simulation mechanisms? We propose, yes: such a level could be represented by the neural matching system constituted by mirror neurons (Gallese et al. 1996; 2002; Rizzolatti et al. 1996; Umiltà et al. 2001; see also Rizzolatti et al. 2001) – or by equivalent neural systems described in the human brain (Fadiga et al. 1995; Iacoboni et al. 1999; Nishitani & Hari 2000). Mirror neurons could underpin a direct, automatic, nonpredicative, and noninferential simulation mechanism, by means of which the observer would be able to recognize, understand, and imitate the behavior of others. The authors maintain that "mirror neurons . . . provide concrete cellular evidence for the shared representations of perception and action" (see target article, sect. 3.1). They fail, nevertheless, to draw the correct conclusions from such a statement. It is true, as they argue, that mirror neurons do not produce per se any empathy. However, if an action-perception matching is crucial for the production of empathy, as the authors suggest, mirror neurons represent the most parsimonious neural system so far described, enabling such a matching to occur. The trick here is not to confound the phenomenal aspect of behavior, its functional level of description, and the neural mechanism at its base.

Preliminary results suggest that a mirror matching system could be at the basis of our capacity to perceive in a meaningful way, not only the actions, but also the sensations and the emotions of others (see Gallese 2001). Single neuron recording experiments in humans have demonstrated that the same neurons become active when the subject either feels pain or observes others feeling pain (Hutchison et al. 1999). Furthermore, a recent fMRI study has shown that the amygdala becomes active not only during the observation, but also during the *active expression* of facial emotions, especially when imitation is involved (Carr et al. 2001).

In conclusion, these recent findings suggest that a neural matching system is present also in a variety of *apparently* non-motor-related human brain structures. Thus, different *simulation mechanisms* are applied in different domains, being sustained by a mirror-matching, dual-mode of operation (*action-driven* and *perception-driven*) of given brain structures. We propose that such simulation mechanisms may constitute altogether a *shared manifold* of intersubjectivity (see Gallese 2001).

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## Cognitive empathy presupposes self-awareness: Evidence from phylogeny, ontogeny, neuropsychology, and mental illness

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**Abstract:** We argue that cognitive empathy and other instances of mental state attribution are a byproduct of self-awareness. Evidence is brought to bear on this proposition from comparative psychology, early child development, neuropsychology, and abnormal behavior.

The subcategory of empathy that Preston & de Waal (P&deW) identify as cognitive empathy represents an instance of a more general phenomenon known as mental state attribution. Twenty years ago a model was formulated that stipulates self-awareness as a necessary condition for making inferences about mental states in others (Gallup 1982). According to the model, inferential knowledge of mental states in others builds on a knowledge of mental states in oneself. Organisms that can become the object of their own attention (i.e., recognize themselves in mirrors) can use their experience to model/infer comparable experiences in others. Because humans share similar receptor mechanisms and brains that are organized in roughly the same way, there is bound to be considerable overlap between their experiences. Moreover, people that have access to their own mental states and take note of their relationship to various external events, have a means of making inferences about mental states in others. Knowledge of self, in other words, paves the way for achieving an inferential knowledge of cognitive states in others.

Since the ability to recognize oneself in a mirror varies as a function of species, age, neurological status, and mental illness (Gallup et al. 2002), this model can be tested in each of these domains. According to the model, variation in mirror self-recognition ought to predict comparable variation in the ability to take into account how others feel, and variation in being able to accurately infer what they want, know, or intend to do. In instances in which self-recognition is deficient or absent, there should be a corresponding deficiency or absence of mental state attribution.

Thus, whereas chimpanzees that recognize themselves in mirrors show evidence of cognitive empathy (Povinelli et al. 1992a), rhesus monkeys, which fail tests of self-recognition, show no evidence of cognitive empathy (Povinelli et al. 1992b). Monkeys seem incapable of taking into account what other monkeys may or may not know, want, or intend to do. Indeed, monkeys may not even know what they know (Cheney & Seyfarth 1990).

The same holds for humans. People who are incapable of recognizing themselves in mirrors are typically unable to make inferences about mental states in other people. For instance, it is only after children learn to recognize themselves in mirrors (usually between 18 and 24 months of age) that they begin to show evidence of being able to take into account what other people are seeing or feeling (e.g., Carruthers & Smith 1996). Likewise, the emergence of prosocial and altruistic behaviors in children is related to the age at which they show self-recognition (Johnson 1982).

There is a growing evidence that self-recognition is localized in the brain. Patients who are incapable of identifying their own faces often have damage to the right prefrontal cortex (e.g., Spangenberg et al. 1998). Breen (1999) described a patient with damage restricted to the right prefrontal cortex that could recognize other people in a mirror, but insisted that his own reflection was someone else. Keenan and Wheeler (in press) summarize a number of neuropsychological studies which show both right hemispheric lateralization and localization of self-recognition in the prefrontal cortex. As support for the proposition that mirror self-recognition is a valid index of self-awareness, it is important to note that self-evaluation and autobiographical memories are also localized in the right prefrontal cortex (see Keenan et al. 2000).

Consistent with the model, the same part of the brain that is important for self-recognition also appears to be crucial for mental state attribution. In contrast to patients with brain damage elsewhere, Stuss et al. (2001) found that those with lesions restricted to the right frontal lobes showed deficits in visual perspective taking and detecting deception. Likewise, Happe et al. (1999) report that patients with damage to the right hemisphere evidence an impaired ability to interpret mental state attribution narratives and fail to appreciate instances of humor that require making mental state attributions.

Deficits in mirror self-recognition are also characteristic of a number of psychological disorders (Gallup et al., in press). Schizophrenics often react to themselves in mirrors as though they were seeing other people (Harrington et al. 1989). Similarly, people who score high on measures of schizotypal personality show impairments in self-face recognition (Platek & Gallup 2002). There is mounting evidence that schizophrenia is associated with frontal lobe pathology (e.g., Frith 1997) and schizophrenics show pronounced mental state attribution deficits (e.g., Frith & Corcoran 1996). The same parallel holds true for autistic children. Mirror self-recognition is developmentally delayed and sometimes even absent in children suffering from autism (Spiker & Ricks 1984), and autistic children are impaired in their ability to take into account what other people are thinking (Baron-Cohen 2000).

Thus, the model that stipulates self-awareness as a necessary condition for mental state attribution has been subject to considerable convergent validation. The underlying network that integrates these processes would also appear to be responsible for cognitive empathy.

## Empathy, simulation, and PAM

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**Abstract:** The wealth of important and convergent evidence discussed in the target article contrasts with the poorly conceived theory put forward to explain it. The simulation theory does a better job of explaining how automatic "mirroring" mechanisms might work together with high-level cognitive processes. It also explains what the authors' PAM theory merely stipulates.

The target article brings together a variety of interesting studies the authors believe to be convergent. I agree that the studies converge, but I do not find the account of what they converge on particularly helpful.

Preston & de Waal (P&deW) initially appear to be putting forward the very bold empirical hypothesis that all the various phenomena commonly considered species of empathy share a particular underlying mechanism, namely, the Perception-Action Mechanism. Upon closer inspection, however, what the authors are doing is defining the term "empathy" to include just those "sub-classes of phenomena that share the [PAM] mechanism." This is an acceptable move, provided the definition offers clarification and insight without deviating too far from our understanding of the term. The burden of proof then shifts to the adequacy of the definition. I find it inadequate. It seems arbitrary to exclude from the scope of "empathy" empathetic responses induced by memory, by imagination, or by perception of verbal narratives such as newspaper reports and fiction. If "empathy" is to cover these responses, then "perception" must be taken to include remembering, imagining, and reading or hearing about another's behavior. Although the authors say they are taking "a broad view of the perception-action model," a view broad enough to count imagination as perception does not really move the field forward. It confers on the various perspectives on empathy only a specious nominal unity.

Another problem is that the apparent simplicity of the PAM model is blemished by what seem to be ad hoc amendments.[1] For example:

> With the Perception-Action Model, whether or not a subject perceives the state of the object depends crucially on their interdependence or interrelationship. . . . The more interrelated the subject and object, . . . the easier it is to process the state of the object and generate an appropriate response. (target article, sect. 1.1.3)

Let's be clear that this generalization was not predicted by PAM; rather, here as elsewhere, the authors tacked it on to PAM to accommodate the evidence. An adequate account should help explain why interdependence/interrelationship is a factor. This would have to be an account that shows how automatic perception-action mechanisms might be integrated with cognitive processes.

The authors briefly discuss the simulation theory, noting that a number of recent papers in neuroscience have presented evidence in support of it (Adolphs 1999; Adolphs et al. 2000; Gallese & Goldman 1998; Iacoboni et al. 1999; Motluck 2001; Williams et al. 2001; Wolf et al. 2001; I would add Blakemore & Decety 2001; Gallese 2000a). One of the reasons why the theory has been attractive to neuroscientists is precisely that it sketches a plausible way for automatic (perception-action and perception-emotion) mechanisms to work together with high-level cognitive processes.[2] The automatic mechanisms allow us to mirror the other's emotions and motor plans; the relevant cognitive processes, according to the simulation theory, marshal situational, biographical, and behavioral information for such purposes as reasoning and decision-making in the role of the other (Gordon 1996). For example, suppose A has a mechanism that takes as input B's facial expression of emotion and produces in A an emotion similar to B's – "off-line," that is, not behavior-guiding but rather restricted to A's first-person "role-taking" representation of B. If "off-line" emotions influence vicarious decision-making in the way that "on-line" emotions influence real decision-making, then one can see how automatic mechanisms for mirroring emotions would be complementary to the cognitive processes involved in "putting oneself in the other's place."

Perhaps even more obviously, mirror neurons are likely to "talk" to the cognitive processes that underlie vicarious decision-making. Suppose A has a mechanism that takes as input B's object-directed action sequence (for example, B's reaching for a cup, grasping it, and removing it from the table) and produces in A an intention or (at least) a motor plan to perform the same sequence – an intention or plan that runs "off-line," not to be acted on by A but rather confined to A's first-person "role-taking" representation of B. Then A has in effect already made a decision in the role of B. The decision must now be integrated with a broader simulation of B, to generate possible reasons for grasping and removing the cup – that is, reasons suitable to B at the time of action.

Unlike PAM, the simulation theory also helps explain why interrelationships are likely to affect empathy. Consider vicarious decision-making. It requires less of an imaginative stretch for an agent A to take the role of another agent B in imagination (or overtly, as in stage-acting) if B is similar to A, or in certain respects closely related. It is not surprising, therefore, that in such cases it is "easier . . . to process the state of the object and generate an appropriate response" (target article, sect. 1.1.3). Here (and, I believe, elsewhere) the simulation theory explains what the PAM theory merely stipulates.

NOTES

**1.** Further, the authors add some perplexing generalizations. For example: All forms of empathy involve some level of emotional contagion. . . . This would seem to rule out empathetic responses to memories, fantasies, and verbal accounts, unless the concept of contagion extends to these. All forms of empathy involve . . . personal distress (if only at the representational level). So sharing another's pain is empathy but sharing another's joy is not? Does PAM respond, then, only to "negative" emotions?

**2.** Here I follow the tradition in cognitive science of using the term "cognitive" to cover states and processes that implement any person-level intentional states and processes, be they conative, emotional, or cognitive in a narrow sense.

## Emotion: The relation between breadth of definition and explanatory power

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**Abstract:** Attempts to integrate diverse phenomena in terms of common processes are much needed in psychology, but definitional precision is a necessary preliminary to explanation. It is also preferable to use caution in juxtaposing concepts from different realms of discourse.

In this target article Preston & de Waal (P&deW) attempt to integrate in terms of a common process a number of psychological phenomena that are usually regarded as distinct. This is an important task to undertake, for the identification of common processes could lead to a more basic understanding of diverse psychological phenomena. The authors survey a broad range of literature from psychology and the neurosciences. While the attempt must elicit one's admiration, repeated reading of the article left this commentator concerned over definitional matters and over the juxtaposition of behavioural, psychological, and neurophysiological concepts.

Empathy is defined in terms of the object's state generating a related state in the subject. The "Perception-Action-Model" (PAM) of empathy takes it one stage further, stating that the activation of the representations induced in the subject *"automatically primes or generates the associated autonomic and somatic responses, unless inhibited"* (target article, sect. 1.1.3, author's emphasis). Thus, while the PAM of empathy includes action, empathy does not. Empathy is seen (perhaps confusingly) as a "superordinate category" "underlying" all phenomena sharing empathy as a common process, such as emotional contagion and helping behaviour. But it is not clear why the authors' Figure 1 indicates that imitation involves perception-action but helping behaviour does not: surely both involve action? And if empathy induces a related state in the subject, but only with the PAM does the subject act appropriately as a consequence, what does it mean when the authors speculate that a perception-action organisation was an evolutionary precursor to empathy? Is action necessary for empathy? Does the perception-action hypothesis merely state that perception can lead to action? If so, what is so new about that? More explanation would have been welcome.

Definitional clarity is not enhanced by the juxtaposition of distinct levels of discourse. The explanation of the definition of the PAM involves behavioural concepts (e.g., imitative actions), psychological concepts (empathy, perception), and concepts from neuroscience (connectivity of neurones). This mixture of languages pervades much of the discussion – as, for instance, when, on the basis of behavioural data, experience is said to "fine tune the circuits for responding." In my opinion, an attempt to relate the behavioural and psychological phenomena under discussion at a neural level requires a clear definition of empathy in behavioural terms, a proposed explanation in terms of (psychological) hypothetical constructs, and demonstration of parallel neural mechanisms. This may sound like regression to the bad old days of learning theories characterised by disciplined system-building, but there is much to be said for definitional precision. If we construe empathy "broadly," take a "broad view of the perception-action model," and use a "flexible definition" of perception, we could explain almost anything.

As another instance of lack of definitional clarity, empathy is said always to involve "some level of personal distress" (sect. 1.1.3), but a few paragraphs later the authors state that it can involve matching "joy to joy."

None of this implies that the behavioural phenomena are insignificant. Babies do distort their faces to match the caregiver's expression, and anyone who has hand-reared nestling birds knows how impossible it is not to open one's own mouth when encouraging them to gape – an observation that incidentally is not in keeping with the postulated role of similarity or relatedness between subject and object. The PAM does indeed seem to offer a plausible explanation of many such observations. But this project requires careful and accurate description. If a monkey, as the result of experience, ceases to give a response that causes another monkey to emit signs of distress, is its act performed "to terminate the object's distress" or to terminate its own? The data show only that ending the subject's distress was a consequence of the change in the object's behaviour, not that it was a goal.

The reservation that the PAM generates associated responses in the subject "unless inhibited" allows P&deW to include phenomena where empathy seems not to occur. But precise explanation of why it sometimes does and sometimes does not is lacking. A rat may or may not act in a way that relieves the distress of a conspecific. Humans do not always help others in distress, but to say that in the latter case their behaviour is inhibited is hardly an explanation.

The authors' aim is to illustrate the range of phenomena that could be explained by the PAM. This enables them to include many cases that do not require it – such as the elicitation of escape by a conspecific's alarm call. We are a long way from being able to show that the PAM explanation is needed. Particularly dubious is the inclusion of the experience of guilt. Guilt does not need a subject and is surely better described in terms of a discrepancy between an internalised moral code and perception of one's own actual or intended action. Many of the neuroscience data and the characteristics of autism cited by the authors fit with PAM but do not require it.

To integrate diverse phenomena in terms of a common process is an important enterprise, but precision of definition is inevitably inversely related to the range of phenomena that are explained, and a clear distinction is required between those that require such a process and those where it might operate.

## How automatic and representational is empathy, and why

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**Abstract:** The claim that empathy is both automatic and representational is criticized as follows: (a) five empathy-arousing processes ranging from conditioning and mimicry to prospective-taking show that empathy can be either automatic or representational, and only under certain circumstances, both; (b) although automaticity decreases, empathy increases with age and cognitive development; (c) observers' causal attributions can shift rapidly and produce more complex empathic responses than the theory allows.

