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Rat Pups Reduce Ultrasonic Vocalization After Exposure to an Adult Male Rat

ABSTRACT: We examined how the experience of a threatening stimulus alters subsequent behavior in a situation where the immediate threat is absent. A small huddle of 12-day-old rats was exposed to a potentially infanticidal adult male rat for 5 min. During male exposure, pups were significantly more immobile than control pups. Thirty, 60, and 180 min after male exposure, the pups were isolated for 5 min from litter and dam in an unfamiliar environment. When isolated, pups that had been previously exposed to the male emitted significantly fewer ultrasonic vocalizations than controls, but did not differ in immobility. Low levels of vocalization were apparent 30 and 60 min after male exposure and were not evident at 180 min. The pups seemed to have adjusted their behavior to a potential male threat in a different context for a limited period of time. © 2003 Wiley Periodicals, Inc. *Dev Psychobiol* 42: 386–391, 2003.

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Animals have repertoires of defensive behaviors to respond to threat. Typical defensive behaviors in a variety of species include risk assessment, becoming immobile (freezing), fighting, or escaping (Lima & Dill, 1990). Besides inducing an immediate response, the threatening situation may have enduring effects and lead to changes in the individual's subsequent behaviors. When the individual is confronted with similar or related threatening situations, it may adjust its behavior according to the previous experience. These modifications may therefore provide survival benefits (Alcock, 2001).

It is well known that one single exposure to an extremely aversive, life-threatening situation can have long-lasting consequences and is sufficient to induce behavioral, neural, and endocrine changes for an extended

period of time. Predatory cues, for example, may have a strong impact on the subsequent behavior of adult rats. Rats that were exposed to a cat or to cat odor for a short period of time withdrew into a burrow system and increased risk assessment behavior over the following 24 hr (Blanchard & Blanchard, 1989), hid in a shelter for an extended period of time during the next 24 hr (Dielenberg, Arnold, & McGregor, 1999), and showed increased anxiety-like behaviors in an elevated plus maze for 3 weeks (Adamec & Shallow, 1993). Rats thus seem to alter their behavior in contexts that are different from the situation in which they were threatened, and they also may display behavior patterns not exhibited during the actual exposure (Blanchard & Blanchard, 1989). Such selective modulation of behavior may be adaptive because the animal can maintain behaviors that counter the threat and inhibit behaviors that increase the threat.

Little is known about the impact of a single aversive situation on subsequent behaviors in young rats. A multitude of studies have demonstrated that pups respond immediately to ecologically relevant threatening situations with a coordinated pattern of behavioral responses. Separation from the dam is a life-threatening situation for a preweaning rat. Pups rely heavily on the mother for

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protection, nutrition and warmth (Hofer, 1996). When isolated from littermates and dam in an unfamiliar environment, pups emit ultrasonic vocalizations (USVs) and show exploratory behavior (Hofer & Shair, 1978). USVs direct the searching behavior of the dam and make it more likely that the pup is retrieved (Brunelli, Shair, & Hofer, 1994; Smotherman, Bell, Hershberger, & Coover, 1978). Infanticide is another threat to preweaning rats. A conspecific male that kills unrelated infants can accelerate estrus in the female and increase its own reproductive success (van Schaik, 2000). Although there are no data about infanticide in rats in the wild, laboratory studies have demonstrated a high prevalence of infanticide (Brown, 1986; Jakubowaki & Terkel, 1985; Paul & Kupferschmidt, 1975). When confronted the first time in their life with an unrelated, unfamiliar adult male rat, pups in a nest area immediately stop any activity and become immobile (Wiedenmayer & Barr, 1998). Immobility could decrease detection by the male because males are more attracted to active juveniles (Thor, Wainwright, & Holloway, 1981). When preweaning rats are separated from the dam and littermates and exposed to an adult male rat, they suppress isolation-induced USVs (Takahashi, 1992a,b). Inhibition of USVs may decrease the likelihood that a nearby male detects and attacks the isolated pup (Takahashi, 1992b). USVs remain suppressed for a couple of minutes after the adult male is removed (Brunelli, Masmela, Shair, & Hofer, 1998; Shair, Masmela, Brunelli, & Hofer, 1997). However, it is not known whether threat-induced changes in behavior persist for extended periods of time in rat pups.

