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The Development of Strain Typical Defensive Patterns in the Play Fighting of Laboratory Rats

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During play fighting, rats attack and defend the nape, which if contacted is nuzzled with the snout. While all strains of rats use the same suite of defensive tactics to protect the nape, different strains use some tactics more frequently. This study tests two hypotheses for this strain difference: (1) each strain has a preference for using particular tactics and (2) strain differences in defense are a byproduct of strain differences in patterns of nape attack. Juvenile Long-Evans (LE) and Sprague-Dawley (SD) males, raised in same strain quads from shortly after weaning to the early juvenile period (i.e., 24-31 days), were tested with unfamiliar same-strain and different-strain partners (Experiment 1) and LE and SD males raised in mixed LE-SD quads were tested with both familiar (Experiment 2) and unfamiliar same-strain and different-strain partners. If hypothesis (1) were true, they would maintain strain-typical defense patterns irrespective of the strain of the attacking partner, whereas if hypothesis (2) were true, it would vary with the strain of the attacking partner. Hypothesis (1) was supported in the first experiment; all the rats maintained their strain-typical patterns regardless of the partner's strain. However, Experiments 2 and 3 supported neither hypothesis, as each animal displayed strain-divergent behavior when playing with partners of either strain. Given that in Experiments 2 and 3, subjects were reared in mixed-strain groups, it is possible that, during the early juvenile period, play fighting experiences shape strain-typical patterns of use of defensive tactics.

Play fighting is one of the most commonly studied forms of play behavior in mammals with laboratory rats being one of the most studied species (e.g., Bolles & Woods, 1964; Meaney & Stewart, 1981; Panksepp, Siviy, & Normansell, 1984; Pellis & Pellis, 1998; Vanderschuren, Niesink, & Van Ree, 1997). However, there are many different strains of laboratory rats that are used in experimental research and these have been shown to differ in many features of their behavior (e.g., Pisula, Gonzalez Szwacka, & Rojek, 2003; Pisula, Turlejski, Stryjek, Nalecz-Tolak, Grabiec, & Djavadian, 2012; Prusky, Harker, Douglas, & Whishaw, 2002), including aspects of their play behavior (e.g., Reinhart, Pellis, & McIntyre, 2004; Siviy, Baliko, & Bowers, 1997; Siviy, Love, DeCicco, Giordano, & Seifert, 2003; Siviy, Crawford, Akopian, & Walsh, 2011). Moreover, laboratory strains of rats are domesticated versions of wild rats and domestication is known to change many aspects of physiology and behavior (e.g., Castle, 1947; Coppinger & Coppinger, 2001; Lockard, 1968; Pisula et al., 2012; Takahashi & Blanchard, 1982).

A recent pair of papers used a standardized testing and scoring scheme (B. T. Himmler, Pellis & Pellis, 2013a) to compare the play behavior of four domestic strains to that of a strain of wild rats (B. T. Himmler, Stryjek, Modlinska, Derksen, Pisula, & Pellis, 2013b; S. M. Himmler, Modlinska, Stryjek, Himmler, Pisula, & Pellis, 2014). In both domesticated and wild rats, play fighting involves competition for access to the partner's nape of the neck, which if contacted, is gently nuzzled with the snout (B. T. Himmler et al., 2013b; S. M. Himmler et al., 2014; Pellis & Pellis, 1987; Siviy & Panksepp, 1987).

Competition for the nape not only involves attacking the nape but also the recipient defending its nape from such contact (Pellis & Pellis, 1987). There are two main types of defense that rats can employ when defending against an attack, (a) evasion and (b) facing defense. Evasion involves the defender moving its nape away from its attacker by running, leaping, or pivoting away, and, in so doing, turning its face away from the attacker. Facing defense involves the defending animal turning to face its attacker, while simultaneously withdrawing the nape. In turn, facing defense can take one of two forms: rotating around its longitudinal axis or rotating around a vertical axis. Moreover, rotation around the longitudinal axis can also take one of two forms: rotating fully until the rat is lying supine, or partially, in which the forequarters are rotated toward its

partner, with one or both of its hind feet planted on the ground (B. T. Himmler et al., 2013a). When rotating around the vertical axis, the defender maintains ground contact with all four paws. Rotation around the vertical axis and partial rotation around the longitudinal axis can end in the same configuration if the rats rear up onto their hind feet and face one another (B. T. Himmler et al., 2013a). Facing defenses, especially full rotation to supine, increase the occurrence and duration of body-to-body contact as the animals wrestle one-another, while evasion decreases body contact as the defender withdraws from the attacker.

