

Empathy: Its ultimate and proximate bases

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Short abstract:

Our proximate and ultimate model of empathy integrates diverse theories, reconciles conflicting definitions, and generates specific predictions. Focusing on the evolution of perception-action processes connects empathy with more basic phenomena such as imitation, group alarm, social facilitation, vicariousness of emotions, and mother-infant responsiveness. The latter, shared across species that live in groups, have profound effects on reproductive success. Perception-action processes are accordingly the driving force in the evolution of empathy. With the more recent evolutionary expansion of prefrontal functioning, these basic processes have been augmented to support more cognitive forms of empathy.

Long 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:

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

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

	Familiarity	Similarity	Learning	Past experience	Salience
Rats				Church 1959; Watanabe & Ono 1986	Lavery and Foley 1963; Rice & Gainer 1962

Monkeys	Aureli et al. 1989; Aureli et al. 1992; Cords & Thurnheer 1993; Demaria & Thierry 1992; Masserman et al. 1964; Miller et al. 1959	Miller et al. 1966; Miller et al. 1967; Miller et al. 1959	de Waal 1996; de Waal et al. 1996	Masserman et al. 1964; Miller et al. 1967	Miller et al. 1959; 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; Zahn-Waxler et al.; 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 et al. 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

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.).

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.

0.1. Terminology

0.1.1. 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, it is 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.

0.1.2. Definitional distinctions

Much of the empathy literature focuses on whether empathy is an emotional or cognitive process and distinguishing empathy from emotional contagion, sympathy, and perspective taking (e.g. Eisenberg 1986; Feshbach 1975; Hoffman 1978; 1982; 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 italics).

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	Usually	Not necessarily	Yes	helping, succorance

	distress.				
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TABLE 2: Usage of terminology by most current researchers divided into main variables of classification, updated for a perception-action view of the phenomena.

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; Wermlund 1949). McDougall observes in his Introduction to Social Psychology "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" (1908/1923, p. 93). McDougall includes imitation of facial expressions from mother to infant, feelings of tenderness evoked in observers of mother-infant interactions, and the 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 and b, 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 un-paired 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 and 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. 1992). Hoffman 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 (1982, 2000).

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 itself is empirically when existing behavioral data on empathy is combined with recent data from physiology and functional neuroanatomy. Applying the perception-action mechanism broadly recoheres the discrepant views into a unified whole, and changes the ultimate model.

0.1.3. 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 definition of empathy (2000), 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 sub-classes of phenomena that share the same mechanism. This includes emotional contagion, sympathy, cognitive empathy, helping behavior, etc. (Figure 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 Figure 1).

