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Development of “Anchoring” in the Play Fighting of Rats: Evidence for an Adaptive Age-Reversal in the Juvenile Phase

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During play fighting, rats often assume a pinning configuration, where one animal stands over its supine partner. The on-top partner can stand on the ground or on its supine partner with its hind paws. When standing on the ground, the rat is more stable and is better able to respond to its partner's actions. The frequency of this more stable pattern of standing during pinning (called anchoring) is higher following puberty than during the juvenile phase. Two hypotheses explaining this developmental change in anchoring were tested. The first hypothesis maintains that the lower level of anchoring in juvenile rats reflects an immature sensorimotor capability. The second hypothesis suggests that, since rats are more playful as juveniles, such heightened levels of play may interfere with movements otherwise used to maintain the stable anchored position at this age. Neither hypothesis was supported: infants have similar anchoring levels to postpubertal rats, and juveniles have a relatively low level of anchoring irrespective of how frequently they play fight. Therefore, the lower level of anchoring in the juvenile phase appears to be a developmental peculiarity of this age. These findings support the view that play fighting in the juvenile phase may be organized in a manner to increase the occurrence of the experiences that are developmentally beneficial in this activity.

Play fighting in rats, as in other mammals and birds (Fagen, 1981), peaks in frequency in the juvenile stage of development (Thor & Holloway, 1984). However, play fighting also changes in content with age (Biben, 1986; Meaney & Stewart, 1981). In rats, play fighting involves attack and defense of the nape, which, if contacted, is gently nuzzled (Pellis & Pellis, 1987; Siviý & Panksepp, 1987), whereas during serious fighting, bites are directed to the rump and face (Blanchard & Blanchard, 1994; Pellis, 1997). While the target of attack remains the same for play fighting at all ages, juveniles appear to be more gentle in their play than adult rats. This can be explained by the tactics most likely used for defense (Pellis & Pellis, 1990). When contacted on the nape, juveniles more frequently rotate around the long axis of their body to a fully supine position (Pellis & Pellis, 1990). With the onset of puberty, male rats are more likely to rotate only their forequarters, thus keeping ground contact with one or both hind paws (Pellis & Pellis, 1987). During the juvenile period, then, when play fighting is most frequent, the rats are also more likely to roll over and wrestle. That is, they are more likely to exhibit the on-bottom/on-top pinning configuration (Panksepp, 1981). However, even when both juvenile and adult rats perform pins, adult rats still seem more rough.

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In a previous study using Laban Movement Analysis (LMA) to evaluate the age-related increase in roughness during pinning in play fighting, it was found that during pins, juvenile rats are more likely to stand on their supine partner with all four paws (Foroud & Pellis, 2003), rather than maintaining ground contact with their hind paws (i.e., anchored). By doing so, juvenile rats are in a less stable position and so are more likely to fall over as they and their partners move (Foroud & Pellis, 2003). As rats mature from the juvenile (postnatal days 30-40) to the postpubertal phase (50-70 days), the on top rat is more likely to anchor itself during a pin. The most plausible hypotheses to account for this change were tested in this study. Firstly, young animals are motorically less competent (Bâ & Seri, 1995; Pellis & Pellis, 1997), and so may be unable to sustain a stable posture. Reduced anchoring in juveniles may simply represent immaturity of the motor system. Secondly, juveniles are more playful, and when at a heightened state of arousal, they may be less able to organize their movements so as to maintain the stable anchored position. That is, lower levels of anchoring may simply be an effect of hyperactive play fighting.

If the increase in the frequency of anchoring from the juvenile to the postpubertal phase reflects the maturation of motor competence, then infant rats should show low, or even lower, levels of anchoring than juvenile rats. To test this prediction, we assessed anchoring in rats from the infantile (19-29 days) to the juvenile period. If reduced anchoring arises from the result of the heightened frequency of play in juveniles, then anchoring should be negatively correlated with measures of the frequency of play fighting. We used two methods to test this prediction. Firstly, the play fighting of pairs of juveniles was used to ascertain whether more playful animals have lower frequencies of anchoring. Secondly, we made use of the finding that after social isolation, rats engage in more play fighting than those not isolated (Panksepp, 1981; Pellis & Pellis, 1990). This effect is especially marked for rats that are socially isolated from weaning to 30 days (Panksepp, 1981; Panksepp & Beatty, 1980). If anchoring is reduced when rats play fight more often, then isolation-reared rats should have lower levels of anchoring than non isolation-reared rats.