Like domesticated rats, wild rats use all these tactics during play fighting (B. T. Himmler et al., 2013b; S. M. Himmler et al., 2014). However, wild rats use evasion more frequently and supine defense less frequently than do the domestic strains, but the domestic rats differ from one another in how they differ to the wild rats. The largest strain difference in defensive tactics among the strains compared was between Sprague-Dawley (SD) and Long-Evans (LE) rats. SD used evasion more frequently than facing defense and LE used facing defense more frequently than evasion. Also, when engaging in facing defense, LE used the full rotation to supine tactic more often than SD. Two hypotheses that could account for the strain differences in the use of defense tactics are tested in this paper.

The first hypothesis posits that different strains have a strain-typical bias for using some tactics more frequently than others. An analogy would be with sex-typical behavior. In rats, females are less likely to mount and more likely to exhibit lordosis than males, which exhibit the opposite pattern. The male-typical pattern is established by perinatal hormonal influences on the neural mechanisms that regulate these behaviors (Baum, 1984). The same mechanism of sexual differentiation has been shown to account for the sex-typical differences the frequency of play fighting, with males usually engaging in more play (Meaney, Stewart, & Beatty, 1985). That there may be strain-typical preferences for using certain defense tactics is supported by findings that differences in neural function have been correlated with some aspects of the differences in the play between some strains (e.g., Siviy et al., 2011). Moreover, the bias to use the full rotation to supine defense in LE has been shown to be dependent on a specific area of the brain. Removal of the motor cortex selectively reduces the frequency of rotating to supine (Kamitakahara, Monfils, Forgie, Kolb, & Pellis, 2007). The rats with motor cortex damage attack and defend at the same frequency as intact controls, and like intact LE rats, use facing defense more frequently than evasion. The motor cortex damage-induced change selectively decreases the frequency of using supine defense and increases the frequency of partial rotation. With regard to facing defense, cortex damaged LE rats are like intact SD rats (B. T. Himmler et al., 2013b; S. M. Himmler et al., 2014). Therefore, it is possible that the strain-typical differences in the use of supine defense and evasion in LE and SD may be due to differences in strain-typical neural biases. This is the brain-bias hypothesis.

The second hypothesis does not focus on brain mechanisms regulating the selection of preferred defensive tactics, but rather, on possible differences in the conditions that create the opportunity to use different tactics by different strains. For example, compared to wild rats, domestic strains of rats are less acrobatic and tolerate closer proximity when attacked (B. T. Himmler et al., 2013b, S. M. Himmler et al., 2014). It remains to be determined whether these differences arise from differences in rearing, caging and feeding patterns or from genetic differences. Regardless of their origin, subtle differences in sensorimotor capabilities can have an impact on the execution of behavior patterns in various contexts (e.g., Berridge, 1990; Whishaw, Gorny, Foroud, & Kleim, 2003). The differences between LE and SD rats may make the attack of an LE rat contextually different enough to that of an attack by an SD rat to make supine defense in the former and evasion in the latter the more effective tactics. There is precedent for such sensory and biomechanical factors influencing choice of defense tactics.

During serious fighting, short-bodied species, like hamsters, are more likely to use a rotation to supine tactic to block a bite to the rump, while long-bodied species, like voles, are more likely to use a rotation around a vertical axis (Pellis, 1997). The number of body movements and the time taken to block a bite in these species show that supine defense is faster and more efficient in short-bodied rodents and vertical rotation is

more efficient in long-bodied rodents (Pellis, 1997). A sensorimotor difference affecting the successful use of some defense tactics used during play has been found between male and female LE rats. When attacked directly from the rear, rats are likely to use the vertical axis rotation tactic, but in this attack configuration, females begin to rotate to face when the attacker is further away than do males. This difference in timing of initiation means that females are more successful in facing the attacker before contact is made and so can block the attack in a face-to-face orientation. In contrast, the males, by beginning to turn later, give the attacker time to close the distance and pounce on the back and so contact the nape with the snout, leading the male to turn to supine to withdraw the nape (Pellis, Pellis, & McKenna, 1994). That is, the successful execution of particular tactics may depend on biomechanical factors arising from small sensorimotor differences (Blumberg, 2005), such that attacks by members of a particular strain are more likely to create the context for particular kinds of defensive tactics to be used. This is the biomechanical hypothesis.