Preston & de Waal's (P&deW's) empathy theory is: The perception of an object's state automatically activates the subject's corresponding representations, which in turn automatically activate the associated autonomic and somatic responses, unless inhibited. Their paper covers a lot of ground, relating the theory to human evolution and reproductive success, mother-infant responses in animals and humans, and the effect of past experience, learning, cue salience, and familiarity/similarity on empathy. They claim the theory is uniquely process-focused, but do not explain the underlying processes except for a foray into neural substrates.

The idea that empathy is automatic and representational is not new. It has been said before, and five processes underlying empathy's automatic and representational dimensions have been advanced; some of them explain empathy's *nonautomatic and nonrepresentational* dimensions as well (Hoffman 1978a; 2000). Three processes are preverbal and involuntary: (1) mimicry, where one automatically imitates another's facial, vocal, or postural expressions of feeling, and the resulting changes in one's facial or bodily musculature trigger afferent feedback that produces feelings resembling the other's; (2) classical conditioning, where empathic distress becomes a conditioned response to others' distress by observing others' distress while experiencing actual distress; (3) direct association of cues from others or their situation with a similar past experience, which evokes the distress of that experience. Being preverbal, these processes enable infants and toddlers to empathize. They also give empathy an automatic dimension through life (this is good for P&deW's model), but they can arouse empathy without representation (bad for the model).

Two higher order cognitive processes do the opposite; they are representational but subject to voluntary control, hence not necessarily automatic (very bad for the model); (4) mediated association, where language communicates the victim's distress, and through semantic interpretation we connect his situation to our own painful past experience; (5) perspective-taking, where we feel the victim's distress by imagining how we would feel if the stimuli impinging on him were impinging on us (self-focused) and/or imagining how the victim feels based on what we know about him (other-focused). Perspective-taking can be voluntary; it can also be activated automatically by the automatic preverbal processes but then one can decide whether to continue or terminate it. Perspective-taking can also initiate a preverbal process (one hears about a familiar victim's misfortune and imagines his facial expression, which triggers empathy).

Multiple processes are important because they assure an empathic response regardless of age and available cues: facial, vocal, or postural cues can be picked up by observers of any age through mimicry; situational cues, through conditioning or association; feelings expressed verbally or in writing can arouse empathy through mediated association or perspective-taking. Automatic preverbal processes can activate, or be activated by higher-order cognitive processes. Empathy is thus a multi-determined, *largely though not entirely automatic and representational,* highly reliable human response, which fits the argument that it survived natural selection and has a hereditary component (Hoffman 1981; Zahn-Waxler et al. 1992b).

P&deW claim that empathy's automaticity is high at birth and decreases with age and experience due to increased prefrontal functioning, segregation of self and other representations, and learned display rules – all of which inhibit the automatic response. This suggests empathy itself decreases with age and cognitive development. Not so. Prefrontal development and self-other differentiation allow the higher cognitive empathy-arousing processes to kick in, enabling children to empathize with an increasing variety of emotional states and with unseen others (in newspapers, television). By 8–10 years they empathize with another's life condition, which can override empathy based on immediate situational and personal cues: seeing a child happily playing, one automatically feels empathic joy, but remembering the child is terminally ill changes to empathic sadness or sadness mixed with joy (Hoffman 2000; Szporn 2001).

Another problem for P&deW's theory is that people spontaneously attribute causes to events (Weiner 1985) and causal attributions shape one's empathic response to another's state (Hoffman 2000). Furthermore, many events witnessed in life produce a rapid shifting of causal attributions from moment to moment. This creates a complex empathic response – a series of interconnected sequences of attributions and rising and falling levels of empathic distress (Hoffman 1978a; 2000). Here is an example. A young man who didn't witness the accident saw the driver of an expensive sports car being wheeled away in a stretcher. He reported an instant feeling of horror:

> but I first thought it was probably a rich, smart-aleck kid driving while drunk or on dope and I did not feel for him [blaming the victim possibly to reduce the pain of empathic horror]. I then thought, this might be unfair, maybe he was rushing because of some emergency, suppose he was taking someone to the hospital, and then I felt for him. But then I thought, that was no excuse, he should have been more careful even if it was an emergency, and my feeling for him decreased. Then I realized the guy might be dying and I really felt bad for him again.

This person's empathic response to the accident victim wasn't just the initial automatic horror or the final empathic distress, but the entire series of interconnected attribution-empathy sequences. How would P&deW's model handle this?

P&deW do tackle an important problem bearing on their view that empathy is both automatic and representational. They report that observing someone grasping an object, and imagining grasping it have similar reaction times, and they seem to conclude the same thing for perception-based and imagination-based empathy. But grasping has little to do with empathy. We need a study of imagination-based and perception-based empathy reaction times. If imagination-based took longer, which I predict, it could be the inevitable result of cognitive appraisal taking longer than direct perception. Or we might predict, as P&deW might, the reaction times would be equal if measured from the moment cognitive appraisal is completed and the other's state comprehended. Either way, this line of research would raise our level of understanding of empathy.

## Mirror neurons, the insula, and empathy

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**Abstract:** Neurophysiological studies in monkeys and neuroimaging studies in humans support a model of empathy according to which there exists a shared code between perception and production of emotion. The neural circuitry critical to this mechanism is composed of frontal and parietal areas matching the observation and execution of action, and interacting heavily with the superior temporal cortex. Further, this cortical system is linked to the limbic system by means of an anterior sector of the human insular lobe.

Preston & de Waal (P&deW) suggest that a simple mechanism for empathy is provided by the Perception-Action Model (PAM), according to which there exists a shared code between perception and action. Recently, neurons with neurophysiologic properties compatible with this mechanism have been described in the monkey inferior frontal cortex (Di Pellegrino et al. 1992). These neurons, called "mirror" neurons, fire not only when the monkey executes an action but also when the monkey observes another monkey, or a human, performing the same action (Gallese et al. 1996). Neurons with similar properties have also been found in the posterior parietal cortex of the monkey (Rizzolatti et al. 2001). Further, higher order visual neurons coding complex actions have been described in the superior temporal sulcus of the monkey brain (Perrett & Emery 1994). In a series of fMRI studies on human imitation, our group has reported a similar cortical circuitry in the human brain (Iacoboni et al. 1999; 2001). What we call the "minimal circuitry" for imitation and action understanding would be composed as follows:

1. The superior temporal cortex provides an early visual description of the action to be imitated to specific parietal areas with neurons that have the unique function of matching observation and execution of action.
2. Parietal neurons with observation/execution matching properties add additional somatosensory information to the movement to be imitated.
3. This more complex information is sent to the inferior frontal cortex, which in turn codes the goal of the action to be imitated.
4. Sensory copies of the imitated actions are then sent back to the superior temporal cortex for monitoring purposes ("my actions are like the actions I have seen").

If we want to apply these same neural and functional mechanisms to the domain of emotion and empathy, then a problem arises. The areas so far identified with mirror properties, in fact, belong to a fronto-parietal circuit that is generally not associated with emotions, but rather with "cold" sensorimotor paradigms. However, actions have an emotional correlate, and observers of an action participate empathically with the performer. Hence, the question of interest here is as follows: How does the limbic system get information from the fronto-parietal mirror system when empathy takes place? If one looks at available anatomical connectivity data, a region of the primate insula – precisely, the dysgranular field – connects limbic areas with the inferior frontal, anterior part of the posterior parietal and superior temporal cortex. Thus, the dysgranular field of the insula has all the requisites for being the relay station between the "minimal circuitry" matching observation and execution of action with a system more directly relevant to emotional processing.

We recently performed an fMRI study to test this hypothesis (Iacoboni, in press). We asked subjects to either simply observe or to observe-and-imitate emotional facial expressions. Our prediction was that during imitation of facial expression the insula would be activated on account of its hypothesized relay function from the frontoparietal mirror system to the limbic system. As control conditions, we asked our subjects to either simply observe or to observe-and-imitate only the eyes or only the mouth extracted from the same faces expressing emotions that were used in the previous conditions. We did so because the single-unit data in the macaque brain suggest that in frontoparietal mirror areas there are representations of hand and mouth movements, but not of eye movements. We hypothesized that the imitation of eye movements with emotional valence may not invoke the activation of the frontoparietal mirror system and, consequently, not require the activation of the insula as relay station to the limbic system. This is because, in the monkey, the inferior frontal cortex where mirror neurons are found does not contain a cortical representation for eye movements. The results we obtained clearly demonstrated the activation of the insula during all imitation tasks. We interpret this as in favor of our hypothesis about the insula having a key role in affect generation and serving as a relay between frontal cortices and limbic structures, thus representing a possible pathway for empathic resonance. It is possible that in humans eye movements have an emotional-empathic correlation stronger than in monkeys, but in our opinion, the activation of the insula even during emotional eye movement imitation was probably due to the fact that imitating a facial expression is a holistic act that can hardly be decomposed. In fact, in all three imitation tasks, substantially identical maps of activation were obtained. And when we compared the activation obtained in each imitation task with that in the other imitation task, no reliable differences were observed.

Moreover, when imitation and observation tasks were compared, a complete spatial overlap of activation between imitation and observation of facial emotional expression was found. This overlap supports the main claim of the Perception-Action Model and suggests that the functional mechanism that this model advocates could be applied to the realm of emotion and may be at the basis of empathy, as P&deW suggest. The only difference in BOLD signal that we observed between imitation and observation of facial expression was in magnitude of response, with greater activity during motor execution than during observation, a feature found also in mirror neurons. Interestingly, even the amygdala was more active during imitation than during observation of facial expressions.

All in all, we understand the emotion of others, and empathize with them, by invoking the very same neural activity associated with our own emotions. A functional or an anatomical lesion in the circuitry we have described here may impair our capabilities for empathy.

## Elucidation of the brain correlates of cognitive empathy and self-awareness

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**Abstract:** Self-awareness is thought to be tied to processes of higher-order perspective taking including empathy. These abilities appear to be reserved for humans, great apes, and possibly, dolphins. Recent examinations reveal that both self-awareness and empathy may have origins in the right hemisphere. It is possible that, as in language, lateralization plays a key role in the development of higher-order perspective taking and self-awareness.

Cognitive empathy shares a strong family resemblance with other neurocognitive abilities that can be broadly subsumed under the umbrella of "self-awareness." It is likely that lateralization plays a prominent role in the development of many of the most sophisticated neurocognitive abilities. While language processes are typically mediated by left-hemisphere structures, other available evidence is consistent with the idea that self-awareness, perspective taking, and, perhaps, cognitive empathy, are largely dependent upon the right hemisphere.

When contemplating what regions of the brain are responsible for any given cognitive ability, it has previously been suggested that the brain be viewed as a mobile (Keenan 2001). While it is tempting to ascribe a particular module of the brain as being responsible for a given behavior, one must realize that even subtle functional changes in one region may affect distal regions. Thus, like a mobile, even minor changes in one region may alter the entire balance of the brain, or individual regions that are not directly connected.

It can be instructive to consider the neural correlates of cognitive empathy in conjunction with similar, related functions. Cognitive empathy, a complex phenomena, must be viewed with such considerations. The ability to represent another's thoughts (e.g., Theory of Mind; see Premack & Woodruff 1978) and representing one's own thoughts may be intimately tied together and may thus have similar origins within the brain. Tracing a more detailed analysis of both self-awareness and empathy reveals that right hemisphere function may be a further distinction between cognitive empathy and more basic elements of a motor action planning model. However, as with the mobile, regions not specifically implicated in cognitive empathy or self-awareness are likely to have a great bearing on the function.

As indicated, the capacity for self-face recognition appears to be reserved for only a few primates and possibly dolphins. Patients with disruptions of self-recognition appear to have either lesions within the right hemisphere (Feinberg & Shapiro 1989; Spangenberg et al. 1998) or right hemisphere dysfunction (Breen et al. 2001). Inactivation of the right and not the left hemisphere appears to disrupt both self-face recognition (Keenan et al. 2001b) and awareness of one's own limbs (i.e., asomatognosia; Meador et al. 2000; for a review on asomatognosia and the right hemisphere, see Feinberg 2000). Functional imaging of the self-face indicates the involvement of primarily right prefrontal regions (Keenan et al. 2001a), in particular when the own-face is being actively rather than passively viewed (Sugiura et al. 2000). Kircher et al. (2001) found right anterior cingulate, right temporal regions and left prefrontal activity in a version of a self-face task.

Autonoetic awareness (see Wheeler et al. 1997) of the past comprises episodic memory, and damage to the right prefrontal and temporal polar regions may induce disruptions in episodic recollection (Markowitsch et al. 1993), while circumscribed left-hemisphere damage may leave autobiographical processing intact (Markowitsch et al. 1999). Employing PET, it has been found that personal autobiographical memories activate a widespread region of the right hemisphere as compared to little right hemisphere activity for nonpersonal retrieval (Fink et al. 1996). Further, the evaluation of self may also employ right prefrontal regions as well (Craik et al. 1999). Self-related tasks have also been tied to medial prefrontal regions, as determined by fMRI (Gusnard et al. 2001).

In terms of Theory of Mind, it has been found that right hemisphere damaged patients are significantly more impaired than left hemisphere damaged patients (Happe et al. 1999; Stuss et al. 2001), and anterior left hemisphere damage alone does not lead to Theory of Mind deficits compared to anterior bilateral damage (Stone et al. 1998). Interestingly, Stuss et al. (2001) found that inferring deception, another indicator of higher-order perspective taking, was impaired in right hemisphere patients. Imaging data has been much less clear. Whereas some studies have found a right prefrontal activation in terms of related Theory of Mind tasks (Baron-Cohen et al. 1994), others have not (Fletcher et al. 1995; Goel et al. 1995). These studies have, in part, also indicated the possible importance of the cingulate gyrus.

Vogeley and colleagues (see Vogeley et al. 2001) recently addressed the possibility that there may be both common and unique elements involved in both the perspective taking of self and of other by use of fMRI. Employing tasks that used perspective taking and stories, it was found that during Theory of Mind, the anterior cingulate gyrus was involved, while during the self task, in addition, right temporal-parietal regions were activated. Further, the interaction of both the conditions (i.e., the regions that significantly activate in the presence of Theory of Mind and self) revealed significant right lateral prefrontal activation.

Greater hemispheric lateralization has been found in animals that are considered capable of performing tasks related to cognitive empathy and self-awareness (Yeni-Komshian & Benson 1976). For example, regions of the brain implicated in language (e.g., planum temporal) are found to have a high degree of lateralization in humans (Galaburda et al. 1978) and the great apes (Gannon et al. 1998; Hopkins et al. 1998). As in language, it is possible that lateralization of other brain structures may be involved in cognitive empathy, Theory of Mind, self-awareness, and similar abilities. With findings that indicate that humans and the great apes are also similar in functional asymmetries (e.g., Hopkins 1997)), right hemisphere involvement in self and other perspective-taking may be an indicator of the brain origins of these abilities.

## Similarity versus familiarity: When empathy becomes selfish

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**Abstract:** Preston & de Waal conflate familiarity with similarity in their attempt to account for empathy. If distinguished, we may have at hand two different kinds of empathy: egocentric empathy and empathy proper.

Preston & de Waal (P&deW) observe that similarity facilitates empathy. Then, without argument, they treat similarity as analytically indistinguishable from familiarity. Obviously, *ceteris paribus,* familiarity matters. As Adam Smith (1976, pp. 136–37) notes, a European man would, justifiably, be more disturbed over losing his finger than over earthquake victims in China. Smith criticizes the moralists and argues that human sentiments are based on familiarity. Familiarity is the vehicle that allows the subject to perceive the object. Familiarity permits the subject to transport himself from his own station to the object's station.

Concerning similarity, why, *ceteris paribus,* should conspecifics empathize with each other more than with dissimilar actors? Why should a male subject empathize more with male than female objects? Or, why should a human subject empathize more with an object that shares the same culture than with a foreign object, or with a monkey than a dog? P&deW note that juveniles prefer to play with others of similar age and gender. However, if boys prefer to play, for example, basketball with other boys, does it mean they are more empathetic towards boys than girls? Actors, it seems to me, seek similar play partners to maximize the fun. Similarity does not enhance empathy if, to start with, play is not empathy.

