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Review

Effects of pre-pubertal social experiences on the responsiveness of juvenile rats to predator odors

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ABSTRACT

The extent to which social variables may modulate the fear associated with a predator cue was assessed in juvenile rats. Cat odor reduced play to a comparable extent in both socially housed and isolate-housed rats, although socially housed rats exhibited more risk assessment during extinction. Rats that had played previously in the context used for assessing fear hid slightly less when exposed to cat odor than those rats that had not played previously in the testing context. However, no other differences were found between these two groups suggesting that prior social experience with the testing context has minimal effects on fear. In a direct test of a 'social buffering' hypothesis, rats that were tested for contextual fear conditioning in the presence of an unfamiliar partner were less fearful than those rats tested alone. These data are consistent with a social buffering hypothesis and suggest that positive social cues may help animals cope with the threat of predation.

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1. Introduction

Anxiety is one of the most common psychiatric disorders among children, with approximately 9% of all children being diagnosed with some type of anxiety disorder. Anxiety among children and adolescents also appears to have increased in prevalence in recent decades. For example, one recent report (Twenge, 2000) noted a significant increase in the incidence of anxiety among both young adults (college students) and younger school children from 1952 to 1993. In fact, the average anxiety score measured in the 1980s for school-age children was higher than that seen among psychiatric patients in the 1950s. Anxiety in children and adolescents can lead to additional problems, such as difficulty in school, alcohol and drug abuse, and other psychiatric conditions such as depression (Williams and Miller, 2003). Childhood and adolescence is also a vulnerable developmental period during which the foundation for developing an anxiety disorder during adulthood could be established (Heim and Nemeroff, 2001). Until fairly recently, however, little attention has been directed to understanding the phenomenology and neurobiological substrates of fear and anxiety as exhibited by children and adolescents (Heim and Nemeroff, 2001; Kagan, 2001).

The ability to detect situations that should elicit fear and/or anxiety and to exhibit appropriate responses in such situations appears fairly early in development. Using factor analysis, Doremus et al. (2006) determined that adolescent and adult rats exhibit the same constellation of behaviors in the elevated plus maze, suggesting that the underlying processes that lead to anxiety in this model are comparable before and after puberty. While the mechanisms that can lead to anxiety may be present in adolescents, there do seem to be differences in what can elicit anxiety between adolescents and adults. For example, adolescent rats exhibit more anxiety in a light–dark box test (Slawecki, 2005) but fail to exhibit an anxiogenic response in the elevated plus maze following withdrawal from acute alcohol exposure (Doremus et al., 2003). Gender may also be a factor as adolescent male rats will exhibit an anxiolytic response to chronic nicotine administration, while adolescent females have an anxiogenic response to chronic nicotine, as do both adult males and females (Elliott et al., 2004). Stimuli that can produce fear in the young animal also seem to vary somewhat within the age period prior to puberty as well. For example, the presence of an unrelated adult male rat can induce fear, as measured by immobility and analgesia, in rats younger than 14 days of age but not in 26-day-old rats. On the other hand, cat odor is ineffective as a fear stimulus at 14 days of age but produces fear in the 26-day-old rat (Wiedenmayer and Barr, 2001). A subsequent study found that 18-day-old rats exhibit fear towards cat odor that is comparable to that of adult rats (Hubbard et al., 2004). All of this suggests that the neural machinery necessary to elicit fear is fully operational at a fairly early age, although there do seem to be age-related differences with regard to the types of stimuli that can elicit fear and anxiety in rats. These data highlight the importance of using caution when generalizing to the adolescent condition from studies conducted in the adult rat.

While fear circuits appear to be fully engaged by the time of weaning, pre-pubertal rats still engage in a number of behaviors that can easily place them in jeopardy (Laviola et al., 1999; Spear, 2000). As maternal care begins to wane, the young of most mammals also begin to engage in varied forms of play behavior. In the young rat, play generally takes the form of rough-and-tumble wrestling among littermates and same-age conspecifics (Panksepp et al., 1984; Vanderschuren et al., 1997; Pellis and Pellis, 1998; Siviy, 1998; Burghardt, 2005) which begins around the time of weaning, peaks at about 35 days of age, and then slowly wanes around puberty. Rough-and-tumble play is neither subtle nor quiet and, as such, might be expected to increase the likelihood of being detected by predators. As with any behavior, play must occur against a backdrop of everyday threats to survival and is fairly sensitive to disruption by a number of threats such as hunger (Baldwin and Baldwin, 1976; Siviy and Panksepp, 1985), sudden changes in lighting (Siviy and Baliko, 2000), and non-specific stressors such as restraint (Romeo et al., 2006). Fear of predation might also be expected to have an impact on play and, indeed, cat odor has been shown to be a potent inhibitor of play (Panksepp, 1998; Siviy et al., 2006). For example, we found that play was virtually abolished when rats were exposed to the smell of a cat in a familiar testing chamber and remained suppressed for up to 7 days after exposure when returned to the same chamber where the cat odor had been experienced (Siviy et al., 2006). Providing an opportunity to hide had no effect on either the unconditioned or conditioned suppression of play; play was reduced to a comparable extent in rats with or without an opportunity to hide. This highlights the relatively fragile nature of play when faced with a putative threat to survival and suggests that changes in playfulness may be a sensitive barometer for fear and/or anxiety in the young animal.

How an organism responds to threats in the environment may depend to some extent on the social context in which the animal lives and in which that threat is experienced. The social life of young mammals can be fairly rich and social experiences that occur prior to puberty may have a significant impact on how the adult phenotype unfolds (Champagne and Curley, 2005). Before independent locomotion is attained, the primary social contact for the newborn is with the mother and active interactions directed by the mother towards the infant can have a lasting influence on the later development of that infant (Suomi, 1997; Meaney, 2001; Parent et al., 2005). For rats, the quality of maternal care during the first couple of weeks of life seems to be particularly important for laying down a foundation of emotional tone that pups from a particular litter will carry with them as they mature. Rats that are raised by dams that naturally engage in more licking and grooming tend to be less fearful (Menard et al., 2004), are more likely to explore a novel environment (Caldji et al., 1998), and have an attenuated startle response (Zhang et al., 2005) when compared to those raised by dams that engage in less licking and grooming. All in all, these data have shown that increased maternal care during the first couple of weeks of life results in a rat that responds to anxiety-provoking stimuli in a way that suggests lower levels of fearfulness and anxiety (Anisman et al., 1998; Meaney, 2001; Parent et al., 2005).

The effects on offspring that are associated with naturally occurring higher levels of licking and grooming by the mother can be experimentally mimicked through brief periods (e.g., 15 min) of daily separation during the first 2 weeks of life. Since two landmark studies published roughly 50 years ago (Levine et al., 1957; Denenberg and Karas, 1959), a number of studies have characterized the behavioral and hormonal consequences of brief daily separation (Meaney et al., 1991; Boccia and Pedersen, 2001; Brunson et al., 2001). The effects of this manipulation, commonly known as "handling", seem to be due to increased maternal care (i.e., more licking and grooming) induced by the repeated separation and reunion (Caldji et al., 1998; Meaney, 2001, Champagne et al., 2003b; Zhang et al., 2005). In order to determine whether early maternal experiences could have an impact on how young rats deal with a predator threat, we recently assessed the extent to which handling could affect predator odor-induced reductions in play (Siviy and Harrison, 2008). Using a standard protocol for handling (Meaney et al., 1985; Meaney et al., 1991; Meerlo et al., 1999) we separated pups from the dam for 15 min each day from post-natal day 1 through 15. Pups were weaned at