In order to test which of these two hypotheses may best explain strain differences in defensive tactics, the present study compared how SD and LE rats defended when attacked by either SD or LE partners. This was done in two ways. First, rats were housed in same-strain quads and then tested in the standard play paradigm (B. T. Himmler et al., 2013a) with unfamiliar partners of the same-strain and the opposite strain (Experiment 1). Second, rats were housed in mixed-strain quads and then tested with either familiar (Experiment 2) or unfamiliar (Experiment 3) same-strain and opposite-strain partners. If the brain hypothesis were correct, then irrespective of the rearing and testing paradigm, all rats should have used strain-typical patterns of defense. If the biomechanical hypothesis were correct, then rats should have used the strain-typical pattern of defense when attacked by same strain partners and some modified version when attacked by opposite strain partners. However, it is possible that rats could undergo experience-based learning, which would enable them to modify their pattern of defense to deal with the idiosyncrasies of the attacks by partners of the opposite strain better. Experiments 2 and 3 should detect such experience-based modifications. Nonetheless, while this modified brain hypothesis would account for experience-based changes in defending against an opposite strain attacker, it would still predict that when defending against a same-strain attacker, the pattern of defense should remain strain-typical. The modification should only occur when rats have had prior experience with opposite strain partners, especially familiar ones.

Method

Subjects

A total of 96 male rats (48 LE and 48 SD) were used. The rats were obtained from Charles River Laboratories (St. Constant, Quebec) around 23 days of age and housed at the Canadian Centre for Behavioral Neuroscience. All subjects were randomly housed in quads with two animals in each serving as the experimental subjects. The quad design was used to allow for a comparative measurement of the experimental animals playing with a partner of the same strain and a partner of the different strain (see below). The rats were maintained at a constant 21-23°C on a 12:12-hour light-dark cycle and were kept in 46cm X 25cm X 20cm polyethylene tubs, with processed corncob bedding. Food and water were provided *ad libitum*. All animals were handled and cared for in accordance with the Canadian Council for Animal Care regulations.

Procedure

Play was tested between 31 and 35 days, which is within the peak period for play behavior in rats (Thor & Holloway, 1984) but before the age at which dominance hierarchies begin to form in males (Pellis & Pellis, 1991; Takahashi & Lore, 1983). For 3 days before play testing, all animals were habituated, in their quads, to the testing enclosure for 30 minutes each day. Short periods of social isolation preceding testing increases the frequency of play fighting (Niesink & van Ree, 1989; Panksepp & Beatty, 1980); the present study used 24 hours of social isolation (B. T. Himmler et al., 2013a). Rats were tested twice, with a 24-hour rest period between the two test days in order to avoid having animals socially isolated longer than 24 hours. Test trials lasted for 10 minutes each, providing enough time to capture most aspects of playful interactions (B. T. Himmler et al., 2013a). Both habituation and testing occurred in complete darkness as it has been shown that social behaviors such as play increase when in the dark compared to light conditions (B. T. Himmler et al., 2013a).

Experiment 1: Same-Strain Rearing and Play with Unfamiliar Partners

Forty-eight rats were divided in 12 quads with each quad composed of rats of the same strain. Two of the rats from each quad were designated the experimental subjects and were tested with unfamiliar rats from other quads – one from the same strain and one from the opposite strain. In this way, one experimental rat from each quad was tested with a same strain partner and one experimental rat was tested with an opposite strain partner. That is, no rat was exposed to the unfamiliar partner more than once, ensuring that the behavior of the rats was not influenced by previous experience with those partners. Three groups were tested with the same strain first, and then a day later with the opposite strain partner, and the other three experimental subjects were tested in the reverse order, so counter-balancing for any order or age effects.

Experiment 2: Mixed-Strain Rearing and Play with Familiar Partners

Twenty-four rats were divided in six quads with each quad composed of two LE and two SD rats. One LE and one SD from each quad were designated the experimental subjects and were tested with the other two quad members. In this way, each experimental rat was tested with an LE and an SD partner. As in Experiment 1, the testing of the quads was counter-balanced.

Experiment 3: Mixed-Strain Rearing and Play with Unfamiliar Partners

Twenty-four rats were divided in six quads with each quad composed of two LE and two SD rats. One LE and one SD from each quad were designated the experimental subjects and were tested with two members from a different quad. In this way, each experimental rat was tested with an LE and an SD partner. As in Experiments 1 and 2, the testing of the quads was counter-balanced.