While familiarity allows the subject to have a richer representation of the object, how does similarity work? Maybe similarity acts like a common language, allowing the subject to understand particular signals. If so, once a man learns the "language" of dogs, for example, the man should empathize with a dog's pain with the same intensity as he would empathize with the pain of a conspecific. Once a man is educated about how females signal pain, such as in labor, the similarity issue should not matter.

Nonetheless, P&deW marshal evidence that shows that similarity matters. But this does not necessarily entail that similarity and familiarity are analytically indistinguishable. There is an alternative: The empathy prompted by familiarity may differ from the one prompted by similarity. Smith (1976) suggested this alternative over two centuries ago (see Khalil 1990; 2001; 2002). He chided the exemplar of the egocentric explanation of empathy of his time, Thomas Hobbes. Hobbes regarded empathy as merely vicarious pleasure. He maintained that altruism is aimed at enhancing the donor's pleasure by imagining the conditions of the recipient *as happening to the donor's own station.* As told by John Aubrey:

> One time, I remember, goeing in the Strand, a poor and infirme old man craved his [Hobbes'] almes. He, beholding him with eies of pitty and compassion, putt his hand in his pocket, and gave him 6d. Sayd a divine (scil. Dr. Jaspar Mayne) that stood by – "Would you have donne this, if it had not been Christ's command?" – "Yea," sayd he. – "Why?" quoth the other. – "Because," sayd he, "I was in paine to consider the miserable condition of the old man; and now my almes, giving him some reliefe, doth also ease me" (Aubrey 1898, p. 352)

Modern economic theorists basically follow Hobbes. Gary Becker (1981), for example, argues that benefactors donate for the reason that, by imagining how recipients are enjoying the goods, they can increase their own utility.

In response to the egocentric view of empathy, Smith stressed that altruism promoted by empathy, which he called sympathy, involves putting one's self in the other's station *rather than judging the other's pleasure from one's own station.* Sympathy would be a "selfish sympathy" if it entails imagining the other's conditions as happening to one's station, that is, one's "own person and character":

> Sympathy . . . cannot, in any sense, be regarded as a selfish principle. When I sympathize with your sorrow or your indignation, it may be pretended, indeed, that my emotion is founded in self-love, because it arises from bringing your case home to myself, from putting myself in your situation, and hence conceiving what I should feel in the like circumstances. But though sympathy is very properly said to arise from imaginary change of situations with the person principally concerned, yet this imaginary change is not supposed to happen to me in my own person and character, but in that of the person with whom I sympathize. When I condole with you for the loss of your son, in order to enter into your grief I do not consider what I, a person of such character and profession, should suffer, if I had a son, and if that son was unfortunately to die: but I consider what I should suffer if I was really you, and I not only change circumstances with you, but I change persons and characters. My grief, therefore, is entirely upon your account, and not in the least upon my own. It is not, therefore, in the least selfish. How can that be regarded as a selfish passion, which does not arise even from the imagination of any thing that has befallen, or that relates to myself, in my own proper person and character, but which is entirely occupied about what relates to you? A man may sympathize with a woman in child-bed; though it is impossible that he should conceive himself as suffering her pains in his own proper person and character. (Smith 1976, p. 317)

For Smith, it cannot be similarity, but rather familiarity, that prompts men to empathize with women in labor. P&deW come close to distinguishing familiarity and similarity when they note that empathy differs from projection: Empathy involves the mapping from object to subject, projection *vice versa.* In light of the above, projection is crude egocentric empathy: the object is not even experiencing any pain that reminds the subject of his misery. In projection, the subject uses similarity, the only thing available, in order for the subject to "empathize" with himself. It is difficult to operationalize the proposed difference between egocentric empathy and empathy. But this is not different from the difficulty of operationalizing the distinction between projection and empathy.

## Empathy requires the development of the self

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**Abstract:** Two major problems exist in studying development: Similar behaviors do not need to reflect the same underlying process, different behaviors can reflect the same process; earlier behaviors do not necessarily lead to later behaviors. Empathy, rather than social contagion, is supported by different processes; contagion supported by prewired species behavior, empathy by cognitions, in particular, the cognitions about the self – a meta-representation.

Newborn infants exhibit behaviors that appear empathic. These behaviors are predicated on social contagion rather than on cognitions, in particular, the cognitions that make inferences about the other by utilizing the knowledge of the self. This developmental sequence, going from social reflexes, such as contagion, to cognitions, such as self-representation, constitutes an important shift in the human child's development.

In this target article, the authors give only passing attention to the issue of self-development. Yet, in development we have evidence for two processes: one, an immediate prewired and species-specific process requiring little learning; the other, a delayed process requiring experience and higher mental functions (Lewis 1999) that impact on behavior. LeDoux (1989), for one, has shown a direct emotional response mediated by the amygdala, hardwired and having an evolutionary history, which allows for action without thought. The indirect system, which goes through the cortex, allows for learning, or unlearning, of responses and is very much influenced by experience and culture (see also, Gilbert 1991). For example, it has been claimed, although the phenomena are certainly not robust, that newborn infants imitate; also that infants show empathy – if we accept empathic distress responses as empathy – in response to another's distress. A newborn's responses are not supported by the same process that supports behaviors for similar responses in adults. When I imitate someone's behavior I do so intentionally and with planning. Likewise, my empathic distress upon seeing starving children is caused by my ability to imagine what I would feel if I were like them or in their position.

In these examples, the role of the self in adult human behavior is obvious, while no self need be postulated for the newborn. A central milestone in human development takes place somewhere between 15- and 18-months when toddlers show three behaviors indicative of the emergence of consciousness and the meta-representation of the self. This emergence allows for cognitions such as, the child "knows it knows." Only later, somewhere toward the third year, does this meta-representation lead to knowledge that they "know something that another does not know"; the classical theory of mind paradigm. The emergence of self also allows for the self-conscious emotions. Simultaneously with the emergence of self-representation there is embarrassment and also empathy – to be discussed below; and within a short time, another year, the emergence of the self-conscious, moral or social emotions, such as shame, guilt, and pride. In social development, this meta-representation gives rise to relationships. Although we see complex social interactive behavior in infancy, social relationships appear unlikely to be possible without a self as part of that representation of "we" (see Lewis 1992).

What behaviors support the idea of this meta-representation? My colleagues and I have been able to demonstrate that infants come to recognize themselves in mirrors, using the nose-directed technique (Lewis & Brooks-Gunn 1979). Another example is children's use of personal pronouns, "me" and "mine," in conjunction with moving objects toward themselves in time-space and pretend play. The rise of the self meta-representation is connected with a variety of cognitive and social emotional behavior (Lewis 1992; Lewis & Michalson 1983). Notable in this discussion is the work of Bischof-Kohler (e.g., Bischof-Kohler 1988). What Bischof-Kohler demonstrated was that the distress expressions and motor actions designed to alleviate the stress of another appear coordinated only after the emergence of mirror-recognition. The emergence of a self-representation is vital for the emergence of an empathic response. After all, how can it be that I have an empathic response without there being a cognitive representation of myself? As Preston & de Waal (P&deW) have pointed out, there are certainly elaborate, empathic-like responses seen earlier; however, the actual adult human form of the behavior is unlikely to emerge until the emergence of a self-representation. From a developmental point of view, we are often confronted with the conundrum of the same behavior or similar behaviors being supported by very different processes, and we should be very careful to make sure that we do not commit the error whereby we conclude that just because behaviors appear similar in similar situations, they are supported by the same underlying process. Indeed, one of the difficulties in the study of development is that the same process may result in very different behaviors during the developmental sequence, while, on the other hand, the same behavior at different points in time may be supported by very different processes. I think it is safe to conclude that any theory of the development of empathy needs to incorporate the emergence of a self-representation. The distress of the newborn to the cries of other newborns, and the generous charitable donations given by U.S. citizens to others distressed by the World Trade disaster, to take two examples, should not be considered as having similar underlying processes; nor does one necessarily lead to the other.

This last point is especially important since a second developmental error has to do with the proposition that something which occurs before something else is, in fact, the cause of it. The analysis presented in support of this, although scholarly and knowledgeable, needs to be tempered by our understanding that there are behaviors that are served by potentially very different processes and that behaviors which occur earlier do not necessarily lead to, nor are related to, behaviors which occur later in ontogeny. The emergence of self-cognitions deserves more attention.

## The Perception-Action Model of empathy and psychopathic "cold-heartedness"

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**Abstract:** The Perception-Action Model of empathy (PAM) is both sufficiently broad and sufficiently detailed to be able to describe and accommodate a wide range of phenomena – including the apparent "cold-heartedness" or lack of empathy of psychopaths. We show how the physiological, cognitive, and emotional elements of the PAM map onto known and hypothesized attributes of the psychopathic personality.

According to Preston & de Waal (P&deW), empathy is based on simulation or mimicry of another's "embodied representation" (see Humphrey 1992; Lakoff & Johnson 1999). Their Figure 1 distinguishes between identification, emotional contagion, and "true" empathy, by emphasizing that physical "identification" is a prerequisite for psychological identification. If true, then similarity of body is a key factor in the extent to which two parties can empathize with one another. Thus, a failure to empathize (or to regenerate another's "embodied representation") altogether, may be not unlike the inability of a person to fully empathize with another kind of animal, the inability of a person of one sex to fully empathize with a person of the opposite sex, the inability of a younger person to fully empathize with an older person, or in fact, the inability of anyone (subject) to fully empathize with anyone else (object) who has experienced an event that the subject has never experienced (e.g., disease, rape, loss of a loved one, being caught in a fire, etc.). Reinforcing this point, paragraph 9 of section 4.1.1 of the target article states that: "The more similar or familiar the subject and object, the more their representations will be similar, which in turn produces more state-matching, better accuracy, and less 'projection'." Conversely, the more dissimilar or unfamiliar the subject and object, the less complete and/or accurate the subject's representation of the object's state will be.

According to P&deW, the PAM "specifically states that *attended perception of the object's state automatically activates the subject's representations of the state, situation, and object, and that activation of these representations automatically primes or generates the associated autonomic and somatic responses, unless inhibited*" (sect. 1.1.3, para 3, emphasis in original). We would add *"or unless the subject does not have any such representations, or the subject does not normally generate autonomic or somatic responses to such representations."* This, we would claim, is the case for psychopaths, who do not exhibit typical autonomic or somatic responses to situations and stimuli which elicit such responses in "normals" (e.g., Hare 1998; Lykken 1957; Newman 1998; Newman & Wallace 1993; Patrick 1994; Patrick et al. 1994).

Personal, phenomenological experience of emotion is crucial to the development of empathy. P&deW acknowledge this in the second para. of sect. 3.1 of the target article, where they refer to the comments of Brothers (1990) that "understanding the emotion of others entails to some degree experiencing the emotion observed," and Gallup (1998b) that "information about the self is used to model the states of others." Following from these observations, in the single paragraph of the target article that discusses psychopaths (para. 3 of sect. 3.4.5), they claim that "without the ability to be aroused by the distress of others, [psychopaths] cannot understand and learn about the state of others through their own substrates." We fully agree. The psychopath's low sensitivity, particularly to aversive stimuli, manifests in a state of relative emotional poverty: psychopaths, therefore, cannot experience "true empathy" with others, because they do not produce the same bodily representations as others.

If "true" empathy is the embodied representation of another's perspective, we should consider that the psychopath's deficit is not in "perspective taking" per se, but in the ability to embody or represent certain feelings at all. That is, we suggest that psychopaths do not have a "deficit" of their mind-reading mechanism (Blair et al. 1995; 1996), but rather, have a "deficit" in their own personal experience (phenomenology) of certain emotions (Mealey & Kinner, in press). The "representations" and "simulations" therefore, that feed into the Theory-of-Mind Mechanism (ToMM) of a psychopath, are limited: the psychopath simply cannot project onto others what he cannot experience himself (Mealey 1997). Take, for example, the following quote from a psychopathic rapist, commenting on his victims: "They are frightened, right? But, you see, I don't really understand it. I've been frightened myself, and it wasn't unpleasant" (Hare 1993, p. 44).

Nevertheless, as P&deW note, "individuals with . . . psychopathy may use . . . alternative strategies to compensate for an impairment in empathy" (para. 1 of sect. 4.1.3). More specifically, we would argue that although psychopaths cannot "feel what another feels" (idiographically), their "alternative strategy" is that they can learn how to "read minds" nomothetically (Mealey 1992). In other words, since the psychopath cannot "simulate" emotions he cannot experience, he must rely almost exclusively on cognitive inputs to his ToMM.

Use of this alternative strategy would explain the curious ability of the adult psychopath to accurately "push all the right buttons" despite the inability to "get into another's skin." Further, it would explain the difficulty of socializing a psychopathic child and the consequent increased probability of antisocial behavior – which, note, is not a necessary outcome of lack of empathy (Kinner 2002). As P&deW claim (final para. of sect. 2.2.1 of the target article) "if an infant is aroused by the display of emotion in the parent (especially fear or distress), then the infant can use the mother's reaction as an unconditioned stimulus to learn about danger." Yet an infant with a psychopath's "different" nervous system will not be aroused by a parent's (or anyone else's) displays of emotion, and will thus fail to learn from aversive experience and remain relatively unsocialized (Eysenck 1983; Hoffman 1978a; 1982; Kochanska 1991; 1993; Lykken 1995; Magid & McKelvie 1987; Mealey 1995). With their "diminished ability to experience anxiety and to form conditioned associations between antisocial behavior and the consequent punishment, [they] will be unable to progress through the normal stages of moral development" (Mealey 1995).

We agree with P&deW that "simulation theory" and "theory theory" are not incompatible, and suggest that psychopaths tend to employ the latter strategy – as exemplified in the "paint-by-numbers" approach of one psychopathic offender who "read self-help psychology books to learn the appropriate emotional responses to everyday events" (Hare 1993, p. 54). We further believe that it is the failure of the psychopath's emotional simulations, and consequent forced reliance on theory, which allows the intelligent psychopath to be functionally and successfully Machiavellian while demonstrating a marked lack of empathy and apparent "cold-heartedness."

## Empathy and the action-perception resonances of basic socio-emotional systems of the brain

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**Abstract:** Mammalian brains contain a variety of self-centered socio-emotional systems. An understanding of how they interact with more recent cognitive structures may be essential for understanding empathy. Preston & de Waal have neglected this vast territory of proximal brain issues in their analysis.

Preston & de Waal (P&deW) provide a compelling analysis of empathy. Progress on such important emotional/cognitive topics requires us to "dock" effectively between intrinsically fuzzy psychological concepts (best operationalized behaviorally) and emerging neuroscientific knowledge. Here we will bring related issues of positive emotional resonance into focus, and supplement P&deW's impressive effort with several critical concerns, the foremost being the need for a neurobiological understanding of social attachments in order to understand how empathy is created in the brain-mind.

In addition to the *perception-action* schema emphasized by the authors, equal weight should be given to long neglected *action-perception* approaches to understanding the mind. Self-initiated actions markedly modulate sensory and perceptual fields (Held & Hein 1963; Sparks 1988), and evolutionary emotional-action systems of the brain may be especially important in the generation of empathic perceptual tendencies. Along with the show-cased "mirror neuron" work of Rizzolatti et al. (2001), motor-intentionality modulates how perceptual world appreciation is created in the brain (Iriki et al. 1996). The degree of perceptual neglect following right parietal damage is modulated by how individuals respond to the neglect (with visually distal actions reducing the neglect, and proximal ones restoring it: see Berti & Frassinetti 2000).

Empathy may be critically linked, especially developmentally, to genetically-ingrained instinctual emotional-motor systems, which focus perceptual-attentional resources (MacDonell & Flynn 1966).

Basic emotional-action systems may project feelings onto objects in the world, creating mood-congruent experience-expectant cognitions essential for empathetic responses.

Consideration of core emotional systems might have coaxed P&deW to emphasize the relevance of various subcortical socio-emotional systems (Panksepp 1998). Although they in passing mention amygdaloid-based fear research, emotional systems deserving attention are the separation-distress (Panksepp et al. 1988) and social attachment (Nelson & Panksepp 1998) circuitries of the brain. All basic emotional systems are built around instinctual action processes, which are not as unconscious as many investigators assume. Such circuits generate "intentions in action" that may create a primitive affective consciousness (Panksepp 2000a) essential for empathy. Without such social response systems, which facilitate social attachments, we doubt if empathy could exist.