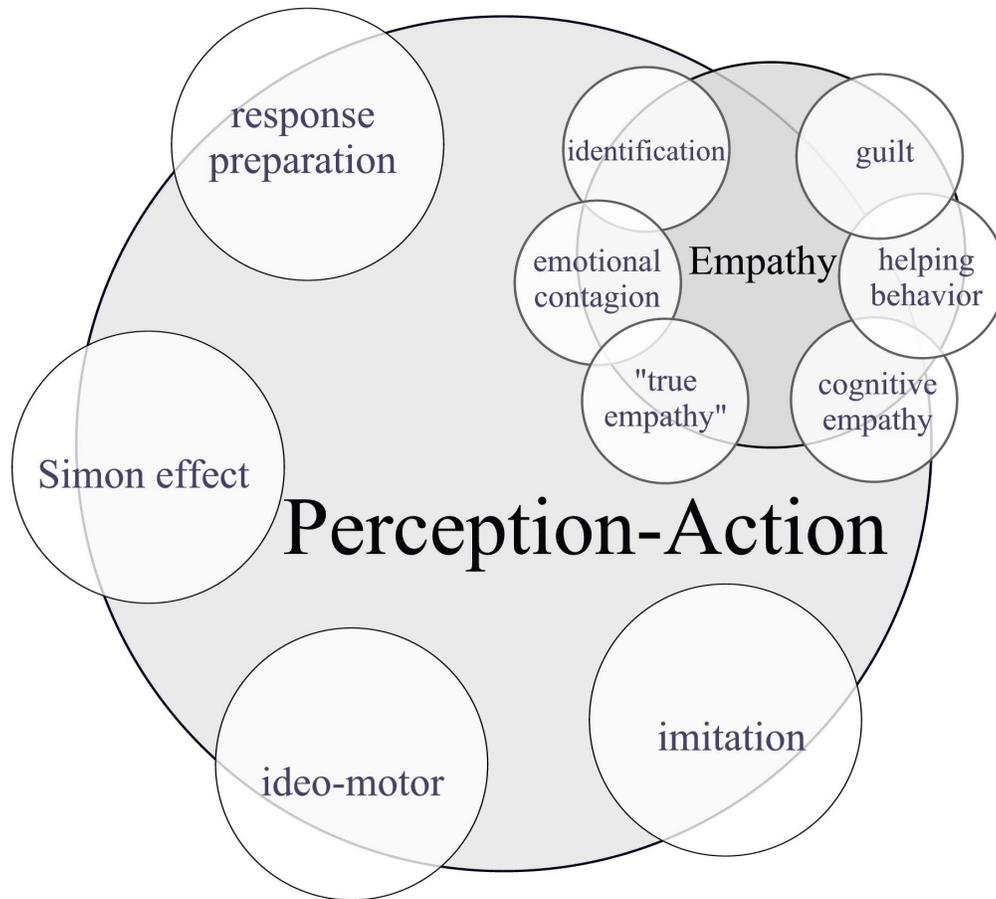


Figure 1. In order to unify the various perspectives, empathy needs to be construed broadly to include all processes that rely on the perception-action mechanism. Thus, perception-action is a superordinate class, which includes two basic level categories, motor behavior and emotional behavior. Both of 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.

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).

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 stimuli. Formed by the combination of developmental tuning biases and connectivity of neurons as well as alterations due to experience.
unless inhibited	Imitative action are inhibited during observation of action, centrally (from prefrontal inhibition), peripherally (with spinal cord inhibition blocking the motoneurons that execute the action), or both.

TABLE 3: Clarification of terms from the summary of the model that are used throughout.

With the Perception-Action Model, whether or not a subject perceives the state of the object depends crucially 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 non-human 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 and to 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 (Harman 1994; Gunnar et al. 1984; 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 model". 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.

1. 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 non-offspring.

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 non-related individuals (Aureli et al. 1989; 1992; Demaria & Thierry 1992). In chimpanzees, where male alliances are very important for intra and inter-group conflicts, reconciliation is higher among males than among females (de Waal 1986; Goodall 1986; 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 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.

1.1. 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 (Powell 1974; Kenward 1978). 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 system. 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, Figure 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.

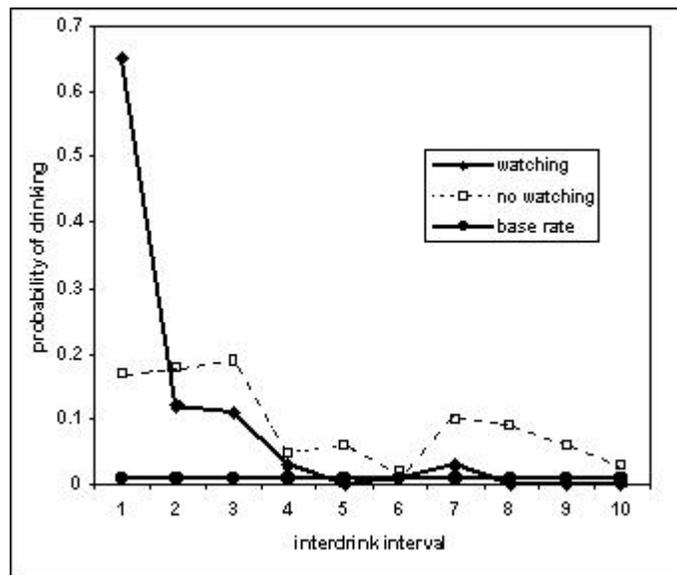


Fig. 2. Social facilitation of drinking in captive hyenas (adapted from Glickman et al., 1997).

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. 1992).

There are a few main reasons not to reject the continuity of these phenomena. Firstly, 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 like 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 section 2). Finally, although there are surely differences in the cognitive capabilities across species (discussed in section 4), 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.

1.2. 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 and Plutchik 1987). Infants are emotionally affected by the state of their mothers and mothers are emotionally affected by the state of their offspring.

1.2.1. 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. 1996; Eisenberg & Okun 1996; Eisenberg et al. 1994, 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 can not 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 social 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. This is in accordance with findings from other fields, and with the importance of alarm and distress contagion on reproductive success.

1.2.2. 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 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 (1971/1974). 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.

1.3. 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 non-offspring. 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 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 (Eibl-Eibesfeldt 1971/1974).

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 in press).

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 non-interrelated objects (like psychopathy). The latter case is an impairment in the perception-action circuit for emotional states, addressed in section 2.4.5. "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.

2. 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).

2.1. Existing theories

Previous theoretical accounts of empathy have implicated a perception-action model to varying degrees (Adolphs 1999; Brothers 1990; Boodin 1921; Levenson & Reuf 1992; Lipps 1903; McDougall 1908/1923; Meltzoff & Moore 1997). Lipps' theory (1903) 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 1998). 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 & Wellman 1992; Gopnik 1993). 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 Pellegrino 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 simulation theory of empathy (Adolphs et al., 2000; Adolphs 1999; Ruby & Decety 2001; Gallese & Goldman 1998; Iacoboni et al., 1999; Williams et al.; in press; 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 last century, with small upsurges 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, non-human 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 2.4.

2.2. 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 confirms 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 movement 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 Decety 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 1996; 1995; Jeannerod & Frak 1999). Response times (RTs) for imagining walking in a 3-dimensional environment follow Fitt's 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.

2.3. 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 likely 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 section 3.).