Equipment

Play trials occurred in a 50cm X 50cm X 50cm plexiglass box encased in a soundproofed chamber (61cm X 61cm X 84cm). The inside of the plexiglass box was filled with 1-2cm of CareFresh® bedding. A DVD103 Sony Handycam was used to film all play trials at a 45° angle using the night-shot option to film in the dark.

Behavioral Analysis

Playful interactions were scored for attack and defense (Pellis & Pellis, 1987). A playful attack was scored when the tip of the snout of one partner was either in contact with its partner's nape or when one partner made a targeted movement towards the nape of the other. The recipient of the attack could either respond to the attack using one of many defenses or simply ignore the attack. Playful defense of the nape could take one of two major forms: (a) evasion, which involves the defender moving its nape away from its attacker and does so by running, jumping, or pivoting away, and (b) facing defense, in which the defender moves its nape away by turning to face its attacker in order to block access to its nape by opposing its teeth between its partner and its own nape. Facing defense can take one of three forms: (a) complete rotation, which involves the defender rolling completely over onto its back, (b) partial rotation, which involves the defender rotating its forequarters while maintaining contact with the ground with one or both of its hind feet, and (c) other, which involves rotations or other movements in other dimensions. The first 2-3 video frames were used to determine the type of defensive tactic first attempted by the defending rat rather than recording the eventual outcome of an attack (Himmler et al., 2013a).

To assess possible cross-strain effects on overall playfulness, the frequency of nape attacks and probability of defense against attacks was recorded (B. T. Himmler et al., 2013a). To test the predictions arising from the two hypotheses, the probability of evasive defense as a proportion of total defense and the probability of supine defense as a proportion of total facing defense was calculated (B. T. Himmler et al., 2013b; S. M. Himmler et al., 2014).

Statistical Analysis

The data were analyzed from both experiments using a two-way analysis of variance (ANOVA), with identity of experimental subject (LE or SD) and identity of the play partner (LE or SD) as independent factors; for significant analyses of variance, the Least Significant Difference test with the Bonferroni correction was used for subsequent pair wise comparisons. Differences were considered significant for p values of ≤ 0.05 . For graphical representation of the data, values are given for group means and standard error.

Validation of Testing Protocols and Behavioral Analyses

The experimenter (Himmler) who performed the behavioral analysis for this study had previously scored with a high degree of inter-observer reliability in two previous studies (B. T. Himmler et al., 2013b; S. M. Himmler et al., 2014). Given the consistency across studies in inter-observer reliability, it can be concluded that any significant differences in the current study were due to differences in manipulation of rearing rather than inconsistent behavioral scoring.

Results

Experiment 1

For all analyses of variance, three factors were compared, the identity of the performer, the identity of the partner and their interaction. A 2 X 2 ANOVA for the frequency of launching nape attacks revealed a significant effect for identity of attacker ($F(1, 20) = 5.780, p = 0.026$), but not for the identity of the partner; nor was there a significant interaction. SD rats launched more nape attacks than LE rats irrespective of the partner's identity (Figure 1a). There were no main effects for the probability of defense ($F(1, 20) = 2.816, p = 0.095$) (Figure 1b).