As noted, a time-honored hypotheses is that empathy reflects some type of emotional contagion. Because we now know where the separation-distress systems are situated in the brain, we can inquire whether "the activation of distress circuits in young and relatively helpless animals generate 'resonant' activity in the same circuits of nearby adults who could provide care?" (Panksepp 1989/1999, p. 56). Such straightforward views provide clear neuroanalytic strategies for probing the nature of empathy, in ways compatible with human brain imaging (Lorberbaum et al. 1999).

The positive side of emotions also deserves more attention. Surely the interanimal resonances of several positive emotions, from sexual reward to maternal nurturance, sustain empathic tendencies. Surely the basic play/joy systems of the mammalian brain, engaged through vigorous "ticklish" touch, operate through a reciprocating neural "dance" in similar brain regions of interacting animals (Gordon et al. 2002). Such action-perception brain dynamics may promote joint-attentional pragmatics that are disturbed in autism spectrum disorders (Panksepp & Sahley 1987).

Ludic circuits can be detailed through the study of play vocalizations, and such tickle-induced play chirps in rats may have evolutionary relations to the infectious, joyous laughter that characterizes the youthful play of our own species (Panksepp & Burgdorf 2000). One endearing finding is that young rats seek the company of adult males who "chirp/laugh" much more than those that do not (Fig. 1). Might the capacity for empathy be preconditioned by such basic early social interactions and bondings? Tickling-induced, chirping-laughter is highly heritable in rats, and we anticipate that genetic profiling of such basic neuro-emotional tendencies with modern microarray and suppressive subtractive hybridization technologies will reveal candidate genes that promote neuro-empathic responsivity.

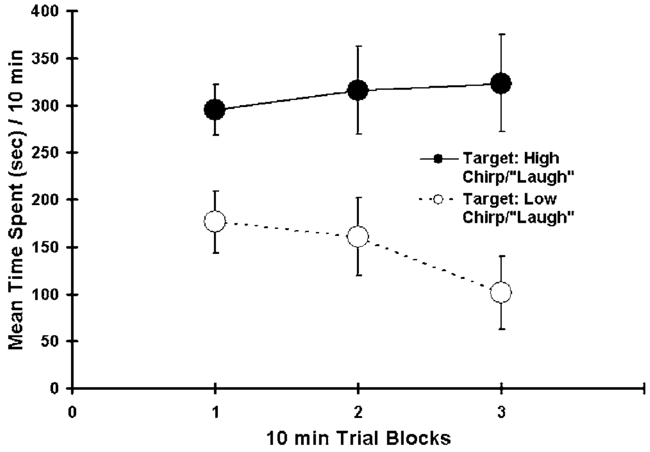

Figure 1 (Panksepp et al.). Mean ± SEM time spent by an adolescent animal with either an adult animal that shows low versus high levels of 50-kHz ultrasonic vocalizations in response to manual tickling by an experimenter. Adolescent rats were given free access to 3 chambers containing a low tickle adult, high tickle adult, and middle empty chamber. The three chambers were connected in series by two, 4 cm in diameter, tunnels which only permitted the adolescents to shuttle between the chambers. Adolescent rats spent more time with the high tickle adult rats as compared with the low tickle animals ($F(1, 12) = 26.62$, $P < .0005$).

Even as P&deW share a provocative vision of empathy, they have neglected approaches that allow investigators to interrelate basic psychological and proximal neurological processes that could yield useful therapeutic interventions for the abundant empathy deficit disorders of our species. Can we really understand the concept of empathy without dwelling on the ancient recesses of the animal brain-mind that are essential for creating basic social emotions such as separation distress and joy? Were such systems to suddenly disappear from human brains, the concept of empathy may have little meaning for our species. Might neurochemical modifications of these ancient socio-emotional circuits modulate our cognitive capacities for empathy? We suspect such ancestral sources of love, created during deep evolutionary time, remain essential for creating feelings from which compassion *emerges* via interactions with recently evolved cortico-cognitive abilities. Subcortical emotional action-perception processes may regulate the cortico-cognitive, perception-action schema upon which P&deW rivet their attentions.

## Understanding other's emotions: From affective resonance to empathic action

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**Abstract:** Empathy is a developmental process whereby individuals come to understand the emotional states of others. While the exact nature of this process remains unknown, PAM's utility is that it establishes empathy along a continuum of behavior ranging from emotional contagion to cognitive forms, a very useful distinction for understanding the phylogeny and ontogeny of this important process. The model will undoubtedly fuel future research, especially from comparative domains where data are most problematic.

> . . . every "intuitive" percept and every "empathic" relationship is dependent upon some nonverbal communication of affect. Although the precise nature of this form of communication is still obscure, it undoubtedly plays a significant role in the social relations among men, among animals, and between man and animals. (Miller et al. 1959b)

Preston & de Waal (P&deW) provide a comprehensive model to explain the evolution of empathic behavior by adapting the Perception as Action model (PAM), originally proposed by Prinz (1997). PAM allows for proximate and ultimate level explanations, an important feature since emotion, as a critical factor involved in the central regulation of behavior, is garnering increased scientific attention across multiple disciplines. The need for putative models and testable hypotheses that go beyond anecdotal descriptions is long overdue.

The basic tenet, however, that perception leads to action, is such a general feature of animal behavior, social or nonsocial, that the model's specificity is often lost in its scope. PAM, for example, appears capable of explaining almost every aspect of emotional behavior, from mother-infant attachment to altruism, rather than specifying how empathy differs from general emotional processes or environmentally contingent behavior. But perhaps this criticism is not so much a flaw of the model, as it is a prominent statement about emotion itself. Emotional processes have such an extended impact on daily life that it is difficult to think of a situation in which their involvement could not be invoked, making operational definitions elusive. This is undoubtedly one reason why researchers are only just beginning to speculate about the role of emotion as a factor capable of influencing animal behavior, from individuals, to groups, and even societies (Flack & de Waal 2000).

In this regard, PAM provides a serviceable and refreshing classification of empathic behavior, ranging from affective resonance to cognitive empathy (see Table 2 of target article). This is critically important for comparative and developmental research, as empathy emerges slowly in conjunction with the developing nervous system and social competence (Hoffman 1978b). Previous studies on primates, for example, have relied on cognitive definitions of empathy, such as mental perspective taking, providing little insight into the relationship between empathy and emotion, or how empathy may fit into an evolutionary scheme (Povinelli 1998). Without a basic and progressive model, comparative research on emotion will remain on the fringe of contemporary disciplines.

How the PAM will be supported by empirical studies in nonhumans remains to be demonstrated. The reviewed studies fail to provide convincing support for even the most basic levels of empathy, like physiological linkage. This is particularly true of conditioning studies in which a distressed conspecific serves as the conditioned stimulus (CS) for the subject's own distress/shock (Miller et al. 1963; Watanabe & Ono 1986). The authors cite Miller and colleagues' cooperative avoidance paradigm as providing evidence of physiological linkage between monkeys, but these results are questionably interpreted (Miller et al. 1967; readers are referred to the target article for a description of this intriguing paradigm). In the study, similar changes in cardiac response were observed in two animals. Both animals, however, were wired to receive shock. Thus, their cardiac responses would not be expected to differ, but rather show similar changes based on similarly perceived personal threat, that is, a CS that predicts shock. A more detailed examination of the data, however, shows that the cardiac responses were, in fact, *not* identical. While both monkeys showed cardiac acceleration, the heart rate of the stimulus animals had significantly greater acceleratory slopes. This is particularly interesting with regard to psychophysiology, as the stimulus monkeys were helpless to avoid the shock, perhaps contributing to greater anxiety during the CS presentation. Additionally, the numerous anecdotes for empathic responding within animal groups, such as tolerance of handicapped, aged, or retarded individuals, do little to advance the model since alternative explanations are not considered. The literature is full of examples of brutality and intolerance within species, and any anecdotes should be tempered as such (de Waal 1986b; Goodall 1986a; Wrangham & Peterson 1996).

It should be noted that most emotion theories, PAM included, are biased towards predicting responses to negative events. Miller, for example, trained monkeys to avoid shock (avoid) or obtain food (reward) and then presented their facial responses to other monkeys to indicate avoidance or reward trials. Significantly reduced responses and modest cardiac acceleration occurred in the reward versus avoidance trials (Miller 1967). These findings, in addition to recent neuroimaging data, suggests that the way in which information about positive events is communicated and represented at the behavioral and neural level is much less clear than for negative events (Canli et al. 1998; Davidson 1992; Lane et al. 1997).

Interesting support for empathy in animals is covered only briefly. In the pioneering work of Miller and colleagues, an extinguished avoidance response was not only reinstated when the CS was changed to a conspecific's fear expression, but spontaneously more responses were maintained *in the absence of* the unconditioned stimulus (US) (Miller et al. 1959a). These data suggest that the perception of facial expressions in primates may involve a basic understanding of their emotional significance, a finding recently demonstrated in chimpanzees and one that has guided much of the contemporary research on human emotion (Ekman 1972; Parr 2001). Studies are underway at the Yerkes Primate Center to document physiological responses to the perception of pleasure and distress in monkeys and apes. Preliminary results suggest that changes in peripheral skin temperature differ depending on the emotional valence of video scenes: temperature increases in response to positive scenes, like play or greetings, and decreases in response to negative scenes, like aggression and threats (Parr, unpublished data). Understanding the extent to which nonhuman animals resonate to the perceived emotion of conspecifics may be the most fruitful starting point for comparative studies of empathy.

In summary, although understanding emotion in others is a critical feature of social organization, researchers are still searching for viable models to explain this basic process. One starting point is to examine the extent to which different species are able to resonate to emotion perceived in others. This unconscious and nonverbal process would not only provide comparable data across different species and developing age groups, but it stands as the most causal link to empathic action.

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## Various kinds of empathy as revealed by the developing child, not the monkey's brain

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**Abstract:** The comparative study of empathy should be based on the developmental taxonomy of vicarious experiences offered by the abundant literature on infants and children's cognitive, social, and emotional development. Comparative research on the topic should refer to the various kinds of empathy emerging in an orderly fashion early in human development.

A major function of today's brain research is to substantiate well-known psychological phenomena by giving them, literally, molecular flesh. For better or for worse, psychologists seem to gain intellectual comfort by increasingly seeking neuroscience's molecular and mechanistic "high-tech" stamp of approval. As a case in point, the recent discovery of mirror neurons in the monkey's brain provides some molecular and mechanistic credence to the old idea of a common code between perception and action systems. Long before this discovery, the idea was already driving major psychological theories on visual perception (Gibson 1979; Gibson & Pick 2001), emotions (Levenson 1996), speech perception (Liberman & Mattingly 1985), early imitation (Meltzoff 1990), and the origins of social cognition and intersubjectivity (Gergely & Watson 1999; Rochat 2001a; 2001b; Trevarthen 1979).

The evidence of mirror neurons in the monkey's brain give Preston & de Waal (P&deW) mechanistic backup for their idea of a biological continuity in the evolution of empathetic feelings. To put it simply, if the monkey's brain possesses nerve cells that fire equally when performing an action or perceiving the same action performed by a conspecific, then even nonhuman species possess the biological potential to experience the world vicariously. If this is a legitimate and interesting proposition that substantiates evolutionary continuity in empathetic feelings (i.e., that sharing feelings is not the monopoly of humans), it eludes the more difficult question of what it means to share feelings with others, whether human or not.

Here, I contend that patterns of firing in the monkey's brain do not, and will probably never decisively illuminate the question. Rather, the levels and multifaceted aspects of vicarious experience are probably best captured by looking at how infants and young children develop in relation to others.

My dictionary defines empathy as "the intellectual identification or vicarious experiencing of feelings, thoughts, or attitudes of another" (*Random House Unabridged Dictionary*). This definition calls for a distinction of psychological levels and meanings. In its modern acceptance, empathy covers all aspects of the process by which individuals can vicariously experience the world, whether at a sensory, perceptual, or higher cognitive level. Espousing this broad construal of empathy does not help in specifying what is covered by the concept in terms of psychological processes and mental involvement.

We can sort this conceptual mishmash by looking at how children express different kinds of vicarious experience with others as a function of their development (see Goldie 1999 for a taxonomy of adults' empathy). Between birth and 4 to 5 years of age the variety of vicarious experiences expressed by children increase dramatically and in an orderly fashion. The developmental literature points to at least 6 levels of empathy emerging in succession, each expanding and adding to the repertoire of empathic potential. These might correspond to 6 basic levels of empathy that are naturally unfolding in early development and forming good conceptual anchorage for future comparative research. These levels can be summarized as follows:

1. At birth, infants manifest passive and obligatory emotional resonance. This first kind of empathy is automatically triggered and biologically determined (e.g., Sagi & Hoffman 1976).

2. By the second month, numerous studies demonstrate the emergence of active reciprocation via social smiling and complex dialogical engagement as well as regulation with caretakers in face-to-face exchanges. At this level, and in addition to emotional contagion, infants begin to manifest a new (conversational) stance towards others, actively co-constructing shared experience via imitation and reciprocal games (e.g., Rochat et al. 1999).

3. Starting approximately at 9 months of age, infants expand their repertoire of vicarious experience by attempting to share their attention with others in relation to objects and events in the environment, actively involved in developing so-called secondary intersubjectivity (e.g., Carpenter et al. 1998). At this level, infants' context of empathy expands beyond face-to-face exchanges.

4. By 14 months, infants are shown to identify themselves as unique entities, beginning, for example, to recognize themselves in mirrors. Presumably, from this point on, they can also begin to identify with or project themselves into others. This provides ground for a new kind of empathy (projective empathy). For example, research suggests that it is at around this age that children start discriminating social partners who are imitating them (e.g., Meltzoff 1990; Agnetta & Rochat 2001).

5. By 24 months, children begin to manifest self-conscious emotions including embarrassment (e.g., Kagan 1984; Lewis 2000). At this level, children begin to engage in systematic comparison, categorization, and eventually conceptualization of the self in relation to others. They start construing how they should feel based on how others might feel about them. Embarrassment is presumably the direct expression of such process.

6. Finally, by 48 months, children develop the unambiguous ability to theorize about others' mind, capable of construing false beliefs and beginning to distinguish objective from subjective thoughts, as well as to construe feelings and emotions held by self and by others that are more or less congruent (see Perner 1991). From this point on, children become capable of adopting a theoretical stance towards others, able to conjecture about the emotional state of others in relation to their own.

In short, developmental research indicates that children develop new ways of sharing experiences with others, hence new ways of empathizing, from automatic emotional contagion to reciprocal exchanges and affective resonance via protoconversation, to joint attention, identification, norm formation, and eventually theories of mind. In fact, all of these kinds of empathy are expressed and present all through the life span, developing (at least in humans) in an orderly fashion over the first 4–5 years of life. Because of their orderly emergence, these kinds of empathy are basic, with qualitatively different levels of psychological complexity, namely, with different degrees of higher cognitive involvement. From a comparative and evolutionary perspective, the question is not whether nonhuman species have or have not a capacity for vicarious (empathic) experience. Most probably they do, as suggested by P&deW. Rather, the question is what kinds of empathic capacity are other species capable of, and more importantly, how does this capacity develop?

It is reasonable to posit that because of their highly scaffolded and actively instructed symbolic environment, human children develop more ways to empathize compared to other species. But that remains to be empirically demonstrated. We need more comparative works on this issue, works that should be inspired by the abundant behavioral literature on infant and child development, and not predominantly by recent research pointing to developmental changes in brain functioning, such as the relative involvement of frontal regions. The development of the frontal cortex is just a gross developmental and comparative index. It is void of meaning regarding children's developing multi-level potential for empathy, hence it is not a suitable basis for comparison across species.

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## Psychobiological basis of empathy

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**Abstract:** Empathy represents one of the basic forms of human expression. Empathy evolved to facilitate social behavior. The perception action model, extended to empathy, is an exciting paradigm in which to undertake contemporary cognitive and comparative neuroscience. It renders the perception of events as an active affair, both when watching others, and when performing actions.

