Neuroscience and Biobehavioral Reviews 35 (2011) 1864–1875

Contents lists available at ScienceDirect

Neuroscience and Biobehavioral Reviews

journal homepage: www.elsevier.com/locate/neubiorev

Review

Rodent empathy and affective neuroscience

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ARTICLE INFO

Article history:
Received 11 October 2010
Received in revised form 24 May 2011
Accepted 27 May 2011

Keywords:
Fear
Pain
Distress
Emotion
Social behavior
Mus musculus
Rattus Norvegicus
Reciprocity
Altruism

ABSTRACT

In the past few years, several experimental studies have suggested that empathy occurs in the social lives of rodents. Thus, rodent behavioral models can now be developed to elucidate the mechanistic substrates of empathy at levels that have heretofore been unavailable. For example, the finding that mice from certain inbred strains express behavioral and physiological responses to conspecific distress, while others do not, underscores that the genetic underpinnings of empathy are specifiable and that they could be harnessed to develop new therapies for human psychosocial impairments. However, the advent of rodent models of empathy is met at the outset with a number of theoretical and semantic problems that are similar to those previously confronted by studies of empathy in humans. The distinct underlying components of empathy must be differentiated from one another and from lay usage of the term. The primary goal of this paper is to review a set of seminal studies that are directly relevant to developing a concept of empathy in rodents. We first consider some of the psychological phenomena that have been associated with empathy, and within this context, we consider the component processes, or endophenotypes of rodent empathy. We then review a series of recent experimental studies that demonstrate the capability of rodents to detect and respond to the affective state of their social partners. We focus primarily on experiments that examine how rodents share affective experiences of fear, but we also highlight how similar types of experimental paradigms can be utilized to evaluate the possibility that rodents share positive affective experiences. Taken together, these studies were inspired by Jaak Panksepp's theory that all mammals are capable of felt affective experiences.

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1. Introduction

Historically, empathy has been considered a high-level affective/cognitive process that is expressed exclusively by humans. However, recent scientific developments have placed this anthropocentric view into question. Prompted in part by the research and writings of primatologist Franz de Waal, more principled and evolutionary based perspectives on empathy have emerged (de Waal, 2008). For instance, it is now generally accepted that many primate species have a capacity for empathy, that empathy can be a proximate mechanism underlying the expression of altruistic behavior, and that empathy is the product of an integrated set of brain processes. Moreover, contemporary views of empathy consider its expression to be a product of several behavioral, affective and cognitive processes, each of which can vary with development, context and species (see below). Deconstructing empathy into specifiable components is useful elucidating the biological substrates that contribute to impairments in social interaction.

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doi:10.1016/j.neubiorev.2011.05.013

In this paper, we consider one core feature of empathy in rodents – the ability to share affective experiences. We review and compare the experimental approaches and results of a series of recent papers that explored different aspects of rodent behavior in response to the distress of conspecifics. Rather than reviewing research on empathy in primates (Davis, 1994; Farrow and Woodruff, 2007; Silk, 2007; Decety, 2010), we examine how shared affect can be modeled in laboratory rats and mice. In this regard, studies of shared affect in rodents can provide a level of biological resolution that has never been achieved in empathy research.

Several of the studies that we describe employ a fear-conditioning paradigm in which an individual is challenged to learn an association between a conditioned stimulus (CS), such as a tone or context, and an unconditioned stimulus (UCS), such as a delivery of a shock. In a standard fear-conditioning paradigm, a subject learns to associate the CS with a UCS that engenders pain. However, many of the studies described herein utilize a very different UCS, a distress cue that has been generated by the induction of pain in *another* individual (Section 4). Consistent with the affective neuroscience approach (Panksepp, 1998), we adopt the perspective that such associations can be learned because changes in an animal's subjective state occur while others are undergoing distress. In this scenario, a subject's subsequent responsiveness to a CS thus reflects its previous emotional experiences with a conspecific in pain.

A basic premise of affective neuroscience is that careful behavioral and neuroanatomical manipulations in the laboratory can yield insights into how affective and cognitive processes are distinct both in terms of their overt expression and their respective neural circuitries (Panksepp, 2005). Through the lens of affective neuroscience, we can envision building a robust framework for elucidating the neurobiological substrates that underlie different aspects of empathy in animals.