The aim of this study was to examine if exposure to a potentially infanticidal male affects the behavior of rat pups subsequent to the encounter in another situation. To determine experience-induced changes in behavior, we first exposed a small huddle of pups to a male rat, mimicking a nest intruder situation when the dam is absent. Thirty, 60, and 180 min after exposure, we placed the pups singly in an unfamiliar environment to mimic the situation when a pup leaves the nest and exposes itself to a potential infanticidal male rat. We hypothesized that previously male-exposed pups would be more immobile and produce fewer USVs when isolated compared to nonexposed pups.

MATERIALS AND METHODS

Animals

Pups were the offspring of Long-Evans hooded rats mated in our laboratory. The parental animals were housed in standard laboratory cages in a colony room maintained at 22 to 24°C with a 12:12 hr light:dark photocycle with light onset at 07:00 h. When the females were pregnant, the males were removed from

the breeding cages. Cages were checked twice daily, at approximately 09:00 and 17:00 h. Pups found at either time were termed 0 days of age. On postnatal Day 12, pups from 12 litters were tested. Eight animals per litter were used. A sexually experienced unfamiliar, unrelated adult male (1 year old) was housed under identical conditions in the same room. Treatments were according to the guidelines of the Institutional Animal Care and Use Committee.

Apparatus

The first part of the experiment was conducted in a translucent polycarbonate laboratory cage (46 × 25 × 21 cm) in a testing room (21–24°C). The cage was subdivided by a wire-mesh partition positioned in the middle of the cage, thereby forming two equal compartments. One compartment was provisioned with soiled wood shavings that had been taken out of the home cage to simulate the nest area. For the second part of the experiment, a smaller translucent polycarbonate laboratory cage (27 × 16 × 14 cm) was used. This testing cage was bedded with new wood shavings and had a cardboard top with a small hole in its center from which the microphone of a bat detector was hung. The microphone was placed in the center of the cage and hung approximately 7.5 cm above the floor of the cage. The USVs were converted into audible signals with an ultrasound bat detector D 230 (frequency division factor 10, Pettersson Elektronik AB, Uppsala, Sweden) set to a broadband mode with a range of 10 to 120 kHz. These audible signals were recorded by depressing a button that silently activated an electronic counter.

Test Procedure

Two groups of three pups were taken randomly from each litter, marked with a nontoxic marker on the fur, and assigned to one of two conditions: control exposed or male exposed. The three pups of a group were placed in the compartment of the testing cage with the soiled bedding. The order of testing of these two groups was alternated between litters. The pups were allowed to acclimate to the testing cage for 10 min. The behavior of the three pups (see *Behavioral Observations*) was recorded during a 5-min test period with either the adjacent compartment empty (control exposed) or with the adult male placed in the adjacent compartment (male exposed). Afterwards, the pups were put back into the home cage in the colony room. After a 30, 60, or 180-min interval, one pup from each group at a time was taken out of the home cage and placed in the second testing cage, an unfamiliar environment. A different pup was tested at each interval in a new cage. Two pups from each group were tested at two different time points. In the interval between the two groups, one pup from a third group from the same litter, control unexposed, was tested. These pups had not been manipulated before. Each pup of the three groups was individually isolated and monitored for USVs using the bat detector. The test was administered for 5 min in which the cumulative count of USVs was taken. In addition to USVs, the behavior of the pup was recorded according to the criteria defined later. All tests were conducted in the first half of the light cycle.

Behavioral Observations

Behavioral inhibition in rat pups consists of cessation of ongoing behavior and taking an immobile posture (Wiedenmayer & Barr, 1998). "Immobile" was defined as any posture in which the animal did not exhibit any movement except that necessary for respiration. The behavior of the pups was recorded by scan sampling (Martin & Bateson, 1993). Every 15 s during the 5-min observation periods, it was recorded if the three pups in the testing cage or the single pup in the unfamiliar cage were immobile. For the control exposed and male exposed groups, a mean was calculated from the scores of the three pups when they were initially exposed. Immobility was expressed in percent of the scans.

Statistics

Immobility and USV data were analyzed by factorial analyses of variance (ANOVA), and Newman-Keuls tests were used for post hoc comparisons. For the immobility data from the initial exposure, the two conditions (control exposed, male exposed) comprised the within-litter variable and were treated as repeated measures. For immobility and USV data from the isolation test, the three trials at 30, 60, and 180 min after exposure were analyzed with separate ANOVAs. The three conditions (control unexposed, control exposed, male exposed) comprised the within-litter variable and were treated as repeated measures.

RESULTS

Initial Exposure

In the presence of the adult male rat, pups stopped ongoing behaviors and became immobile. Male-exposed pups were significantly more immobile than pups without the male in the adjacent compartment, the control exposed group, ANOVA, $F(1, 11) = 179.86$, $p < .001$ (Figure 1).