The article by Preston & de Waal (P&deW) on the biological basis of empathy is interesting. They hypothesize that empathic systems are embodied in the brain. These systems are tied to perceptual/action programs that organize intentional action.

P&deW build their hypothesis on the findings that similar motor programs in the cortex are activated both when one performs an action, and when one observes another perform an intentional action. First and third person perspectives are obviously different, but they share part of the same neural substrates and this has been an important scientific finding.

The perceptual action model that P&deW endorse envisions representational capacity to be importantly linked to the organization of action. But cognition does not mean more control; nor does it mean cortex or consciousness. The evolution of the central nervous system has been linked to greater accessibility and greater use of subsystems in the organization of behavior, but cognition is endemic to brain function.

Two investigators set the intellectual context for the discussion of the empathy: Adam Smith and Charles Darwin. Smith expressed the ideas of a number of his contemporaries by asserting that moral sentiments are an important part of our responses to the experiences of others; I see you in pain, I act (though not always, and to varying degrees) to comfort you. The other, Charles Darwin, links the moral sentiments to the origins of social behavior.

Disagreement exists about whether to attribute empathy to any primate other than humans. Is empathic distress found in other species? The authors suggest the possibility; several species look as if they are orienting their response in relation to the experiences of others, specifically the detection of the discomfort of conspecifics and ameliorative behavioral responses toward the conspecifics. But what would it take to persuade those who could explain such behavior without invoking the concept of empathy?

I would not separate cognitive empathy from other forms of empathy, as the authors do. Empathy is, in part, an appraisal of an event. The authors embrace the appraisal model of emotion. And, as they note, some senses of empathy are perhaps less complicated than others. I would suggest that a difference in degree of sophistication is a better way of explaining different kinds of empathy, rather than that one kind is cognitive and the other is not.

After all, a number of cognitive systems are reflexive, rapid, and impenetrable. To undercut misleading connotations, I would again suggest that one talk about multiple appraisal systems, degrees of empathy. The fact that the response can be fast and reflexive is not the issue – surely the perception of syntactical competence is reflexive and rapid. The fact that the response is automatic does not make it noncognitive. The empathic reflexes of the mother/infant reflect appraisal systems that are rapid and reflexive, but also cognitive.

Degrees of perspective taking exist. The perception-action model is a nice way in which to couch the organization of action and the organization of perception, without having to revert, I would suggest, to the cognitive versus noncognitive distinction with regard to empathy.

The authors make the point that similarity affects empathic responses to others; they suggest that the less similar, the less likely a response. The Nazis rendered those chosen to be exterminated as "different" and unlike the "average" German at the time. It was perhaps more easy to destroy those who were different – to act barbarically, to show little empathy. The result was little sympathy, and a greater tendency to do damage.

## Perception-action links and the evolution of human speech exchange

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**Abstract:** A perception-action system may underlie the mechanisms by which human speech exchange in social interaction is managed, as well as the evolutionary precursors of these mechanisms in closely related species. Some phenomena of interaction well-studied by sociologists are suggested as a point of departure for further research.

The proposal advanced by Preston & de Waal (P&deW) that a wide range of phenomena related to imitation and empathy can be accounted for by a perception-action system is not new. Nor is it clear that their formulation has enough precision to be considered a model. However, their treatment of this issue departs from previous reviews in two important respects. The first is that they focus on emotion and empathy, whereas previous authors have focused on the information processing events involved in perception and imitation of conspecifics (e.g., Decety & Grèzes 1999; Meltzoff & Moore 1997; Miklósi, 1999; Prinz 1997; Rizzolatti & Arbib 1998; 1999; Wilson 2001). The second is the review of data from comparative ethology, integrating phenomena from humans, primates, and other mammals into a single framework, and suggesting an evolutionary continuum that can usefully illuminate the human case. This, we propose, can provide an explanatory framework for a range of social phenomena identified by sociologists but heretofore neglected by psychologists and cognitive neuroscientists. We refer specifically to the findings of conversation analysis (for reviews, see Heritage 1984, Ch. 8; Levinson 1983, Ch. 6; ten Have 1999).

Studies of human talk in naturally occurring situations reveal an extremely robust system of practices by which participants organize their interaction turn-by-turn. The domain of this speech-exchange system is "conversation," defined as talk in interaction where the order, size, and content of turns are not structured by the speech-exchange system itself (in contrast to conventional arrangements such as ceremonies, court-room proceedings, and debates). The conversational speech-exchange system provides for turn taking, sequencing (connecting a current turn to prior and next turns), and repair of troubles in hearing and understanding. This speech-exchange system is apparently universal across cultures and languages, is what talk reverts to when conventional arrangements break down, and is the form of talk infants first encounter in language acquisition. Moreover, because the conversational speech-exchange system accommodates an extremely diverse range of content and social contexts, it may provide a mechanism by which a species as biologically uniform as Homo sapiens can produce the startling variety of cultures found across human populations.

To illustrate, turn-taking is a central organizational feature on which much else in conversation depends (Sacks et al. 1974; Schegloff 2000; Wilson et al. 1984). Roughly, a turn is a period during which just one participant has both the "right" and "obligation" to act, in the sense that failure to act is a noticeable occurrence. For example, silence following a question is treated by participants as a noticeable nonaction by the recipient rather than as part of the questioner's turn. Further, turn transitions frequently occur with no hearable gap between speakers (Jefferson 1973), despite the measurable amount of time required for the second speaker to "prime" the vocal apparatus for speech. The timing of this turn-taking mechanism appears to be extremely precise and fine-tuned, and its functioning relies on a shared orientation to that timing by both participants.

Two issues immediately arise. First, what are the cognitive mechanisms by which this speech-exchange system functions? Second, what were the evolutionary precursors that allowed this system to emerge?

With regard to the latter, we can ask whether related phenomena can be observed in situations that do not involve language. Clearly, some human nonverbal activities involve taking turns, and some activities of other species, such as grooming, may do so as well. This of course is an empirical issue, and the extensive primate data collected by de Waal and others might provide evidence. The questions then would be how nonverbal turn taking is managed so that the normal state of affairs is smooth transition from one participant to another, and how episodes of simultaneity and failure to act are dealt with. Obviously, one should not expect that the specific details of human speech-exchange practices will be found more generally, but rather that these are specializations of more basic phenomena which may be found in other species.

With regard to the cognitive mechanisms underlying speech exchange (and more broadly, underlying management of the timing of interaction), it is possible that these are closely tied to the perception-action system discussed by P&deW. To make this link, we must note that mechanisms for imitation and empathy need not be limited to the production of overt behavior but could also be used for internally simulating others' behavior and mental states. Such simulations could be used to track the course of the speaker's turn, predict when that turn will end, and so on.

This raises the question of whether broader and more abstract phenomena in the speech exchange system can be integrated into a perception-action perspective. One example is the phenomenon of turn-completion by another: one person starts a turn and a second picks up and finishes it off with the first person treating the completion as adequate by simply going on with the flow of the conversation and not protesting against an interruption or correcting the second speaker for misrepresenting (Lerner 1991). A second example is the importance of the participants' orientation to context (Arminen 2000; Wilson 1991; Zimmerman 1992). For example, the utterance (taken from a tape recorded telephone conversation), "somebody jus' vandalized my car," could be any of a number of things, such as an excuse for being delayed. In fact, it was treated by speaker and recipient alike as a request for help, based not on the utterance itself, but on the context: a phone call to an emergency dispatching agency. Context turns out to be pivotal for how the speech-exchange system itself functions – for example, a request sets up the relevance of granting or denial, but an excuse does not. In order for this to function effectively, both participants must be able to simulate and predict not only the other's behavior, but more broadly the other's intentions and orientation to the larger context. Whether the kind of simulation supported by a perception-action system is sufficient to explain these broader abilities, remains an open question.

## Caregiving, emotion, and concern for others

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**Abstract:** Few individuals are constitutionally incapable of showing concern for others at an early age, and malleability is possible. Individual variations will be best understood through study of the representational prerequisites of empathy in close conjunction with caregiving environments and affective underpinnings.

The concept of empathy has been questioned, even maligned, throughout time. Galileo classified sympathy with antipathy, occult properties, and other terms thought to masquerade as scientific explanations (Sobel 1999). Early philosophers, theologians, and moralists often viewed individuals as solely motivated by self-serving interests and needs. These beliefs made their way into twentieth century psychoanalytic, psychological, and sociobiological theories opposed to the idea that concern for others could be a central goal of human behavior. Recent theoretical, methodological and empirical advances reveal a rich, rigorous knowledge base about genuine concern for the well-being of others. The PAM model of Preston & de Waal (P&deW) builds upon and extends these discoveries. Particularly encouraging is the emphasis on the mother-infant relationship as the core context within which empathy is first learned. This generalization is now buttressed by solid empirical data (Zahn-Waxler 2000). It represents a departure from most earlier evolutionary theories where, with a notable exception (MacLean 1985), altruism expressed by the young toward family members was seen as impossible. Caring behaviors by the young were discounted as ultimately self-serving.

MacLean's ideas provide an important backdrop to the conceptual framework of P&deW. He viewed empathy as rooted in our biological, evolutionary heritage, a capacity that emerged in conjunction with the evolution of mammals. Mammals as warm-blooded creatures that nurture, nourish, and protect their young, engaged in a "family way of life." This set the stage for exposure (and responsiveness) to distress experiences of pain, separation, and suffering in others. Such stimuli are also the elicitors of empathy.

MacLean proposed interconnections of the limbic system with the prefrontal cortex, in the mammalian triune brain. Linked originally to parental concern for the young, a broader sense of responsibility for others emerged as reflexive reactions of concern were transformed into purposeful patterns.

P&deW develop a plausible argument that the same central nervous system link between perception and action guiding actions in the physical environment also organizes social-psychological processes pertaining to empathic concern. Whether perception-action processes are accordingly *the* driving force is open to question. The authors wisely avoid the rancorous, unproductive debate about the "true" nature of concern for others (i.e., selfish vs. selfless). In their view, definitions of empathy have been overemphasized to the point of distraction. However, conceptual and empirical advances depend upon identification of different forms of empathy, as well as the reasons and motives for different forms of expression. This requires clear definitions.

The focus on the CNS and brain circuitry gives further credence to ideas once deemed inherently unscientific. The successful integration of diverse literatures, theories, and disciplines bodes well for the utility of the PAM model. Now it will be necessary to develop specific empirical tests, to determine what it can and cannot explain. The model is presented in broad terms. To what extent do generalizations and integration of ideas oversimplify the issues? How well can individual differences in both naturalistic and experimental contexts be predicted? Neural disturbances and brain damage may contribute to empathic deficits, explaining variations at the extreme. However, relatively few individuals are constitutionally incapable of caring in the early years of life and malleability is possible. While recognized in many models, these issues are less actively pursued in empirical tests. Both genetics and environment contribute to early individual differences (Zahn-Waxler et al. 2001). Clarity is needed on empathy as a neurologically distributed process, and how interactions of nature and nurture can be examined.

Empathy disorders (e.g., autism, psychopathy) and factors contributing to them (e.g., parental depression) are considered here in the context of a deficit model. Parental depression and other conditions also can heighten empathy, sometimes creating surfeits (Zahn-Waxler 2000). In contrast to basic emotions (anger, fear, and joy), higher-order emotions like empathy and guilt are derivations of primary emotions. Empathy can only occur *in response to* another's emotion. Taking on the emotions of distressed others can create risk for depression, a mood disorder defined by sadness. Whether empathy is expressed as adaptive concern or in a way that drains and demoralizes the self, its first form of expression is affective in nature. Correspondingly, the PAM cognitive neuroscience perspective requires integration with an affective neuroscience approach (Davidson & Sutton 1995) from the outset.

In the PAM theory, emotional contagion is distinguished from, but also part of, a broader category of empathy including other subtypes. Further conceptual and empirical work is needed to clarify the distinctions and commonalities. For example, physiological reactivity to the distress of others (an index of contagion) is viewed as interpersonal connectivity essential to empathy. It is also viewed as personal distress that can turn the potential empathizer away or even against the victim on account of fear. Physiological arousal activated in a caregiver by a crying infant can elicit empathic concern, avoidance, or even abuse. The authors state that emotional contagion proximately guides the parent-offspring relationship, increasing the success of the offspring by eliciting tailored or proper care. Further information is needed on how the PAM theory can be used to generate predictions about (a) the nature of tailored or proper care, (b) when and how it is provided, (c) anticipated outcomes, and (d) interactions with child temperament. Most predictions generated focus on experimental tests of unclear relevance to real life. An exception is the proposed relationship between scope of life experience and scope of situations in which the subject responds appropriately. Defining and testing the constructs of "life experience" and "appropriate response," however, will be a major undertaking.

P&deW cite research by Cummings et al. (1985) where 2-year-olds show increased aggression toward peers following exposure to adult conflict as evidence for how representation changes with experience. This was true, however, only for a subgroup of children, mainly boys, who were already highly aggressive. Moreover, girls mainly showed distress. Generalizations from research can mask important exceptions that, if left unexamined, create risk for the models established. This is why the study of individual differences must accompany research on universals.

The emphasis on the caregiver-infant relationship in progressive, evolutionary models is relevant to the fact that females are more likely than males to show empathic, prosocial behaviors, (Zahn-Waxler 2000). In most species the caregiver typically is the mother. Biological factors as well as socialization experiences undoubtedly contribute to heightened empathy in females seen even in the first years of life. The study of groups who differ in their expressions of concern for others may help sort out the roles of nature and nurture that contribute to individual differences.

# Authors' Response

## Empathy: Each is in the right – hopefully, not all in the wrong

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**Abstract:** Only a broad theory that looks across levels of analysis can encompass the many perspectives on the phenomenon of empathy. We address the major points of our commentators by emphasizing that the basic perception-action process, while automatic, is subject to control and modulation, and is greatly affected by experience and context because of the role of representations. The model can explain why empathy seems phenomenologically more effortful than reflexive, and why there are different levels of empathy across individuals, ages, and species.

*And so these men of Indostan*
*Disputed loud and long,*
*Each in his own opinion*
*Exceeding stiff and strong,*
*Though each was partly in the right,*
*And all were in the wrong!*
*–from John Godfrey Saxe's version of "The Blind Men and the Elephant" (Saxe 1963)*

## R1. The big picture

Making an analogy to the ancient parable, empathy, like the elephant, has been studied from many different perspectives, yielding different and seemingly contradictory descriptions of the phenomenon. The thirty-one expert commentaries on our article echo the cacophony of opinions in the field of empathy research, with reports of empathy as a prosocial response to the needs of others that develops in childhood (**Bard, Brownell et al., Commons & Wolfsont, Eisenberg, Hoffman, Lewis**), as an innate ability for emotional resonance that exists across species (**Aureli & Schaffner, Bard, Bekoff, Gallup & Platek, Parr**), as a conditioned response that develops through experience (**Davis**), and as a high-level, cognitive process that relies on perspective-taking abilities reserved for a certain level of human development and a limited taxonomic group of animals (**Bandura, Constantino, Lewis**). In our target article, we tried to unite the empathy literature by taking a broad perspective that incorporates and validates all of these perspectives, working across all levels of analysis to determine how to mesh the perspectives into a unified model. We believe that "each was partly in the right" and do not exclude the possibility that we may be among those "in the wrong"; we do hope that our response further demonstrates the need to look at the whole beast as we explain how our model accommodates issues raised by our commentators.

We read the commentaries as generally supportive of the approach we have chosen. In fact, it is truly remarkable that empathy has now attracted so many expert opinions in a respectable journal, given that only in recent history has it been considered a serious object of scientific study (see **Zahn-Waxler**'s commentary). Most of the commentators agree in principle that it is time to integrate various levels of empathy into a single model and to elucidate its core mechanisms; this is a common theme throughout this response. Our response follows the structure of the target article, with large divisions on the ultimate (sect. R3) and proximate levels (sect. R4). We will focus on issues that were raised by multiple commentators, and clarify issues that may have been confusing (see Table R1).