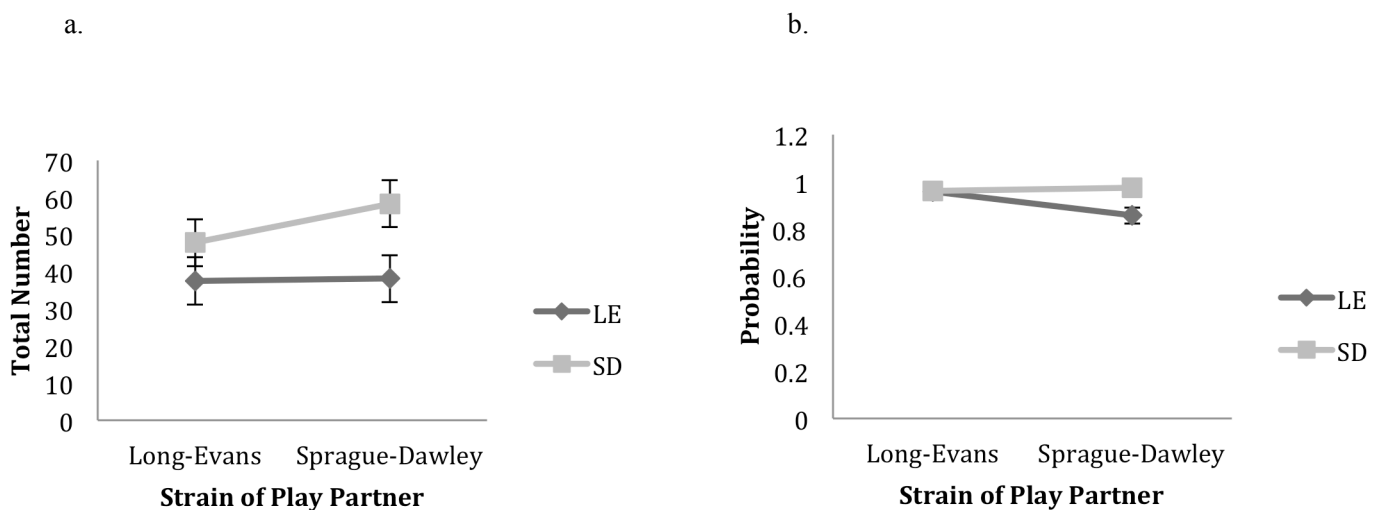


Figure 1. (a). The total number of playful attacks per 10 minute play trial. (b). The probability of defense against a playful attack.

A 2 X 2 ANOVA for the probability that a defending rat would use the complete rotation tactic revealed a significant difference for the identity of the defender ($F(1, 20) = 47.115, p = 0.0001$), but not for the identity of the partner, nor was there an interaction. LE rats were more likely to use the complete rotation tactic than SD rats irrespective of partner (Figure 2a). For the probability that the defending rat would use the evasion tactic there was a significant difference for the identity of the defender ($F(1, 20) = 90.658, p = 0.0001$), and for the identity of the partner ($F(1, 20) = 12.674, p = 0.002$), but there was no significant interaction. SD rats were more likely to use evasive tactics than LE rats irrespective of the identity of the partner (Figure 2b). Moreover, Bonferroni corrected pairwise comparisons showed that being attacked by an SD partner was more likely to lead to evasive defense in both LE and SD rats ($p < 0.05$).

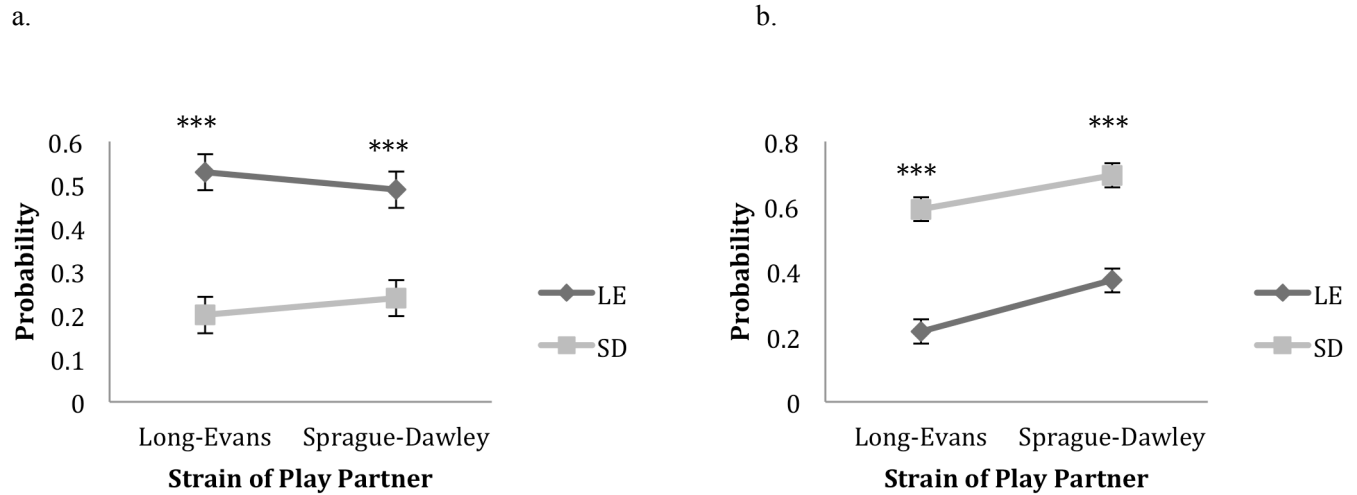


Figure 2. (a). The probability of using the complete rotation defense in response to a playful attack. (b). The probability of using evasive defense tactics in response to a playful attack.