Isolation in Unfamiliar Environment

Immobility did not differ across the three groups during the three isolation periods in an unfamiliar environment (Figure 1). During the 5-min isolation period, pups emitted USVs (Figure 2). There were significant main effects for isolation-induced USVs 30 min, $F(2, 14) = 4.91$, $p < .05$, and 60 min, $F(2, 14) = 4.49$, $p < 0.05$, after exposure. The pups previously exposed to the male had significantly lower USV rates compared to control exposed and control unexposed pups 30 min ($p < .05$) and 60 min ($p < .05$) after exposure (Figure 2). After 180 min, USVs did not differ across the three groups, $F(2, 14) = 1.17$, $p < .4$.

DISCUSSION

Rat pups that were previously exposed to an adult male rat produced significantly less USVs when isolated in an

FIGURE 1 Immobility (means $\pm$ SE) of 12-day-old rats in a huddle ($N = 72$) during exposure to an adult male rat and 30 ($n = 24$), 60 ($n = 24$), and 180 min ($n = 24$) after exposure during isolation from dam and littermates. Control exposed animals were tested without the male present, and control unexposed animals had not been tested before. *** $p < 0.001$, different from control exposed animals.

unfamiliar environment compared to controls. The pups emitted fewer USVs 30 and 60 min, but not 180 min, after male exposure than controls. Because there were no male cues present in the unfamiliar environment, the low levels of vocalization seem to have been caused

FIGURE 2 Ultrasonic vocalization (means $\pm$ SE) of 12-day-old rats during isolation from dam and littermates 30 ($n = 24$), 60 ($n = 24$), and 180 min ($n = 24$) after male exposure. Control exposed animals had been tested without the male present, and control unexposed animals had not been tested before. Gray bars, control unexposed; open bars, control exposed; black bars, male exposed. * $p < .05$, different from control exposed and control unexposed animals.

by the previous experience itself. This inhibitory effect was not general and did not affect another behavior, immobility, indicating that pups selectively adjusted their behavior to a potential male threat in the unfamiliar situation.

When pups are removed from the dam and nest and placed alone in an unfamiliar environment, they emit high rates of USVs that may last at least 30 min (Hofer & Shair, 1978). Several studies have demonstrated that the presence of conspecifics can modulate isolation-induced USV (Carden & Hofer, 1990; Hofer & Shair, 1978, 1980). For example, when the dam was placed with an isolated pup, the pup suppressed its calling (Hofer & Shair, 1978), but resumed calling at an even higher rate when the dam was removed again (Hofer, Brunelli, Masmela, & Shair, 1996). Such potentiation could make rapid retrieval more likely because a previous encounter with the dam may predict her proximity (Hofer, Masmela, Brunelli, & Shair, 1998). On the other hand, the presence of an adult male rat profoundly inhibits USVs in isolated pups. Isolated 12-day-and-older pups were immobile and suppressed calling when in close proximity to an adult, unfamiliar male (Takahashi, 1992a,b), but not to a familiar or adolescent male (Takahashi, 1994). Modulation of USVs can continue even after removal of conspecifics. Immediately after having been exposed to an anesthetized male, for at least 3 min, 12-day-old pups suppressed USVs (Brunelli et al., 1998; Shair et al., 1997). Our study supports and extends these findings and demonstrates that 12-day-old pups, which had been exposed to an adult male and had spent 30 min with the mother, emitted fewer USVs when subsequently isolated compared to pups not previously exposed to a male. Changes in calling rates such as mother-induced potentiation and male-induced inhibition demonstrate that isolated pups are able to regulate their USVs depending on present and previously perceived social cues.

During the actual exposure to the adult male rat, pups in groups of three were most of the time immobile. Immobility is the predominant defensive response when preweaning rats are exposed to aversive stimuli such as cat odor or cues from male rats (Wiedenmayer & Barr, 2001b). However, during subsequent isolation, immobility did not differ between previously male-exposed and control pups. The prior experience of having encountered a male thus did not simply extend the expression of the initial response in time, but rather seemed to modulate a different behavior, USV, that was elicited by a different situation, the unfamiliar environment. Adult rats modify, subsequent to an aversive experience, particular behaviors in other contexts as well. Adult rats that had been previously exposed to cat cues displayed anxiety-like behaviors in situations, such as the elevated plus maze, that were different from the previous cat-exposure

situation (Adamec & Shallow, 1993; McGregor, Schrama, Ambermoon, & Dielenberg, 2002; Zangrossi & File, 1992).