## R2. General features of our model

### *R2.1. The meaning of multiple levels*

In biology, phenomena exist at several simultaneous levels. Nico Tinbergen fleshed out four levels of analysis: evolution, adaptation, development, and mechanism, each with its own questions and explanations of the same phenomenon (Tinbergen 1963). Ernst Mayr similarly divided analysis into proximate and ultimate causation (Mayr 1961). According to both schemes, all levels are necessary for a full understanding of a phenomenon, and the accounts of each level complement rather than conflict with one another.

For example, one might say that birds have feathers to keep warm, while another may disagree and say they facilitate flight. This is an issue of *adaptation* by natural selection, and both proposed functions are considered valid. There is a separable question of *evolution* that deals with how selection of certain genes and changes in gene frequencies produced feathers, and of *phylogeny,* which asks in which kind of animals feathers first appeared (an area with many recent fossil discoveries). Once feathers evolved, one needs to know about their *development* in the individual. Still further, there is the issue of how feathers work, the level of *mechanism,* of how they trap heat, dispel water in water fowl, and aid flight. In order to answer complex questions about behavior (why some birds fly and not others), one needs to investigate across all of these levels of analysis. More importantly, even these four levels of analysis cannot be divided sharply because each overlaps with and "informs" the others.

Our model of empathy touches on all four levels of analysis, and also combines across them, proposing that the *mechanism* itself is *adaptive, evolved* over time, and requires particular *developmental* conditions for maximum benefit in this environment. In fleshing out these levels of empathy, we have touched on everything from group alarm to the intersubjectivity problem. We do not think that this results in a mixing of metaphors (**Hinde, Gallese et al.**) or a definition that is too broad to be useful (**Hinde, Gallese et al., Parr**). Instead, by combining across levels, our model seeks to provide an adequate and accurate description of the phenomenon while supporting most of the existing perspectives.

A broad view covering everything from evolution to neurobiology cannot possibly do justice to the level of detail our colleagues have achieved with many subtopics of empathy, and as such, some commentators expressed a desire for the model to place more emphasis on their particular perspective. This proved especially true of the developmental researchers who thought that more emphasis should have

Table R1. *Major categories of topics addressed by commentators divided into four classifications: General issues, definitional issues, ultimate issues, and proximate issues*

| General Issues | | | Definitional Issues | | | |
|---|---|---|---|---|---|---|
| Positive vs. negative | When you see empathy | Prediction, testability | A broad definition | Representations | Response | Automatic |
| Ainslie & Monterosso, Brownell et al., Anderson & Keltner, Gordon, Panksepp, Parr | Bandura, Parr, Rochat, Schulkin | Atkinston, Gallese et al., Hinde, Parr, Panksepp, Zahn-Waxler | Anderson & Keltner, Gallese et al., Hinde, Parr | Hoffman | Davis, Anderson & Keltner, Hinde | Ainslie & Monterosso, Bandura, Bard, Blair, Brownell et al., Constantino, Davis, Eisenberg, Gordon, Hoffman, Lewis |
| R2.3. | R4.2. | R5. | R1., R2.1., R2.3. | R4.1. | R2.2. | R4.1.1. |

| Ultimate Level Issues | | | | |
|---|---|---|---|---|
| Other species | Interrelationship | Self, self-awareness, MSR | Developmental change | Adaptiveness of contagious distress |
| Aureli & Schaffner, Bard, Bekoff, Brownell et al., Gallup & Platek, Panksepp, Parr | Anderson & Keltner, Aureli & Schaffner, Bandura, Gordon, Hoffman | Gallup & Platek, Beckoff, Keenan & Wheeler, Lewis | Bard, Brownell et al., Commons & Wolfsont, Eisenberg, Gallup & Platek, Hoffman, Lewis, Zahn-Waxler | Bandura, Eisenberg, Constantino, Mealey & Kinner |
| R3.2. | R3.1. | R3.2. | R2.1. | R3., R5. |

| Proximate Level Issues | | | | | | | |
|---|---|---|---|---|---|---|---|
| Need mechanism | Automatic vs. cognitive | Mirror neurons | Simulated processes | Similarlity vs. familiarity | Neurological specifics | Attention | Disorders of empathy |
| Bard, Rochat, Davis | Atkinson, Aureli & Schaffner, Bandura, Brownell et al., Constantino, Hoffman, Lewis | Bandura, Parr, Charman, Davis, Eslinger et al., Gallese et al., Iacoboni & Lenzi, Panksepp et al., Rochat | Atkinson, Gallese, et al., Gordon, Kahil, Keenan & Wheeler | Bandura, Brownell et al., Hinde, Khalil, Mealey & Kinner, Schulkin Keenan & Wheeler, Panksepp | Atkinson, Blair, Eslinger et al., Gallup & Platek, Iacoboni & Lenzi, | Ainslie & Monterosso, Bandura | Bandura, Blair & Perschardt, Charman, Constantino, Mealey & Kinner, Wilson & Wilson |
| R2.3, R4 | R2.2, R2.3, R4 | R4.3 | R2.3, R4 | R4.2 | R4.4 | R2.3, R5 | R4.5 |

been placed on the stages of empathic development (**Bard, Brownell et al., Commons & Wolfsont, Hoffman, Lewis**), the differences among types of empathy (**Eisenberg, Hoffman**), and individual differences (**Zahn-Waxler**). We fully agree that these issues are important; indeed, they comprise the majority of existing empirical research on empathy. We chose not to emphasize this research in our review because it has been the topic of many such reviews in the past (e.g., Eisenberg & Strayer 1987; Hoffman 2000; Ungerer 1990; Zahn-Waxler et al. 1992), and as such we felt that the space in our article was better spent demonstrating how findings from this literature fit with our model. We are grateful to the commentaries that reviewed these findings, providing the reader with a more complete picture.

### *R2.2. "Low" versus "high" levels of empathy*

Some commentators described empathy as a cognitive process, qualitatively different from lower-level versions of empathy such as emotional contagion (e.g., **Bandura, Constantino, Lewis**). We agree that cognitive abilities augment basic perception-action processes in order to accomplish more complex forms of empathy (e.g., "true empathy" or "cognitive empathy," target article, sect. 4.2). However, these higher-level processes rely on perception-action processes, even if their automatic quality causes them to seem less significant. The fact that empathic processes arise automatically does not preclude their implications and expressions from being "filtered" through experience and cognitive evaluation; automatic processes can and do coexist with voluntary ones (contra **Hoffman**).

We agree with **Atkinson** that there are separable patterns of central and peripheral activity for separate emotions (cf. Damasio et al. 2000; Ekman et al. 1983), and that there are emotion-general cognitive processes, such as working memory. But, returning to our familiar theme, this distinction should not be overemphasized because emotion-specific contagion can be generated through emotion-general cognitive processes (e.g., imagery), and cognitive forms of empathy must activate representations of the specific emotion being simulated. Areas that code for shared representations (like somatosensory; cf. Adolphs et al. 2000) are necessary for perception of one's own feeling states, as well as the feeling states of another, and they are activated in both simple and complex forms of empathy, depending on the task.

### *R2.3. Why a process-based model?*

A few commentators did not see the need for a "process-based model" of empathy (e.g., **Anderson & Keltner, Gordon, Hoffman**). The emphasis on process is part of what distinguishes our model from others, so we respond to this in some detail. A process model is primarily useful because it does not require hard and fast divisions among types of phenomena (as is the case with developmental and comparative behavioral models). According to a process-based model, empathic processes are always present to some degree. If a normal subject has perceived the distressed state of an object, there will be some resulting activation of the subject's own distress circuits, even if the activation is not strong enough to generate conscious awareness of distress, an overt expression, or actions to terminate the object's distress. In addition, subjects may have their own goals that conflict with and override the need to attend to or respond to the object. Attention to the object is no minor issue because, as **Bandura** so aptly pointed out, one major way in which subjects avoid resonant distress, or the responsibility to offer help, is to avoid attending to the object altogether. Moreover, empathy deficits such as autism may be primarily due to attention deficits (e.g., Frith 1989; Gillberg 1999).

Thus, we fully agree with **Rochat** that the question is not whether or not nonhumans have a capacity for vicarious experience, but what *kind* of capacity they are capable of, and how it develops. And we agree with **Schulkin** who goes further and suggests that we should not separate empathy and "cognitive empathy," because the latter implies falsely that the former is noncognitive (perhaps "perspective-taking" can be used to describe cognitively effortful versions of empathic process).

On the other hand, some commentators downplay the possible continuity, mentioning the absence of empathy in certain subjects or situations (e.g., **Bandura** for humans, **Parr** for chimpanzees), or contrasting lower and higher levels of empathy in human adults as compared with infants or nonhuman animals (**Bandura, Brownell et al., Constantino, Lewis**). These comments reflect the fact that while we are placing empathy within a continuous, process-based model, another established tradition places empathy within a categorical model based on overt behavior or subjective experience. The latter has generated intense disagreement on the phenomenon and the placement of boundaries (e.g., Becker 1956; Cialdini et al. 1997; Eisenberg 1986; Hoffman 1978; Omdahl 1995; Shantz 1975; Wispé 1986).

Some theoretical models of empathy stipulate an overt prosocial response because of the practicality that overt states are often the only ones available for study (e.g., conditioning, comparative behavior, prosocial development). Because we think it is informative to know what is inside the "black box," we emphasize the ways in which perception activates the neural substrates of visceral and somatic states, which in turn activate the substrates of overt action. We used the term "response" in the target article to refer to the neural activation, which may have been mistaken by some commentators to refer to overt acts of imitation or helping (e.g., **Davis, Anderson & Keltner**, and **Hinde**).

Kim **Bard** presents data that advocate a process-based model of empathy. In an experiment by Coles et al. (1999), the response of 8-week-old infants to a social partner depended on their prior experience (presence of prenatal drugs and parental stability). This reaction was only evident in the heart-rate physiology of the subjects, however, not in their overt behavior. The heart rate response in question was seen only for social stimuli. In the target article, we presented similar human neonate data (sect. 1.1.3). These data demonstrate the importance of looking at physiological data, and of including mechanism-level descriptions, discussed further below. Obviously, behavioral data remain essential, because in the end we wish to know which model best explains behavioral outcomes, and our process-based model makes specific predictions for behavior, not all of which are shared by other theories.

In opposition to the process-based aspect of our model, **Gordon** emphasized his rather more cognitive model of mental simulation. Applying the theme of multiple levels, we believe that simulation theory, as well as its counterpart theory-theory, are compatible both with each other and with our model. Simulation theory is very similar to our perception-action model in that it deals with the way individuals model the world, but it is largely metaphorical, or "disembodied." In our model, "mental simulations" would derive from activating one's own substrates for feeling and action, but at a low enough level that there is no overt action, and/or with added neural inhibition to prevent overt action (perhaps like the "offline" processing of **Atkinson** and **Gordon**). In situations that are ambiguous or require overt action, concomitant executive processes can help switch activation among multiple, stable representations in order to determine the correct interpretation or the appropriate action (like **Hoffman**'s shifting of cognitive appraisals). Theory-theory is also metaphorical, but is a higher-level description of how individuals approach, and learn about the world. With our model, theories would be the stable representations created through experience with the world that dictate what one predicts to find and perceives. The shifting among these stable representations is equivalent to theory testing, à la the scientist in the crib (Gopnik et al. 1999). Moreover, since simulation theory and theory-theory exist at different levels, simulation theory could explain how theory-theory is instantiated (subjects simulate the object's behavior to test a theory).

Advocating a process-based model does expand the term empathy beyond the traditional, prosocial affective states or actions (as used by **Anderson & Keltner, Aureli & Schaffner, Davis, Hinde**), to include all affective forms of the perception-action process, any state that resonates between the subject and object (as noted by **Anderson & Keltner**). As such, the model includes the spread of both positive and negative states (addressing **Ainslie & Monterosso, Brownell et al., Gordon, Panksepp et al.**). Although, we reiterate with **Parr** that positive emotions are not just the inverse of negative because the two have different neural substrates to a large extent.

Since it is problematic to alter the meaning of an existing term, we suggest using the term "empathic processes" to refer to affective forms of the perception-action mechanism, and to reserve the term empathy *per se* for the traditional definitions (which depend on the discipline). We believe it is valuable to use the term "empathic processes" to characterize even low-level versions of these perception-action processes like emotional ideomotor actions and predator alarm. We do not think that responses to grasping (**Hoffman**) or predator alarms (**Aureli & Schaffner**) *are* expressions of empathy, or that they feel or seem similar to higher-level forms of empathy, but these phenomena belong in the same family of affective perception-action mechanisms. Our characterization of seemingly nonempathic states and behaviors as empathic processes may unsettle those preferring a phenomenological description (e.g., **Gallese et al.**). However, phenomenology ignores aspects of the underlying mechanism beyond conscious thought and awareness, and thus discourages understanding of the phenomenon in continuity with simpler phenomena, some found in other species. In addition, not everyone's phenomenology is the same. Someone who perceives empathy as a cognitive process will not resonate with an affective characterization, explaining why these different views have persisted in mutual isolation for over two centuries. Only by fleshing out the phenomenon in a way that includes all perspectives can one understand it.

## R3. Ultimate bases

Empathy is founded on the basic perception-action nervous system arrangement, which originated with the nervous system itself and can be assumed to be adaptive since it facilitates responses to the environment. In addition to the adaptiveness of perception-action processes in general, we discussed in detail the role of the mother-infant bond for developing socio-emotional concordance, which correlates with many positive outcomes for the individual (we were remiss in not citing the extensive supportive research of Jaak **Panksepp** on this topic in rodents).

Traditional models concerning the adaptation of empathy emphasize the benefits to the subject for helping the object, for example, inclusive fitness, reciprocal altruism, increased esteem within the group. Moreover, **Anderson & Keltner** rightly emphasize the ability of empathy to increase social bonding and cooperation. We do not disagree that all of these are important adaptive functions of helping behavior; but we focused on mother-infant interactions because these are of such direct relevance for the reproductive success of mammals, and were there from the beginning of mammalian evolution, so that they may have served as the evolutionary "engine" for empathic processes.

Significantly, from an evolutionary perspective, many of the distress cues commonly used by mammals to arouse helping responses are directly derived from the infantile behavioral repertoire, as pointed out by Eibl-Eibesfeldt (1971/1974); also MacLean (1985) – thanks to **Zahn-Waxler** for this addition – and Panksepp (1998). A particular kind of distress cue evolved because of its effectiveness in generating help from others. The aversiveness of the object's cue (to the degree that ending it is positively reinforcing), and the effect of the cue on the subject are inherently intertwined in terms of function and evolution. We agree with **Eisenberg** that these factors are partially separable for individual events and that this separation is useful for understanding individual differences in emotion. Eisenberg's research (references in Table 1 of the target article) demonstrates that some subjects exhibit more distress in response to the object's distress than others, and that help given by distressed subjects may differ qualitatively from that given by nondistressed subjects (such as, respectively, forceful termination/avoidance versus tailored care). Moreover, some subjects and situations may be more sensitive to social cues, such as audience effects and reciprocity. These effects are important and instructive to the phenomenon. We also agree with **Bandura** that contagious distress without any control would not be adaptive; as such, we assume the many factors modulating the intensity of perception-action processes prevent distress from occurring in most situations, and to disruptive degrees (salience, familiarity, similarity, attention, inhibition, emotion regulation).

### *R3.1. How empathy relates to relationships and bonding*

Interdependence between subject and object increases the need for the subject to attend to, perceive, and do something about the object's state. **Anderson & Keltner**'s model of social bonding is highly relevant here even if we doubt that the evolution of empathy started out in the context of relationships with a relatively low degree of interdependency (compared to the mother-infant bond), such as among peers or unrelated adults. This use of empathy, although highly relevant in the complex societies of most primates, seems to have been reached later on in evolution.