Failure to support these hypotheses provides indirect support for a third possibility. The lower level of anchoring in the juvenile phase may be a programmed developmental change that along with other such changes in the juvenile phase (Pellis, 2002a), provides rats with the experience needed as juveniles to gain appropriate social skills (Pellis, 2002b).

Experiment 1: Anchoring in the Prejuvenile Phase

This study was designed to quantify a rat's frequency of anchoring when pinning a partner during the infantile onset of play fighting (19-24 days; Bolles & Woods, 1964; Pellis & Pellis 1997) and to evaluate any changes in the frequency of anchoring from the postweaning infantile phase (25-30 days) to the juvenile phase (30-40 days).

Method

Subjects. A total of 37 Long Evans hooded rats from three litters were used. Litter 1 had six males and five females, Litter 2 had seven males and six females, Litter 3 had seven males and six

females. Subjects were housed with their mothers until weaning at 22-24 days in 46 cm x 25 cm x 20 cm polyethylene tubs with a 2.5 cm layer of processed corn cob for bedding. At weaning, mothers were removed and the litters were moved into similar, but larger, tubs (46 cm x 42 cm x 20 cm). All animals were maintained on a 12:12 h light:dark cycle (lights on at 07:00 h) and kept at a constant room temperature of 21-23°C. Water and food (Purina rodent chow) were available ad libitum.

Procedure. Two methods were used for videotaping play fights. In the first method, litters were subdivided into male and female groups, and at 19, 20, 21, 22, 23, and 24 days, each same-sex group from each litter was placed in the testing enclosure. Such group testing is important for the youngest ages, as the pups may otherwise be inhibited from playing by the combined novelty of the test enclosure and the separation from their littermates and mother (Pellis & Pellis, 1997). In the second method, at 24, 29, 34, and 39 days, each animal was isolated for 24 h as such isolation has been shown to increase the frequency of play fighting (Panksepp & Beatty, 1980; Pellis & Pellis, 1990). Following isolation, same-sex pairs of rats (9 male pairs, 8 female pairs) were tested. The same pair mates were used at each age.

The floor of the testing enclosure was covered with a 2.5-cm layer of processed corncobs. To ensure a clear view of all body parts and partner orientations, subjects were videotaped from an oblique lateral view with the camera pointing down at an angle of 45°. The testing enclosure (50 cm x 50 cm x 50 cm) had a mirror at the back that further facilitated observation of the otherwise hidden parts of the rats' bodies. The trials lasted 10 min and were videotaped in the dark using the "night shot" function on a Sony 8 mm camcorder. The animals were returned to their home cages following testing.

Data Collection and Analysis. As in a previous study (Foroud & Pellis, 2003), the posture of the on-top rat when pinning a partner was analyzed. While in the on-top position, the rat typically places its forepaws on the on-bottom partner. However, the placement of the hind paws can vary: the rat either stands on the ground or on its partner. When the rat has its hindfeet on the ground, it is referred to as being anchored. To quantify this, the base of support was recorded as an end-point measure during each pin. That is, if at least one of the rat's hind paws maintained ground contact and was weight bearing, the rat was scored as being anchored. If at least one of the rat's hind paws maintained weight bearing contact on the partner during the pin, the rat was scored as not being anchored. During each pin, a rat received a score of 1 for being anchored and a score of 0 for not being anchored during a pin. If a rat alternated between anchoring and not anchoring over the course of one pin, it was scored as 0.5. The average anchoring score was then calculated for each rat, and from these individual averages, the overall average for each group (i.e., age) was calculated. Data for pairs performing at least seven pins per trial were analyzed. Where appropriate, the frequency of playful initiations, where one rat nuzzles the nape of its partner (Pellis & Pellis, 1987), and pinning (Panksepp 1981), were scored. Playful initiations and pins were recorded as the number performed per individual per 10 min. An alpha of 0.05 was used for all statistical tests reported in this paper.

Results and Discussion

Analysis of variance (ANOVA) of the paired infant data showed no significant sex difference; however, a repeated-measure ANOVA revealed a significant age effect, $F(3, 123) = 5.16$; Figure 1. Pairwise comparisons using Fisher's PLSD posthoc tests showed a significant difference between Day 25 and Day 30, between Day 30 and Day 40, and Day 35 and Day 40, but not between Day 25 and Day 35, between Day 30 and Day 35, and between Day 25 and Day 40. That is, the juvenile rats (Day 30) had a lower frequency of anchoring than they had shortly after weaning. That young infants can have a high frequency of anchoring was supported by the group data collected between Days 19 and 24. Too few pins occurred over these days to score individual days, so these days were summed for each litter. Over the three litters, males scored an average of 74% and females an average of 67%. That is, infants anchored themselves more often than juvenile rats (see Foroud & Pellis, 2003).

