Review

# Toward a cross-species understanding of empathy

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**Although signs of empathy have now been well documented in non-human primates, only during the past few years have systematic observations suggested that a primal form of empathy exists in rodents. Thus, the study of empathy in animals has started in earnest. Here we review recent studies indicating that rodents are able to share states of fear, and highlight how affective neuroscience approaches to the study of primary-process emotional systems can help to delineate how primal empathy is constituted in mammalian brains. Cross-species evolutionary approaches to understanding the neural circuitry of emotional 'contagion' or 'resonance' between nearby animals, together with the underlying neurochemistries, may help to clarify the origins of human empathy.**

## Introduction

Empathy reflects the capacity of one animal to experience the emotional feelings of another, a process with many cognitive refinements in humans. Thus, investigators commonly distinguish between emotional and cognitive forms of empathy (see below) [1,2]. Studies of empathy make up a relatively new subdiscipline in neuroscience, with human brain imaging providing many correlates of relevant, higher psychological functions [3–5]. Neuroscience research on empathy in other animals has lagged far behind, but simplified animal behavior models based on emotional contagion, the presumed foundations of empathy, have been developed (Figure 1) [6]. Our goal here is to summarize such novel empirical approaches for studying empathy in laboratory rats and mice, and to highlight an integrated neuro-evolutionary strategy for understanding human empathy.

Before proceeding, we consider the meteoric rise of neuro-empathy studies during the past few decades. The study of empathy was sparse in the biologically-oriented sciences of the 20th century until E.O. Wilson's *Sociobiology* (1975), where constructs such as kin selection and reciprocal altruism were seen as major evolutionary explanations for individuals behaving unselfishly, even 'altruistically', toward others, provided that such behaviors supported the survival of one's own genes [7]. Indeed, in *Descent of Man*, Darwin suggested that 'We are thus impelled to relieve the sufferings of another, in order that our own painful feelings may at the same time be relieved' and 'those communities which included the greatest number of the most sympathetic members would flourish best, and rear the greatest number of offspring' ([8], p. 88). Thus, inspired by writings of philosophers such as John Stuart Mill and Adam Smith, together with American social psychologists such as William McDougall [9] and Russian evolutionist Pyotr Kropotkin [10], a prosocial perspective emerged in late 20th century suggesting that individuals might be constitutionally more cooperative and emotionally interdependent than previously considered.

By the late 1990s human brain imaging offered robust approaches for identifying brain regions aroused during emotional states, encouraging systematic neuropsychological studies of empathy [11,12] that have now yielded diverse affective, cognitive, and social neuroscience perspectives [1,13–15]. Concurrently, primatologists recognized signs of empathic sensitivities [16,17] and now neuroscientists, inspired by classic early behavioral studies [18–20], are fashioning reliable simplified models to study the evolutionary roots of empathy (Box 1 and Figure 1)

## The vagaries of 'empathic' terminologies

The term 'empathy' continues to have a diverse as well as nebulous usage, with 'sympathy' and 'compassion' being perennial colloquialisms used to describe related phenomena. One must remember that the term is a recent contribution to the vernacular, emerging in the early 20th century from the Greek *empatheia* (from *em-* 'in' + *pathos* 'feeling') and translated into the German *Einfühlung*, namely 'feeling into', especially when humans aesthetically appreciate the beauty of art. The English version of the term was coined in 1909 by Titchener [21] who was interested in describing the structure of the mind, and was further developed by Lipps [22] to recognize that humans have an intrinsic ability to recognize and appreciate the emotions of others through their bodily gestures and facial expressions.

Considering the variety of definitions and the relatively new intellectual coinage of the concept, all investigators must be careful to specify how they utilize the term. Obviously, the use of words such as 'understand', 'recognize', and 'imagine' can cause considerable problems for cross-species research because those words typically imply a critical role for higher cognitive functions which are