The differential effect of previous male exposure on USV and immobility needs further consideration. Separate neural pathways seem to underlie responses to threat such as immobility and USV (Bandler & Shipley, 1994). In rat pups, different columns of the midbrain periaqueductal gray (PAG) mediate different behavior patterns. Whereas both the ventrolateral and lateral columns mediate isolation-induced USVs in 12-day-old rats, only the ventrolateral PAG seems to mediate male-induced immobility in 14-day-old pups (Wiedenmayer, Goodwin, & Barr, 2000). Male exposure seems to have affected the two pathways differently as vocalization, but not immobility, was altered after the exposure. A candidate area underlying experience-dependent changes in USV is the amygdala. The amygdala assesses the emotional relevance of stimuli and mediates unconditioned responses to threat (Davis, 2000; LeDoux, 2000). The amygdala also is the locus of experience-induced plasticity (Blair, Schafe, Bauer, Rodrigues, & LeDoux, 2001; Maren, 2001). The amygdala may evaluate signals from sensory pathways during male exposure and pass the signals to brain stem areas such as the PAG (LeDoux, Iwata, Cicchetti, & Reis, 1988), which then mediates the immediate response immobility. At the same time, the amygdala may encode signals that subsequently, in the absence of the aversive stimulus, lead to changes in the USV response. In 14-day-old rats, male exposure activated the lateral amygdala (Wiedenmayer & Barr, 2001a), and in adult rats transmission from the amygdala to the PAG was enhanced after cat exposure, which may have led to the behavioral changes subsequent to exposure (Adamec, Blundell, & Collins, 2001). However, a role of the amygdala in modulating USV has yet to be demonstrated, especially since the amygdala seems to be immature before postnatal Day 12 (Sullivan, Landers, Yeaman, & Wilson, 2000).

The experience of a single aversive event may, under certain circumstances, induce long-lasting changes in behavior. When adult rats were exposed to ecologically relevant threats, such as predator cues, they changed their activity patterns and behavior for a prolonged period of time. A single short exposure to a cat increased anxiety-like behaviors immediately after exposure, and these changes lasted from 24 hr to 3 weeks (Adamec, Kent, Anisman, Shallow, & Merali, 1998; Adamec & Shallow, 1993; Blanchard & Blanchard, 1989). Cat odor alone is a less potent threat as odor-exposed rats displayed less anxiety-like behavior in the elevated plus maze than cat-exposed rats (Adamec et al., 1998). Nevertheless, cat odor induced defensive-hiding and risk-assessment behavior 24 hr after the exposure (Dielenberg et al., 1999;

McGregor et al., 2002). However, even though behavioral changes may be long lasting, they are generally transitory and wane because they reflect trade-offs between threat avoidance and other activities such as foraging (Kavaliers & Choleris, 2001; Lima & Dill, 1990).

In contrast to these adult studies, the inhibitory effect of male exposure on vocalization lasted less than 3 hr in pups. Such a short duration could be explained by infantile amnesia (Campbell & Spear, 1972). In preweaning rats, rate of forgetting tends to be inversely related to age (Spear & Rudy, 1991). Twelve-day-old pups may rapidly forget because brain areas involved in memory formation may still undergo maturational changes. Alternatively, the transitory low levels of USVs in male-exposed rat pups could indicate a trade-off as well. The time that has elapsed since a threat occurred may provide information on the probability that the threat is still nearby (Kotler, 1992). Separation from nest and dam in an unfamiliar environment induces vocalization, which increases the likelihood of retrieval by the dam (Smotherman et al., 1978). Vocalization, on the other hand, could attract infanticidal male rats (Conely & Bell, 1978; Takahashi, 1992a). Low calling rates in pups isolated shortly after having perceived male cues may indicate a trade-off between not attracting the male but still attracting the mother. Three hours after the encounter, the male may not represent a significant threat anymore. In contrast to calling, immobility in isolation did not differ between previously male-exposed and control pups. It could be argued that activities such as locomotion may increase the likelihood to escape the aversive situation, but in contrast to calling, would not attract a distant male.

These findings indicate that a single aversive experience may cause anxiety-like behaviors that are displayed in the absence of the aversive stimulus. Under natural conditions, anxiety-like behaviors may help the animal to be prepared for another encounter with the same threat. The transient nature of low levels of calling indicates that a short male exposure did not affect the rat pups' behavior in a long-lasting way. Rather, the pups seemed to have been able to adjust their behavior temporarily in an unfamiliar situation to a potential threat.

NOTES

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