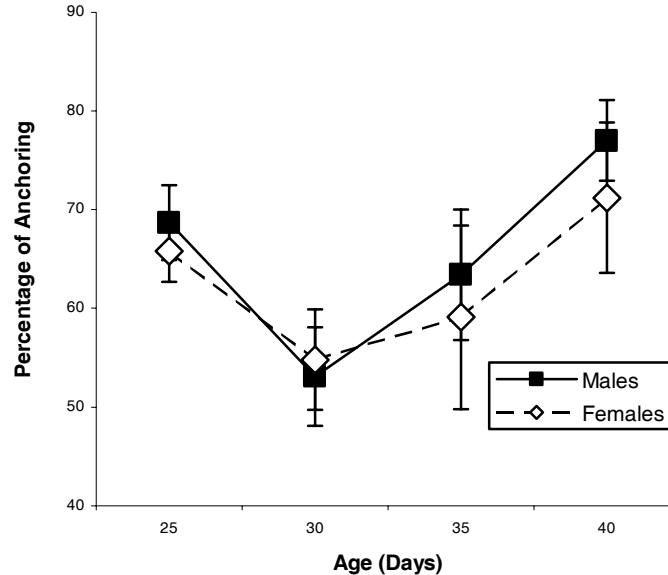


Figure 1. The development of anchoring (means \pm standard error of the mean) from shortly after weaning (25 days) to near the end of the juvenile phase (40 days) in male-male and female-female pairs.

Since infant rats demonstrate higher levels of anchoring than those of juvenile rats, the lack of anchoring in the juvenile phase is most likely not due to motoric incompetence. Rather, it may be that the heightened levels of play experienced during the juvenile phase interfere with movements otherwise used to maintain an anchored position.

Experiment 2a: Do Rats that Engage in more Play Fights Anchor less?

Method

Subjects. Thirty male rats were pair housed at the onset of puberty. Each pair was housed in a 46 cm x 25 cm x 20 cm polyethylene tub with a 2.5 cm layer of processed corncobs for bedding. See Experiment 1 for details on housing and feeding.

Procedure. Subjects were habituated to the testing enclosure for up to 20 min per day for three consecutive days prior to the day of testing. Immediately following the last habituation session, subjects were isolated for 24 h. After the isolation period, each pair was videotaped for a period of 10 min in the testing enclosure. The number of pins per pair was scored, as was the probability of anchoring and the frequency of play initiations for each member of each pair. See Experiment 1 for details on testing and data collection. Unlike Experiment 1, the rats were only tested once in the juvenile phase of development between the ages of 32 and 35 days. The analysis involved comparing the individual scores for anchoring with individual scores for playful initiations and for pair scores of pinning, using Pearson product-moment correlation.

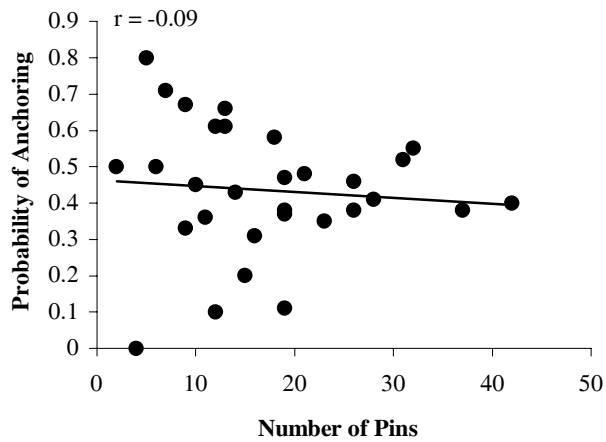
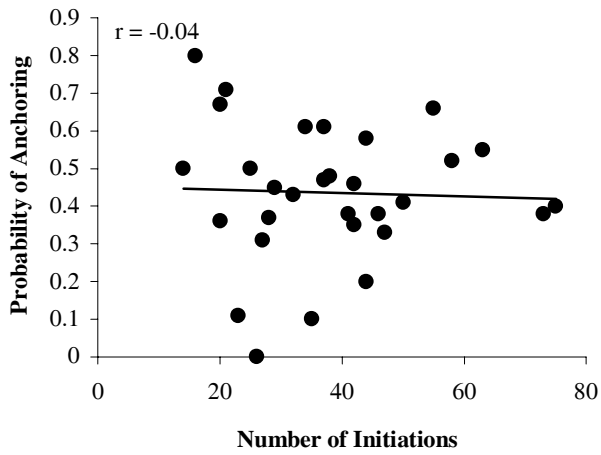
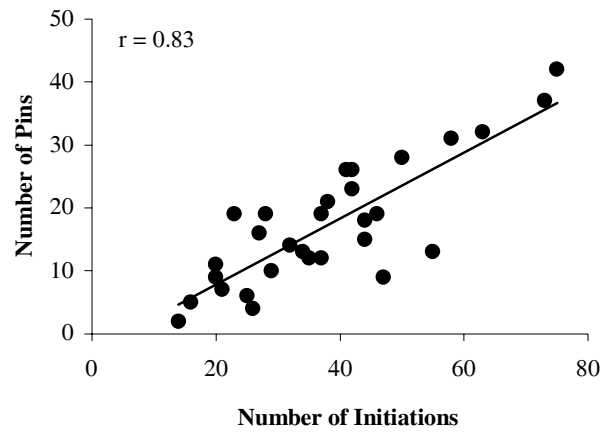