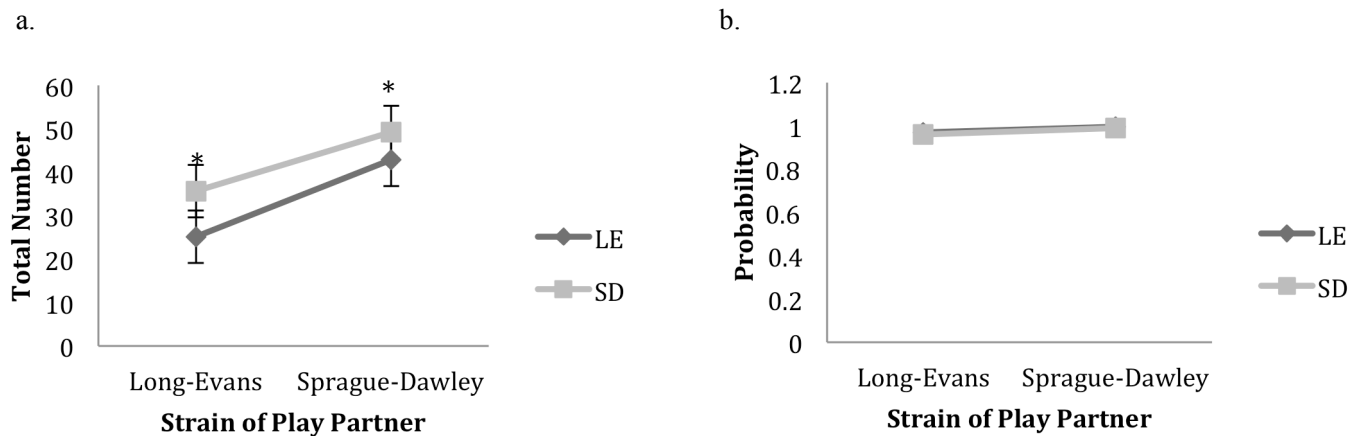


Figure 3. (a). The total number of playful attacks per 10 minute play trial. (b). The probability of defense against a playful attack.

Experiment 2

A 2 X 2 ANOVA for the frequency of launching nape attacks revealed a significant difference for the identity of the attacker ($F(1, 20) = 6.617, p = 0.018$), but not for the identity of the partner; nor was there a significant interaction. SD rats launched more nape attacks irrespective of the identity of the partner (Figure 3a). There were no main effects for the probability of defending against nape attacks ($F(1, 20) = 0.017, p = 0.897$) (Figure 3b).

Similarly, there were no significant differences for the probability that a defending rat would use either the complete rotation tactic ($F(1, 20) = 1.075, p = 0.312$) (Figure 4a) or evasion ($F(1, 20) = 0.173, p = 0.682$) (Figure 4b).