1.1. Empathy

The study of empathy is heavily influenced by questions about terminology, and there continues to be an imprecise and therefore confusing usage of the term 'empathy' both in the scientific literature and among the lay public. In this paper, we will not review this literature or how empathy is expressed in humans (readers are referred to MacLean, 1967; Hoffman, 1981; Davis, 1994; Decety, 2010). Rather, we will point out a few salient definitions that can be useful in developing a concept of empathy in rodents.

The word empathy has undergone a substantial evolution in the last century. Lipps (1903) provided the original definition of empathy as a process by which "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." (Preston and de Waal, 2002, pp. 2). During the next one-hundred years, perspectives on empathy were substantially expanded and refined. Some investigators focused on how individuals perceive and respond to the emotional expressions of others. Such approaches emphasized a role for affective arousal, associative learning and motor mimicry (i.e., imitation). More cognitive approaches to studying empathy were based on describing how an individual comes to understand the perspective of another by actively projecting into the psychology of their social partners. Within this context, major questions involved discerning when and how an individual can distinguish self from other, and whether there was an ability to recognize that the perspective of another could be different from one's own. At the highest level, cognitive approaches to empathy focused on language-based abstractions in which certain words could activate emotions in others because they were relevant to a past experience. Moreover, some cognitive approaches considered a role for compassion in the empathic response, which allowed individuals to relate with the emotional state of others even though they did not necessarily share the same state (for an excellent review of different definitions of empathy and its historical evolution see Davis, 1994).

Theoretical developments in empathy research now view the expression of empathy as the result of an interaction between several component processes, both affective and cognitive (Hoffman, 1987; Preston and de Waal, 2002; Decety and Jackson, 2004). Preston and de Waal (2002) hypothesized that these processes utilize an ancient perception–action coupling mechanism in which a subject's attention to the 'state' of another can automatically activate the same state in the subject. Regardless of the underlying mechanism, this model serves as a very useful heuristic insofar that viewing empathy as a psychological phenomenon which stems from several underlying processes offers a practical strategy for employing biological approaches in empathy research. In the rest of this section, we review what some of these component processes are in attempt to clarify our own hypothesis that rodents are capable of sharing affective experiences.

Emotional contagion is a psychological process that is relevant to empathy and refers to a phenomenon in which the perception of a *behavioral* change in an individual appears to automatically activate the same process in another individual. Emotional contagion is thus a reflexive behavioral process among individuals within the context of a motivationally salient event. By definition, contagion requires that two individuals contemporaneously express a behavior that reflects a common experience. Perhaps the most common examples of emotional contagion in humans are infectious crying among babies and yawning among adults. Although emotional contagion fits within a more generally accepted definition of empathy; "the generation of an affective state more appropriate to the situation of another compared to one's own" (Hoffman, 1975), it is excluded from others, particularly when there is an emphasis on the ability to distinguish self from other. Importantly, emotional contagion does not require an ability to discern whether the source of an affective experience comes from one's self or from another individual (Singer and Lamm, 2009).

The ability to distinguish self from other is a key feature of emotional empathy, in which directed attention to another's emotional state can lead to the same state in a subject. Thus, like emotional contagion, emotional empathy involves 'state-matching' between individuals. However, emotional empathy is exclusively concerned with the *affective* state of individuals, as opposed to a reflexive behavioral response. Importantly, because emotional empathy requires an ability to distinguish one's self from another, it can subsequently lead to helping behaviors and also can be engaged by one's personal recollection of an experience (Davis, 1994; Preston and de Waal, 2002).

While emotional empathy inherently requires that two individuals share an affective experience, its expression also can be modulated by cognitive processes. These cognitive aspects of empathy incorporate changes in the emotional state of one individual that are subsequently experienced by another individual after some degree of additional processing (e.g., top–down processing). Examples of this include contextual appraisals, such as integrating past experiences or familiarity, and high-level cognitive phenomena, such as perspective taking (see below). For instance, in some of the studies described in Sections 2–4, responsiveness of a subject is altered if they have had previous experience with the UCS, if they have lived with or share kinship with their social partner, or if their social partner poses a concurrent threat. Moreover, in humans, empathic responses are modulated by a subject's perceived fairness of an individual suffering from a painful stimulus, as well as by gender (Hein and Singer, 2008). In some situations and species, a distinct form of cognitive empathy may be operational, which requires an ability to distinguish that another can