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 LeDeux'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 subservise 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 in press). 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, while damage to areas where the memories are stored are more devastating late.

2.4. Emotional evidence for the PAM

2.4.1. 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. 1959). 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 (Miller et al. 1959). 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, Wechkin, & Terris 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 in press). 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 submitted). These subjects correctly matched the video with a picture of an emotional expression in a chimpanzee that had the same valence (Figure 3).

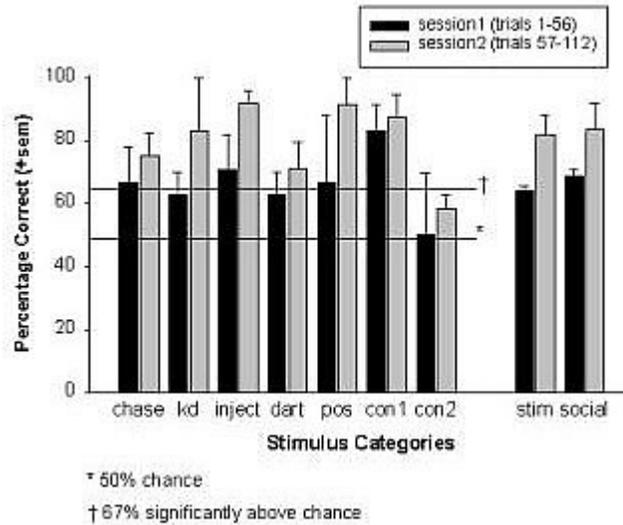


Fig. 3. Mean performance on matching-to-meaning trials on the first and second testing sessions (Parr, in press).

2.4.2. Human developmental evidence

Infant non-human and human primates are known to respond to the distress of others with distress (e.g. Sagi & Hoffman 1976; de Waal 1989). 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 (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, attention to the model, general expressivity of the infant, expression correspondence, and accuracy of an observer of the subject to guess the expression of the object decreased from two to three and four to six months (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. Eimon and Potegal note that the open display of

emotions in 2-year-olds "would be considered pathological in an adult" (1994, 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 (Lhermitte 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 1978; Meltzoff 1993; Meltzoff & Moore 1993), and both are correlated with development of the prefrontal cortex.

2.4.3. Human behavioral evidence

Most behavioral research with humans focuses on the way that representations change with experience. These data are addressed below in section 3. "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.

2.4.4. 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 judgements 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 (Goldman 1992; Gallese & Goldman 1998; 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).

2.4.5. 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 1999; 1992; 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. in press).

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). 20 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 and 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 12 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, the decrease 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.

3. REPRESENTATION AND COGNITION

3.1. 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.

3.1.1. 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 (1915, in Wispé 1987). Hume noted that it is easier to sympathize with someone if you have something in common with that person (1888/1990). 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, etc. 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 in preparation). 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. 1959). 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 in press). Similarly, increased experience is thought necessary for empathy towards differently-abled objects. For example, through learning, non-human primates show increased tolerance towards handicapped individuals. Two chimpanzee juveniles housed with an injured female were anecdotally described to "scrupulously avoided 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. O'Connell 1995; de Waal 1997b).

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 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" (1888/1990; 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). He states: "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 non-primed subject.

3.1.2. 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 (pers. com. from L. Fadiga, in Rizzolatti and 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).

3.1.3. 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.

3.2. 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 1992; 1979; 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 1st 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 non-primate 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; Figure 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; Figure 5).

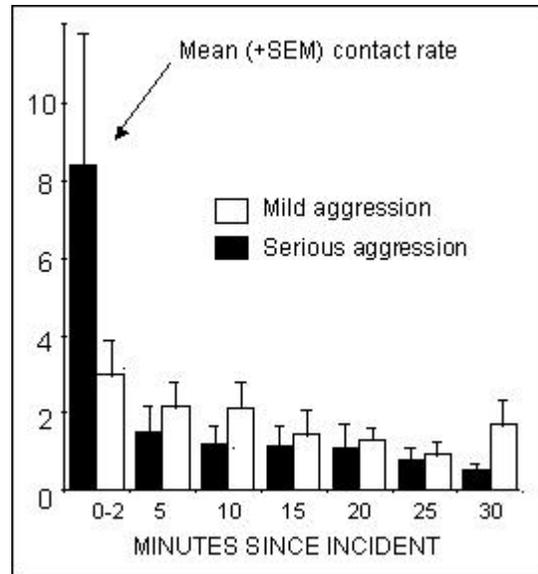


Fig. 4. The rate of friendly contact initiated by bystanders with victims of aggression. Note the extraordinary high rate directed at victims of serious aggression in the first few minutes after the incident. Based on post-conflict observations on captive chimpanzees following agonistic incidents, by de Waal & Aureli, 1996.



Fig. 5. A juvenile chimpanzee comforts a distressed adult.

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 meta-analysis of over 2,000 anecdotal reports of non-human 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 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 reactivity. 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 its absence, remain emotionally distinct from the object, and determine the best course of action for the object's needs.

4. 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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