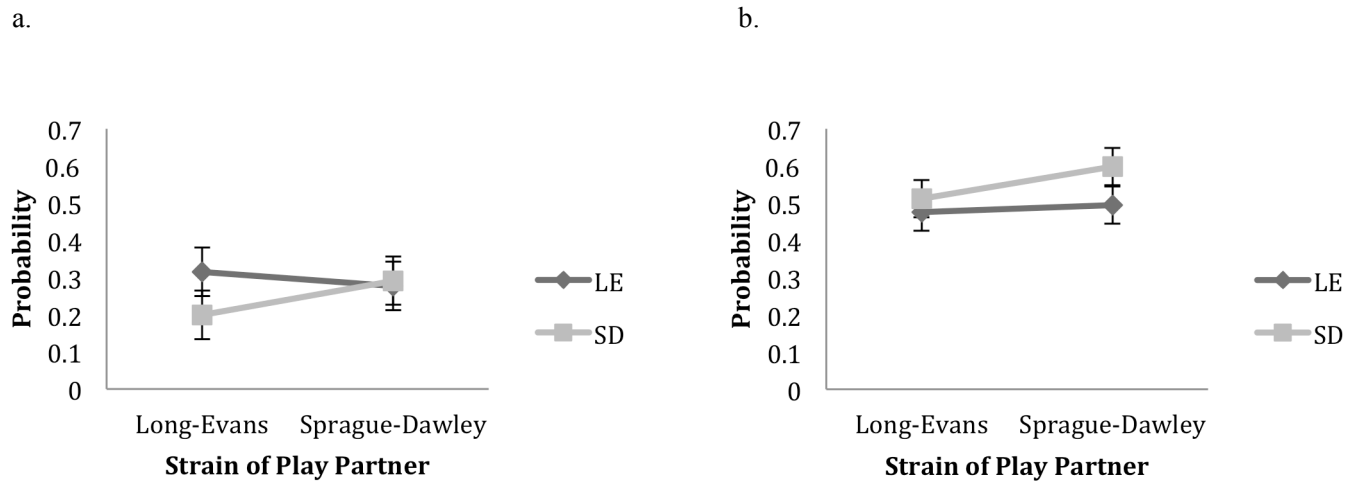


Figure 4. (a). The probability of using the complete rotation defense in response to a playful attack. (b). The probability of using evasive defense tactics in response to a playful attack.

Experiment 3

A 2 X 2 ANOVA for the frequency of launching nape attacks revealed a significant difference for the identity of the attacker ($F(1, 20) = 12.629, p = 0.002$), but not for the identity of the partner; nor was there a significant interaction. SD rats launched more nape attacks irrespective of the identity of the partner (Figure 5a). A 2 X 2 ANOVA for the probability of defending against nape attacks revealed a significant difference for the identity of the attacker ($F(1, 20) = 6.942, p = 0.016$), but not for the identity of the partner, nor was there a significant interaction. SD rats were more likely to defend against a playful attack from either strain of partner (Figure 5b).

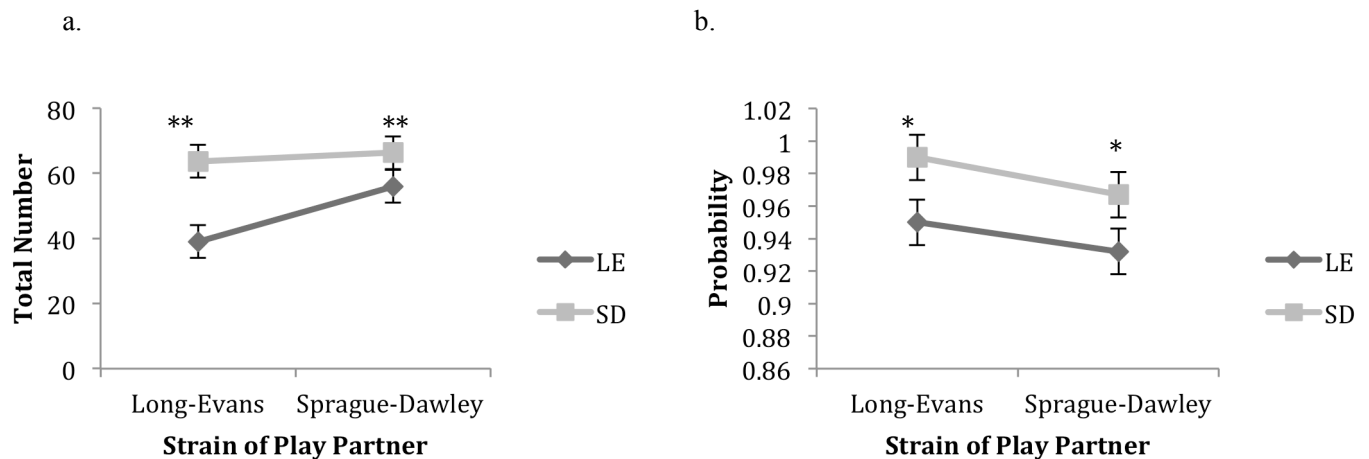


Figure 5. (a). The total number of playful attacks per 10 minute play trial. (b). The probability of defense against a playful attack.

There were no significant differences for the probability that a defending rat would use either the complete rotation tactic ($F(1, 20) = 0.285, p = 0.600$; Figure 6a) or evasion ($F(1, 20) = 1.957, p = 0.177$; Figure 6b).