**Bandura** provides support for the emphasis on interdependence citing experiments where subjects only have concordant emotional reactions when they expect the object to be from their group, or to be cooperative. Only an interdependence hypothesis and not a social bonding hypothesis would predict similar effects of attention and action towards enemies as well as allies, and similar prosocial actions towards strangers who are temporarily necessary to the subject. The empirical work of Aureli and colleagues attests to the fact that relationship quality is equivalent to interdependence. In separate studies, it has been shown that individual primates with high relationship quality are more likely to reconcile (van Schaik & Aureli 2000), and individuals that must rely on each other for food are more likely to reconcile (Cords & Thurnheer 1993).

**Gordon** felt that our emphasis on the interrelationship of the subject and object was an "ad hoc amendment" to the model. On the contrary, the effect of interrelationship on the subject's behavior is a direct result of the perception-action arrangement of the brain, especially when you look across levels of analysis. Brains evolved to respond quickly and appropriately to the environment. Interrelationship and interdependence correlate very highly with the need for a subject to respond to an object. Thus, the adaptive bias towards friends and kin is a direct result of response-based neural design. This underscores the interplay of the ultimate and proximate levels of analysis since the brain mechanisms for response adaptively influence who the subject attends to, which in turn influences tendencies for cooperative and prosocial behavior.

### *R3.2. The inclusion of animal research*

There were no objections to our emphasis on continuity of empathic processes between humans and other animals, in fact we perceived general support (e.g., **Aureli & Schaffner, Bard, Bekoff, Gallup & Platek, Panksepp et al.**). Bard emphasized the fact that chimpanzees and humans go through similar stages of development in socio-emotional abilities. Aureli & Schaffner provided an emotion-mediated model of social decision-making in animals that is similar in qualilty to the somatic marker hypothesis for human decision-making (Damasio et al. 1991). The research of **Parr** is intriguing and instructive for our model, not only as a comparative approach, but because she combines behavioral and physiological measures, accessing the processing aspect of empathy in a way that previous comparative studies have failed to do.

Mark **Bekoff** points out the importance of including social carnivores in research on empathy and the self. If the capacity evolved in relation to mutual dependency and bonding between individuals, this taxonomic group is a logical one to look for empathy. Possibly, attribution-based forms of empathy require a self-other distinction. The mark test with mirrors is thought to tap into this ability, and since, until recently, only apes and humans were known to pass this test, **Gallup & Platek** reiterate Gallup's (Gallup 1982) prediction that cognitive empathy will be found only in this taxonomic group. This hypothesis was picked up by de Waal & Aureli (1996) when they found that only apes, and not monkeys, spontaneously provide consolation to victims of aggression (see also, de Waal 1996). Recently, however, dolphins have been added to the select group of animals with mirror self-recognition (Reiss & Marino 2001), an intriguing finding since dolphins have long been known for their altruism towards each other. Killer whales, and perhaps false killer whales (but not sea lions), also exhibited contingency checking to a mark (Delfour & Marten 2001). These findings seem to support the connection between higher forms of empathy and self-awareness. We agree with Bekoff, though, that the mirror test is unlikely to provide the whole story on self-awareness (Cenami Spada et al. 1995), and that we should remain open-minded about animals that fail this test yet have highly evolved social lives.

The canid research of Bekoff futher provides a nice animal parallel to **Brownell et al.**'s observation that human children "not only dynamically accommodate their behavior to one another and share emotion expression and behavior during play, but they also share one another's goals, desires, and beliefs." Bekoff's comparative research into the play behavior of social carnivores demonstrates that the "play bow" is used to communicate play intentions. The bow is used to initiate play (and according to a perception-action model, instigates a feeling of play in the other), and the frequency of play bows is higher after intense bites, and higher in species more able to inflict pain, communicating the absence of aggression in situations that could be misinterpreted (Bekoff 1995).

## R4. Proximate bases

As said before, there is no hard wall dividing ultimate and proximate levels of analysis; the two are always interrelated in the sense that proximate mechanisms themselves must evolve to serve their ultimate goals. The proximate level is not identical to the neural substrate (it includes all immediate causes of behavior), but it is especially our inclusion of neural data that seemed unnecessary to some commentators (e.g., **Davis, Rochat**). We will therefore first demonstrate that neuroscience is an established and necessary field. This is followed by our clarification of aspects of the proximate model that may have been unclear, then by disorders of empathy and our vision for future research.

Even if neuroscientific tools are currently en vogue and probably overestimated, this is not to be held against them. We do not agree that they represent some flash in the pan: neuroscience has indeed been part of traditional psychology for hundreds, if not thousands, of years. Since Hippocrates (400 BC), we have been learning about the brain using careful studies of behavior and postmortem analysis (e.g., Galen in the second century BC; Gall, Broca, Wernicke, and Meynert in the nineteenth century; see Long 1996/2002). But these indirect methods are often painstaking and limited by time, patience, and the availability of patients with selective impairments. New tools such as brain imaging can catalyse this knowledge with a few well-designed studies. This level of knowledge is necessary to distinguish among competing hypothesis, to select between possible and actual psychological theories.

To illustrate, it has been suggested that empathy is achieved in human adults by the subject's effortful reflection on the object's state and situation; this reflection generates state matching between subject and object (**Constantino, Lewis**, and **Bandura**). Alternatively, our model predicts that the matching state is generated automatically in the subject, but that the subject can use effort to attend to and modulate this activation. The former theory seems to imply that most, or all nonhuman animals lack the capacity for empathy, as they have limited executive skills and hence cannot effortfully consider the object's state. In contrast, our theory predicts that animals will have access to the states of others, even if their executive skills limit the extent to which they can manipulate this information. The demonstration of matching emotional states in young human infants and animals supports our model.

Similarly, one might propose, as **Kahlil** did, that empathy is achieved by "placing yourself in the shoes of" the object, or by "trying on" the emotion of the object. These two hypotheses may seem different theoretically, and this difference may be supported by data (see **Bandura**), but according to our model, both require the perception-action mechanism to generate access to the state of the object. It is more successful to "try on" the object's state than to imagine being the object (cf. Hughes et al. 1981; Stotland 1969) because "trying on" focuses on feeling states, whereas "in the shoes" focuses on the object's position and percept. Careful consideration of the mechanism is the only way to appreciate the similarities and differences between these two options.

Most theories of empathy are based on phenomenology, thus designed to mesh with our subjective experience; yet most are disembodied, and unable to explain how the subject places itself in the shoes of the other. This intersubjectivity problem gave rise to conditioning models that suggested subjects were conditioned to feel distress when their own distress followed that of the object. Conditioning of distress surely happens, as demonstrated by the animal experiments discussed in section 3.4.1 of our target article. But this does not account well for the contagious emotions of newborn infants or for the fact that subjects exhibit distress to the object even when they have never experienced the stressor (contra **Hinde**'s assumption). The weakness of phenomenological models is that they do not instantiate themselves across levels of analysis.

### R4.1. The role of representations

The term "representation" in our account may be confusing if taken to refer to symbolic entities that underlie voluntary processes. If representations were to refer to this level of functioning, they would indeed conflict with basic empathic processes such as emotional contagion, as pointed out by **Hoffman**. However, we are using the term, as is common in cognitive science, to refer to the neuronal connections of the brain that store information. As such, muscle movements, feeling states, associations, conditioning, and so on, are all mediated by representations, and they require no special cognitive abilities beyond the plasticity that exists in any central nervous system (cf. Damasio 1990; McClelland & Rumelhart 1985; Merzenich & deCharms 1996).

**R4.1.1. The meaning of "automatic."** Breathing is most of the time an involuntary, automatic process. Imagine that we would have to concentrate on it all of the time. Yet, we do have control over it, can deliberately speed up breathing, regulate it, and even temporarily stop it till we are blue in the face. This goes to show that the term "automatic" should not be confused with "uncontrollable," as some of the commentators seemed to do in their response to our description of empathy as an automatic process (**Bandura, Brownell et al., Constantino, Davis, Hoffman, Lewis**). What we meant is that neural representations are automatically activated by perceptions associated with them. Thus, we assume along with our commentators that perception-action circuits will not always be engaged (e.g., if the subject is not motivated to attend to the object), and that if they are engaged, many mediating factors will determine the subject's experience and behavioral output.

To give a more concrete picture, witnessing an expression of sadness could activate cortical and subcortical areas (even peripheral muscles; cf. Fadiga et al. 1999) below a threshold that would elicit a facial expression or change in physiology. This lower level of activation would still give the subject access to the state of the object, allowing the subject to understand the object, make inferences and plans, without necessitating conscious awareness of the feelings or overt changes (like "offline" processing, **Atkinson** and **Gordon**). In some cases, however, we predict that the subject *will* actually exhibit/feel the mimicking movement/feeling (high salience, attention, cognitive load). For example, in the Dimberg studies we reviewed (target article, sect. 3.4.4), subjects exhibit facial muscle activity and report a subjective experience matching the depicted emotion (pictures of facial expressions).

The automatic activation of neural representations by no means conflicts with a more cognitive or an appraisal view of empathy. Appraisals are themselves the product of activated, interconnected, neural representations associated with the percept; thus, one can interchange our use of "representations" with **Hoffman**'s use of "appraisals." Similarly, the cognitive and situational factors mentioned by **Bandura** are accounted for, since experience determines the subject's activation via the effect of experience on attention (target article, sect. 4.1.1, 4.2). Inhibition and attention reallocation can up- or down-regulate the activation of representations (target article, sect. 4.2).

### R4.2. Similarity versus familiarity

Familiarity and similarity explain the vast majority of effects on empathy in the literature (see Table 1 of the target article). Batson and colleagues have extensive data on the effect of even superficial, perceived similarity on the likelihood to help (Batson et al.1977; Batson & Coke 1981; Batson et al. 1988; Toi & Batson 1982). **Brownell et al.** also cite a paper by Zahn-Waxler and colleagues showing that preschool children direct prosocial behaviors more to peers than adults (Zahn-Waxler et al. 1982).

**Khalil** brought up the differences between similarity and familiarity, and we agree that they should not be equated. Similarity is the extent to which subject and object share any of a multitude of features (e.g., overlap in genes, body structure, appearance, temperament, past experiences, the way that they carry themselves). Familiarity, on the other hand, is the extent to which the subject has had past experience with the object, directly or indirectly. While similarity often overlaps with familiarity, especially if time is spent with similar individuals, one could be relatively similar to someone one has not met, and one can be very dissimilar to someone one knows well (as in the case of "dear enemies," and interspecies interactions). The two factors differ, but their effects on empathy are similar because they both increase the attention to and understanding of the object – similarity through the representations that the subject and object share, familiarity through the representations created in the subject through experience with the object. The representational overlap between subject and object addresses the concerns of **Bandura** and **Parr** that individuals do not always exhibit empathy for one another. Empathy is prevalent within groups because the individuals are similar, and empathy is lacking during inter or intragroup conflicts because the individuals are dissimilar (or perceive themselves to be). **Schulkin** suggested a similar interpretation for the behavior of the Nazi forces during World War II.

There will always exist some similarities and some differences between subject and object, and there will always be an extent to which they will be familiar with one another (addressing **Bandura, Brownell et al., Hinde**). **Mealey & Kinner** described this well when they stated that some insufficiencies in empathy will exist between people and animals, females and males, young and old, and between any subject and object with differing experiences. The vernacular use of the word "empathy" in English actually restricts the concept such that the word cannot be used (i.e., "I empathize with you") unless the subject has had the same experience. The same is true for the original German *Einfühlung*. Without the same experience one may be able to "sympathize," but not "empathize" (again reflecting a categorical, rather than a continuous model of empathy). Because similarity and familiarity are not discrete categories, the subject and object can be compared on many different dimensions. When the subject observes the object from a distance, body type, posture, and carriage are the only cues available, so these will be the representations of interest. In an emotional, interpersonal conversation between spouses, the outcome will depend more on their shared representations of each other and their relationship.

### *R4.3. Not just mirror neurons*

Many commentators saw our proximate mechanism as basically a "mirror neuron" hypothesis (e.g., **Charman, Davis, Panksepp et al., Rochat**), which is understandable, given the enormous amount of recent press given to these cells. According to our model, however, mirror neurons alone cannot produce or give rise to empathy (as acknowledged by **Gallese et al.**), and much more work on the interconnected brain circuits and their connections to the viscera would be necessary to explain the biological bases of empathy (as done by **Iacoboni & Lenzi**). Importantly, experiments in neuroscience using socio-emotional paradigms (see target article, sect. 3.4.4) do not implicate motor mirror neuron areas, but rather areas where visceral emotional states are represented in the cortex, and the pathways between them. In a recent study, when presented with pictures of faces, schizophrenic patients had increased activation compared to normals in motor and pre-motor cortex areas that control face movement. This indicates that they compensate for their emotion processing deficits by hyperactivating their own face movement substrates during perception (Quintana et al. 2001). The F5 mirror neurons described in monkeys may not be of primary importance for empathic processes, but may play a bigger role in the perception-action processes of language (Rizzolatti & Arbib 1998), where there is a preponderance of neuropsychological data to support their role.

Mirror neurons are interesting because they provide cellular evidence for the perception-action mechanism required by our model, which is far from new (as emphasized by **Rochat**). As reviewed in the target article, perception-action processes were specifically postulated by Lipps (1903) and Merleau-Ponty (1962/1970) long before the discovery of mirror neurons. Also, Prinz and colleagues have been demonstrating perception-action processes in motor behavior for the past few decades (exemplifying that one can infer the biological mechanism from well-designed behavioral experiments) (see, e.g., Prinz 1997). However, it is important not to interpret the fact that we have mostly motor data for perception-action processes as an indication that all perception-action processes are motoric in nature (cf. Gallagher et al. 2002). One can apply perception-action processes to social cognition without it necessarily being a motor theory of social cognition (cf. Gallese & Goldman 1998; Wolpert et al. 2001).

### *R4.4. The search for neural mechanisms: Beyond mirror neurons*

As a circuit-based model, our description of the neural pathways of empathy did not elaborate on the specific role of each brain area. A few commentators came to our rescue, filling in details from recent empirical studies of brain imaging. We are grateful for the imaging study reviews of **Atkinson** (emotion-specific versus emotion general processing), **Blair & Perschardt** (emotion recognition, especially angry vs. fearful faces, and theory of mind), **Gallup & Platek** (self-recognition and mental state attribution), and **Keenan & Wheeler** (lateralization of self-awareness, theory of mind). There have also been other highly relevant and supportive papers published since the call for commentators. Our model accounts for the findings in these papers, but we caution against interpretations of data that localize a particular task to a particular brain area. The commentaries of **Eslinger et al.** and of **Iacoboni & Lenzi** exemplify a dynamic, integrated approach that studies abilities, rather than tasks, and brain systems rather than brain areas.

The substrates for self-awareness are particularly interesting. Self-awareness was addressed by multiple commentators (**Bekoff, Blair & Perschardt, Gallup & Platek, Keenan & Wheeler**) and it is relevant to empathy, since empathy correlates with mirror-self recognition (MSR; cf. Gallup 1982). Self-awareness is also relevant to our model because perception-action processes use the substrates of the self to perceive others, begging the question, how does one differentiate activation caused by one's own actions from that generated by the perception of action in another? We suggested that activation is in general higher when caused by actions in the self than in another, and that particular areas should show more activation for self-generated action. General and area-specific activation could be used to disambiguate self-action from other-action. Other authors have suggested the involvement of reafferent motor signals in the right parietal cortex (Georgieff & Jeannerod 1998; Iacoboni et al. 2001).

Two recent studies by Decety and colleagues found lateralized effects in two PET imaging tasks that compared self- and other-related conditions, but the interpretation of these data is complicated (first- vs. third-person action imagery; Ruby & Decety 2001; imitating vs. being imitated in a complex motor task, Decety et al. 2002). As expected by a perception-action model, they found overlapping neural substrates for self- and the other-oriented action conditions, and there were areas that were only – or more – active in one condition than another, demonstrating that you can use the neural signals to differentiate self from other. Lateralized activity in the inferior parietal cortex was particularly suggested to discriminate between self and other; the right was active when the subject was being imitated by another and when imagining another's action, the left was active when the subject was imitating another and when imagining self-action. But studies reviewed by **Keenan & Wheeler** suggest self-awareness is lateralized to the right hemisphere: Does it make sense for self-action to activate the opposite side of the brain as "self-recognition"? Decety and colleagues suggest that subjects hyperactivate self-representations while processing another's action, to avoid confusion (Ruby & Decety 2001; cf. Hurley 1997).