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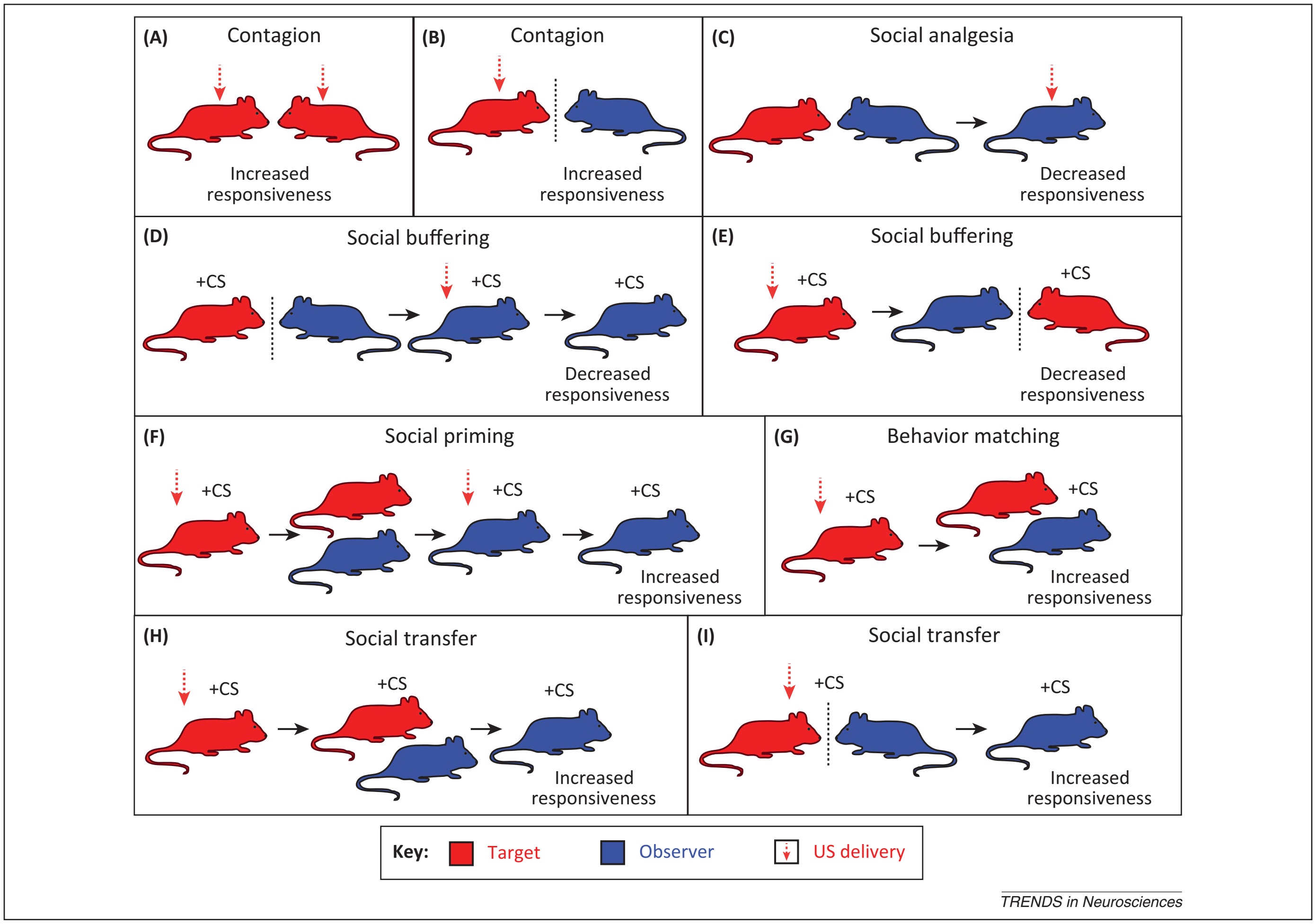


**Figure 1**. Experimental approaches for assessing primal empathy in laboratory rodents. Nearly all of the studies that tap into some aspect of empathy processing in rodents utilize a painful sensory experience that can result in fear. As outlined in this cartoon depiction, the general approach entails presenting a noxious stimulus (often a shock) to a 'target', while an 'observer' witnesses this experience. Measures of behavioral responsiveness in an observer occur during the actual experience, or subsequently when a conditioned stimulus (CS) is presented, or when the target expresses a conditioned response (CR) to the CS. For example, **(A)** mice increase responsiveness to a painful unconditioned stimulus (US) when a familiar conspecific is concurrently exposed [62]. **(B)** Rodents increase freezing or express correlated freezing responses when observing a conspecific receiving a US [38,41,61]. **(C)** Prior social interaction coupled with a subeffective dose of morphine produces thermal analgesia [92], whereas observing a social partner in pain also produces subsequent thermal analgesia [62]. **(D)** Observing a non-fearful conspecific within a context reduces subsequent acquisition of contextual fear [63]. **(E)** The presence of a non-fearful social partner reduces retrieval of a fearful memory [67]. **(F)** Social interaction with a fear-conditioned conspecific increases subsequent acquisition of fear [66]. **(G)** Experienced rats respond to a CR of fear in others with increased freezing behavior [41]. **(H)** The CR of a partner rat is also sufficient to engender subsequent freezing in an observer [68]. **(I)** Mice acquire learned fear and avoidance responses after observing others being conditioned [39,41,69]. Not illustrated above are studies that have explored the role of social factors in fear-extinction (e.g., [64,65]).

difficult to study in animals. In this paper we use the term 'primal empathy' to refer to processes such as emotional contagion and emotional resonance in which there is a convergence of inferred affective states between individuals. This type of 'affect-matching' is monitored via shared emotional behavioral states which can be used as validated proxies of affective experiential states [23], but which do not require the additional ability to reflect cognitively upon one's own states nor upon those of others. Such an approach suggests that primal empathy is a shared neurobehavioral, and we argue a shared neuroaffective, process rather than a unique emotional state *per se*. However, in humans and perhaps particular other mammals (cetaceans? higher primates?), primal empathy may interact with higher cognitive functions, allowing feelings such as compassion or sympathy to emerge (Box 1). Thereby, cross-species approaches to the neural origins of primal empathy may help to clarify how higher (more cognitive) forms of empathy are elaborated in humans.

## Evolutionary affective foundations of empathy: levels of analysis in the brain and mind

Clearly a detailed, constitutive understanding of the mechanisms of empathy must come from cross-species neuroscience. Given the many excellent reviews covering correlative human brain imaging of empathy [3,11,24–27], we focus here on the primal emotional foundations of empathy in mammalian brains. The 'primary-process' emotional systems of the brain, which generate affective feelings (Box 2), are more accessible in animal models than in humans [23,28]. The interaction of primal affective states with 'secondary-process' learning and memory processes may eventually illuminate the higher 'tertiary-process' empathic abilities that are best studied in humans (Box 1).

Such a multi-tiered, cross-species approach to understanding the brain and mind [29] helps to underscore the evolutionary complexities of empathy [4,30,31]. An unparalleled advantage of animal models is the ability to