Figure 2. The relationship between the number of playful initiations and of pins (a), the number of playful initiations and the probability of anchoring (b), and the number of pins and the probability of anchoring (c) in juvenile rats.

Results and Discussion

A Pearson's r revealed a significant positive correlation between playful initiations and pinning ($z = 6.24, n = 30$; Figure 2a). This is consistent with previous research (Panksepp, 1981). However, no significant correlations were found for the frequency of anchoring with either the frequency of playful initiations ($z = -0.21, n = 30$; Figure 2b) or the frequency of pinning ($z = -0.47, n = 30$; Figure 2c). Therefore, anchoring does not appear to be less frequent in more playful animals.

Experiment 2b: Does Increasing the Rate of Play Lead to a Reduction in Frequency of Anchoring?

Method

Subjects. Twenty four Long Evans male rats were weaned at 20 days and divided into two groups of twelve. Rats for the control group were housed as pairs in 18 cm x 63.5 cm x 25 cm hanging stainless steel mesh cages, whereas the rats for the experimental group were individually housed in 18 cm x 25 cm x 21 cm hanging stainless steel mesh cages. See Experiment 1 for details on housing and feeding.

Procedure. At around 27 days of age, each subject was individually habituated to the testing enclosure. Prior to testing, subjects from the control group were isolated for 24 h and then placed, with their pairmates, in the testing enclosure. Subjects from the isolation group were also videotaped in pairs, using two isolates to form each pair. See Experiment 1 for details on testing, data collection, and analysis.

Results and Discussion

There was a significantly higher frequency of pinning in isolation-reared rats than in the socially-reared rats (Mean (\pm SEM): 9.64 (\pm 1.56) vs. 4.29 (\pm 0.97); $t(5) = 3.74$); but no significant difference in anchoring, 61.50 (\pm 8.24) vs. 48.76 (\pm 12.91).

Anchoring does not appear to be less frequent in more playful animals. A problem arises, however, when comparing play behavior between isolated and socially-reared rats; the isolated rats are unfamiliar with their pairmates, and so, regardless of isolation, play fighting may be modified due to interacting with an unfamiliar partner (Kahana et al., 1997; Smith et al., 1998; Takahashi, 1986).

Experiment 3: Partner Familiarity and the Frequency of Anchoring

This study was used to determine the effects of interacting with an unfamiliar partner on anchoring. The following experiment compared play fighting in socially-reared rats paired with familiar and unfamiliar partners.

Method

Subjects. Fourteen male rats were pair housed when weaned at 22 days. Each pair was housed in a 46 cm x 25 cm x 20 cm polyethylene tub with a 2.5 cm layer of processed corncobs for bedding. See Experiment 1 for details on housing and feeding.

Procedures. Testing began at 32 days of age, when subjects were tested twice, once with familiar pairmates and once with an unfamiliar same-sex, same-age partner. In each case, the tests

were conducted following 24 h of social isolation. Three pairs were tested with their littermate first and a stranger second, whereas the other four pairs were tested with a stranger first. See Experiment 1 for details on testing, data collection, and analysis.

Results and Discussion

A matched pairs t-test revealed no difference between anchoring occurring with a familiar and unfamiliar partner, 53.01 (± 4.44) vs. 53.15 (± 5.07).

Partner familiarity does not seem to affect the frequency of anchoring in juvenile rats. Therefore, the results of the isolation study (Experiment 2b) were unlikely to be confounded by differences in partner familiarity.