A more parsimonious model is suggested to explain these data, that fits perfectly with recent applications of motor theory to social cognition (cf. Blakemore & Decety 2001; Wolpert et al. 2001). The left hemisphere may be needed to attend to, or generate, self-action; this explains left lateralization for apraxia, imitation of another, and imagining self-action. Conversely, the right hemisphere is involved when you attend to the action of a person or body part "outside of yourself" (including pictures of yourself or your mirror reflection), explaining right lateralization when the subject is being imitated by another, imagining the action of another (but see Grafton et al. 1996), MSR, theory of mind, and passivity phenomenon. The right parietal cortex is particularly involved when tasks require complex visuospatial processing (Colby & Goldberg 1999; Goldenberg et al. 2001). Thus, one may need more right hemisphere activity to generate complex, precise movements (Goldenberg 2001), to visually process the actions of another (Ruby & Decety 2001; Decety et al. 2002), or to visually process one's own reflected actions (self-recognition studies).

A simple mechanism could explain how one differentiates activity caused by looking at one's self, another person imitating you, or just another person. The cerebellum is thought to activate or prime the sensory areas with the expected feedback from an intended action (a forward model, cf. Wolpert et al. 1998). This predicted feedback can be compared to the actual visual feedback from the person facing you (even if it is yourself), and you can interpret the situation based on the results of this comparison. If the visual feedback from the person facing you correlates precisely in time and space with your expectations, you are looking at your own movement; if the actions correlate, but less precisely in form and timing, you are looking at another person imitating you; if the actions are not correlated with your own, you are just looking at another person. It is known that cerebellar response correlates with the delay between the expected and observed feedback (Blakemore et al. 2001); usually this signals an error, but when the feedback is from another person (you have many cues that it is), you can interpret the increased cerebellar activity as a sign that you are being imitated. When one is conscious that there is a disconnection between what is predicted and observed, there is increased activity in the prefrontal cortex (Fink et al. 1999); this may explain the impression that MSR requires conscious awareness, and the fact that the prefrontal cortex is active during self-recognition tasks. But, it is still conceivable that individuals with less self-awareness or less prefrontal cortex can distinguish self from other using the cerebellar signals.

**Iacoboni & Lenzi** describe their own work on the neural substrates of empathy in a task where individuals either passively perceived emotional expressions, or perceived expressions while imitating them (the "empathy" condition). This experiment found that completely overlapping areas were recruited for the two tasks, which was interpreted as support for a perception-action model of empathy. The only difference between the conditions was in the magnitude of the response, with more activation for the imitation condition, presumably because the subjects were actually moving. This fits with our assumption that perception activates representations, but at a lower level than for overt actions. Iacoboni & Lenzi discussed how the insula was uniquely situated to communicate information from the mirror neuron system to the limbic system, generating the emotional sequelae necessary for an affective version of perception-action processing. They found insular activity in the imitation conditions as suspected, but there seems not to have been significantly more activation in imitation than passive viewing.

Similar to the aforementioned findings, in a PET study of emotional imagery by Bechara, Preston, and colleagues at the University of Iowa, there was almost complete overlap between the areas recruited for imagining an emotion event from your own life, versus imagining an emotional event from the life of another person. These data support a perception-action model of empathy since you understand the experiences of another through your own emotion substrates (see Preston et al. 2002).

In their commentary, **Eslinger et al.** have summarized the areas of the brain stem and cortex that are active during moral judgment. Since these areas (amygdala, thalamus, insula, upper brainstem) are important for both perceiving and feeling emotion, they are in line with our model and the hypothesis of **Iacoboni & Lenzi**. Eslinger also cites data from lesion analysis demonstrating that empathy requires intact brain areas that evoke and interpret visceral states, and places these areas in an interconnected circuit between the frontal lobe and anterior temporal lobe (including the amygdala and the insular cortex) with "distinct but complementary roles" for each of the areas. In line with our suggestion of a significant role for the cerebellum in the ability to predict and attend to emotional stimuli, there was activation of this area during moral judgments.

### R4.5. Instructive pathologies

Some commentaries augmented our description of impairments in empathic perception-action processes in disorders like autism and psychopathy. **Constantino** gave an accurate and eloquent summary of our model and went on to support our review with data from clinical findings on empathy disorders. We fully agree with Constantino that these disorders represent extremes on continua of social and cognitive functioning (see Gillberg 1999). Contstantino also points out that mild social deficits may have been preserved over the course of evolution because they are adaptive. This is actually a theme of a *BBS* target article by Linda **Mealey** (another commentator), who discusses this possibility in depth for psychopathy (Mealey 1995).

**Mealey & Kinner** support the idea that individuals with psychopathy lack the ability to affectively respond to the state of another, stating that these individuals may not have the necessary socio-emotional representations, or that these representations are not linked to the physiological responses that give them substance. We agree with these commentators' assumption that individuals with psychopathy may not have a theory of mind deficit *per se* (contra **Blair & Perschardt**), but rather that their personal experience of certain emotions is different, and thus their experience does not resonate with objects of distress. Their deficit could be due to many different central nervous system problems, and the genesis of psychopathy is not known. Prefrontal dysfunction is not unlikely, but there is probably a more complex problem that disrupts the connections between the prefrontal cortex (especially area 25), the amygdala, and brain stem autonomic structures.

Our hypothesis for the impairment of individuals with autism is different from psychopathy, but similar in the sense that it is also a disruption in the perception-action circuit (which is not "unitary"; cf. **Blair & Perschardt**). Because both are considered "empathy disorders" there are indeed qualitative similarities between them (see Gillberg 1992), but the way in which empathy is impaired, and the types of social deficits that these populations show are different, thus requiring a different explanation (as noted by

**Bandura**, and by Blair & Perschardt). We provided evidence to suggest that autism is not a problem with the prefrontal lobes in particular (as interpreted by Bandura), but rather by an impairment of basic imitation and attention, likely linked to cerebellar damage. Cerebellar damage would cause problems in predicting and attending to the appropriate emotional cues in stimuli, precluding low-level imitative behaviors and proper social development. New data support the importance of early imitative and resonating behaviors in development. Children with autism exposed repeatedly to an adult that imitated them showed increased sociality after the first session (Field et al. 2001). Mothers apparently use imitation in the earliest months of a babies life, but gradually increase the proportion of affect attunement beginning at two to three months; by six months, attunement predominates (Jonsson et al. 2001). However, assuming an early developmental problem in the cerebellum, the extensive cerebellar-frontal connections would not develop properly, resulting in ostensive prefrontal dysfunction. As underscored by **Charman**, abnormalities have been found in basically all lobes of the autistic brain (e.g., frontal [Casanova et al. 2002], parietal [Townsend et al. 2001]; temporal [Casanova et al. 2002; Saitoh et al. 2001]), but there is currently a lack of integration of these various findings.

The imitation deficit viewpoint was supported by **Charman**; he added that there are many possible hypotheses about the cause of this impairment. He suggests that individuals with autism could be impaired at (1) perceiving the state of the object (emotional or motor), (2) mapping the object's states onto one's own states, (3) identifying with the object (Hobson 1993), or, (4) they could have a nonfunctioning mirror neuron system (Rizzolatti et al. 1996). We think that perception is not different from mapping, as perception is the same stage as activating your own representations (equalizing options 1 and 2). Identification is a psychological construct, which we would operationalize as the result of perceiving that state in the object (which autistics may not do), and having similar representations as the object (which psychopaths and dissimilar normal individuals may not have). Again, we are dealing with the ability to attend to the object and the presence of overlapping representations with the object. Individuals with autism have impaired language skills and motor imitation (implicating the mirror neuron system), as well as impaired emotion imitation (implicating empathy processes); this suggests the impairment is "upstream" of both the mirror neuron system and empathy specific processes (Williams et al. 2001). This is again why we emphasize a deficit in these individuals in attending to appropriate stimuli, related to their cerebellar damage.

One could test for the early versus late impairments across populations as suggested by **Atkinson**. Dimberg's facial EMG data (referenced in target article, sect. 2.4.4) represents automatic activation of muscles from emotional expression, and thus an effect of early, low-level processing; but this effect is hard to replicate. Preston and colleagues at the University of Iowa are in the process of developing an alternative protocol to be used with impaired populations that directly compares automatic/covert with conscious/overt processing of emotional states.

An interesting application of the cerebellar hypothesis came from **Wilson & Wilson**'s commentary on perception-action effects in social turn-taking. Recent data suggests that the cerebellum represents temporal relationships among events, even outside the domain of motor behavior, and even when there is no overt response (Ivry 2000). The cerebellum may be responsible for the attention-shifting aspects of behavior (especially response reassignment), while the basal ganglia coordinate successive responses (Ravizza & Ivry 2001). Extensive data on the spatial-attention deficits of individuals with autism mimic the deficits of individuals with lesions in the cerebellum, and correlate with the amount of damage to the vermis of the cerebellum (see Townsend et al. 2001). Turn-taking relies heavily on these cerebellar processes because one interprets the other's goals from the content, timing, and cadence of their speech, in order to predict and time interruptions; this allows for smooth conversation without large pauses or inappropriate overlaps. Most social interactions depend on tight timing of one individual's actions with another's (e.g., greeting rituals, romantic encounters), and our interpretation of others' behavior likely relies on these cues (e.g., Heider & Simmel 1944). This research reminds us, as did **Panksepp et al.**, that the search for deficits in individuals with impaired social behavior needs to include noncortical areas (cerebellum, basal ganglia, other brainstem structures).

## R5. The future of empathy

In the target article, we offered specific experimental ideas for testing our model. Some commentators questioned the predictability (**Hinde**, **Parr**), but we believe that our model is predictive and generates hypotheses because of the way interdependence, familiarity, similarity, and salience affect the extent to which the subject processes the object's state, and is motivated to act. The importance of most of these factors has already been proven in the existing literature (see Table 1 of the target article), and the merit of any new hypothesis is to generate new predictions. Interdependence has been less explicitly looked at, and was controversial to some commentators (**Anderson & Keltner, Bandura, Gordon**). We emphasize interdependence because the nervous system in general, and a perception-action system in particular, evolved to generate responses to the environment. Since objects that are intertwined with the subject require a response, they will attract the attention of the subject and activate perception-action processes.

There is a great need to experimentally separate the subject's ability to attend to the object from the ability to process the object's state. In agreement with **Bandura**, we predict that the allocation of attention is the primary way in which people control and modulate the extent of their resonant emotion with another. There will be impairments in empathy that are correlated with attention deficits (e.g., autism). The role of attention suggests a number of different experimental tests, including the early versus late processing experiments in the previous section. The role of attention also suggests that we need to look more closely at the role of the cerebellum and basal ganglia in the production and interpretation of socially appropriate behavior (e.g., with stroke patients or Parkinson's patients, respectively), and that we need to include measures of attention in behavioral paradigms (such as using a video of the subject, an eye tracker, and/or memory tests of similar nonemotional details).

Possibly, perception-action processes are less evident in existing human laboratory experiments because the stimuli are not salient enough to generate automatic processing (static instead of dynamic, pictures instead of live, faces only instead of whole body). We are sympathetic to the conditions that prevent naturalistic research (e.g., human subjects' approval, time to collect and analyse data, number of technicians needed), but the exceptions to these constraints on research prove that it is possible, and for the testing of our model it may be necessary.

Developmental research has been particularly innovative in studying real-life socio-emotional responses, while retaining experimental rigor (e.g., the home tests of empathy by **Zahn-Waxler**; imitation experiments of Melzoff and colleagues, social referencing studies of Campos and colleagues). This example needs to be followed more directly in research with adult humans because, although these individuals are capable of reporting on their own state and filling out questionnaires, these kinds of data are subject to bias and error and cannot be compared directly to research in animals, infants, and impaired populations. Animal research by necessity has to forego questionnaires, which may be the reason why there are now far more studies on spontaneous reconciliation and consolation in nonhuman primates than in humans, young or old (Aureli & de Waal 2000).

One could use the diffusion of responsibility paradigm from social psychology to investigate empathy, controlling the relevant factors between the subject and a confederate object of distress (familiarity: whether they met in a prior session or did not; similarity: whether they are the same age and class or not; salience: whether the subject is in mild discomfort or is unconscious; interdependence: whether the object is the partner in the experiment or not; other goals: whether the study is "cancelled" or the subject is *en route* to a goal). All of these factors should positively affect the subject's response (salience should have an inverted-U effect), and different designs could combine factors to look at their relative influence. We predict that the subject's goals will override the other effects at lower levels, but that high levels of familiarity and interdependence will override even important goals of the subject (short of reproductive success itself). To look at empathic processes more generally, one should assess the subject's internal reactions to the object, and attention to the object, as well as the overt response.

**Zahn-Waxler** requested that future research flesh out the interactions of nature and nurture and the precise role of "tailored care," and she suggested that individual differences are a good way to do so. We believe this research is best done with animal models, because one can control many of the relevant factors. We reviewed early studies of helping behavior in rodents and birds, and hope that this innovative research can be revived. One can use very similar paradigms to those conditioning paradigms, but increase the number of factors well beyond conditioning and salience to include all of the factors mentioned in the diffusion of responsibility study (familiarity, similarity, interdependence, other goals) as well as conditions that cannot be controlled with humans (past experience, rearing conditions, genetics, species differences). One can also look at psychophysiology, endocrinology, and neural substrates relatively easily in animals, especially rodents (see the emotion and memory research of McGaugh and colleagues, e.g., Guzowski et al. 2001; Roozendaal et al. 2001), but these approaches have yet to be turned on the topic of empathy *per se.* Albeit more difficult, a psychophysiological approach has proven to be successful for studying emotional processing in primates (Aureli et al. 1999; Berntson et al. 1989; Miller et al. 1966; Parr 2001; Parr & Hopkins 2000).

Individual and species differences are benchmarks for genetic differences, especially when rearing conditions can be partially controlled, so one can use breeding techniques to isolate the genetic differences between responders and nonresponders. This is especially interesting with small-animal models since one can look at multiple generations and control the parentage. In this regard, the rodent research of **Panksepp** is well-equipped to deal with these issues; his suggestion to using genetic profiling techniques has become very feasible and should be among planned studies on empathy.

It is more difficult to study nature/nurture issues in human populations because there are so many factors involved and one cannot control them; this results in very small effect sizes, requiring vast numbers of subjects for just correlational results. For human populations, it is best to look at extreme ends of the continua in order to increase effect sizes, which means studying impaired populations. The work of Tiffany Field exemplifies this research, looking at the emotional concordance and responsivity of normal infants compared to infants at risk for developing an acquired disorder, for example, due to premature birth (Field 1979), respiratory problems (Field et al. 1979), or a mood disorder in the mother (Field et al. 1990). In general, research on impaired populations will continue to give insight into the necessary components for normal empathic responses, and into the mechanisms underlying them. This research is hard to interpret without corresponding research into animal models and the substrates of normal humans (using functional imaging, TMS, EEG, endocrinology, etc.). Normal human populations are especially amenable to psychophysiological recording that can look at perception-action effects in the autonomic nervous system online. These processes, only in combination, will clarify the important interaction of nature and nurture, as well as the central and peripheral circuits involved in each stage of the processing.

## R6. Conclusion

The commentators agreed overall that it is useful to extend the concept of empathy into ultimate and proximate domains, and to try to link empathy in humans and nonhumans. Recent data support many aspects of the model, and we can start to be more specific about the neural substrates of emotional perception-action processes. Future research, directed more at the role of interdependence, attention, and the interaction between cerebellum and subcortical structures should prove useful in further elucidating the mechanism and the reason for impairments of empathy. We thank the editors of *BBS*, the original reviewers, and the commentators for their thoughtful suggestions and comments. We hope the process of empathy has begun to emerge from its state as "a riddle in social psychology" (Allport 1968), as we begin to understand the ultimate and proximate mechanisms.

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**[Note: The letters "a" and "r" after authors' initials refer to target article and response references, respectively]**

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