General Discussion

When play fighting, rats attack and defend the nape (Pellis & Pellis, 1987), and many of the movements performed by the participants are explainable in terms of the tactics used to gain or block access to the nape (Pellis, 1988). At any given age, rats seem to be attacking and defending as best as they can (Pellis & Pellis, 1990, 1997). That is, they use the capabilities that they have to the best effect. In the pinning position, the on-top partner uses its limbs to hold and block counterattacks by the on-bottom partner, and then uses moments of advantage to press its own further attacks to its partner's nape (Pellis, 1988). Standing on top of the supine partner with all four paws compromises the ability of the on-top rat to gain and make use of such advantages. That is, while standing on top of the partner with all four paws, the on-top rat has to use its paws to maintain its postural stability in response to both the movements made by its partner and those made by itself (Foroud & Pellis, 2003). Yet, in the juvenile phase, the rats stand on their partner with all four paws more often than is the case with the approach of puberty (Foroud & Pellis, 2003).

One possible explanation for this seemingly poor maneuvering by the juvenile rats is that they lack the sensorimotor skills to position themselves effectively with their hind paws on the ground. In this way, the lower frequency of anchoring may be accounted for by incomplete development of the requisite skills. In the present study, the incidence of anchoring was examined in infant rats during the periweaning period, when play fighting first emerges (Bolles & Wood, 1964; Pellis & Pellis, 1997). The data show that infant rats anchor as frequently as do pubescent and adult rats. In fact, the lower level of anchoring in the juvenile period (between 30-40 days) actually involves a decline from the level present in weanlings. Therefore, the lower level of anchoring in the juvenile period cannot be explained as being due to the incomplete maturation of the sensorimotor system, as younger animals are as capable of exhibiting anchoring as are older ones.

Another possible explanation is that the changes in anchoring arise as a byproduct of the heightened frequency of play fighting in juveniles. That is, anchoring is lowest in the juvenile phase because the hyperplayful animals may be less able to sustain the more stable on top position. The present results do not support this explanation. When comparing individuals, it was not the case that those who play most anchor the least. Similarly, while isolation rearing can increase the frequency of play fighting, it does not affect the age-typical frequency of anchor-

ing. Our data suggest that the likelihood of anchoring is independent of the frequency of play fighting.

Anchoring resembles the age-related modulation in play frequency and switch in playful defensive tactics (Pellis, 2002a), in that its modulation in the juvenile phase occurs whether play fighting with a partner of either sex (Foroud & Pellis, 2003), or whether the partner is a familiar animal or a stranger (this study). Therefore, anchoring appears to have a robust pattern of waxing and waning, occurring at its lowest level in the juvenile phase.

Play fighting in juvenile rats cannot simply be considered as an exaggerated performance of the species-typical behavior patterns present in adult sex and aggression, as may be the case for many other rodents (Pellis & Pellis, 1998b). Instead, play fighting in rats exhibits preprogrammed modulation in its organization that suggests that it may be designed to promote the acquisition of particular experiences. When play is at its most frequent, juveniles are more likely to roll over and wrestle, thus prolonging the play fights and increasing the degree of body-to-body contact (Pellis & Pellis, 1987, 1990, 1997). We have now shown that at this same age, the rat standing on top of the supine partner places itself in such a way as to increase its postural instability, making it more likely that the partner can successfully defend itself and even counterattack (Foroud & Pellis, 2003). The confluence of these design features in the juvenile phase makes it unlikely that they arose by chance – instead, they appear to have the structured organization expected of an adaptation (Williams, 1966). The question is, an adaptation for what?

Some thirty or so functions have been proposed for play (Baldwin, 1986). While it is not clear which of the extant theories (Bekoff & Byers, 1998; Burghardt, 1998) may be supported by the present findings, the greater knowledge that is emerging of the organization and developmental changes occurring in play fighting can be used to test many of these theories. For example, Thompson (1998) posits that play fighting is used to assess one's own prowess relative to that of others. A prediction that emerges from this hypothesis is that an individual should do its best to win the play fight. After all, the proposed function of play in this hypothesis is to assess its relative skill level against that of its peers. Our data on anchoring seems to provide evidence against this hypothesis. By not anchoring itself, the juvenile rat is making it less likely that it will be able to win the contest. However, this conclusion must be viewed as tentative, as it is still not clear what constitutes winning and losing in such contests. Perhaps, instead of competing, the animal is gaining information about itself, for example, how far can it be pushed and how far it is willing to go (Biben, 1998; Pellis & Pellis, 1998b). A fuller understanding of the actions performed during play fighting and how they are modified with age, context, and experience, provides a data base that can be more effectively used to develop decisive tests of specific functional theories.

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