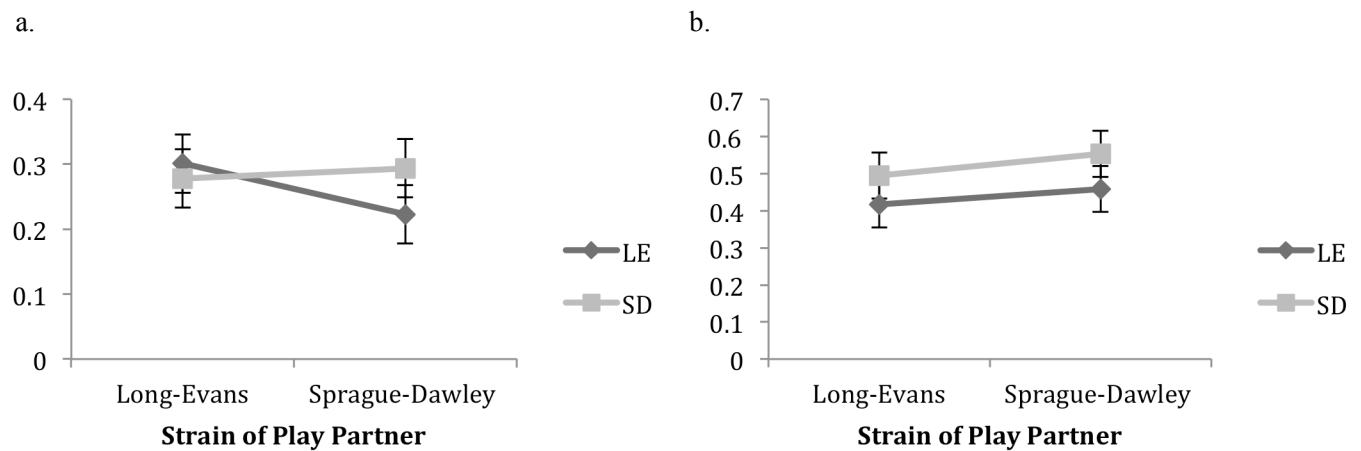


Figure 6. (a). The probability of using the complete rotation defense in response to a playful attack. (b). The probability of using evasive defense tactics in response to a playful attack.

Discussion

The present study was designed to test whether the strain-typical patterns of playful defense in rats is fixed by strain-typical brain mechanisms or arises from strain differences in how partners attack. For motivation to initiate play, as measured by the frequency of nape attacks (Panksepp, 1981; Thor & Holloway, 1983), there were no rearing and testing differences, in all cases SD rats launched more attacks than LE rats. For defensive responses to such attacks, SD rats tended to defend more frequently in all cases, with the difference reaching significance in Experiment 3. Thus, irrespective rearing experience and strain of the partner, with regard to attack and defense, the rate was higher in SD rats as shown in previous studies (B. T. Himmler et al., 2013b; S. M. Himmler et al., 2014). It is how the rats defended themselves that specifically tested whether type of defense is based on a strain-typical preference or a byproduct of how different strains attack.

The findings from Experiment 1 were consistent with the brain hypothesis as all animals maintained their strain-typical patterns of playful defense regardless of the strain of the attacking partner. Although LE rats showed an increase in evasive tactics when playing with an SD partner, this frequency of evasion was not as high as in SD rats. This suggests that, while subtle differences in patterns of attack by different strains may have a small influence on some tactics, the biomechanics of attack is not sufficient to affect the strain-typical preference for using particular defensive tactics. Indeed, the values for percentages of using evasion and supine defense are in the strain-typical range established in previous studies (B. T. Himmler et al., 2013b, S. M. Himmler et al., 2014). This being the case, it would mean that the diversification of defensive tactics among strains following domestication (B. T. Himmler et al., 2013b, S. M. Himmler et al., 2014) would likely have involved differential changes in the neural mechanisms that regulate different facets of play behavior (e.g., Kamitakahara et al., 2007; Siviy et al., 2011). That is, strain differences in defense involve differing biases for use of the different tactics of defense, with the neural mechanisms regulating those biases being changed accordingly. While the results from Experiment 1 clearly support this conclusion, the results from Experiments 2 and 3 suggest that more complex developmental processes in producing strain-typical patterns are involved.

The findings from the second and third experiments were not consistent with either the brain hypothesis or the biomechanical hypothesis. The biomechanical hypothesis predicted that, if strain differences are due to differences in attack styles, then these rats, just like those in Experiment 1, would defend in the

strain-typical manner when tested with a same strain partner, but in a modified form when playing with an opposite strain partner. Given that Experiment 1 was consistent with the brain hypothesis, any change in behavior when defending against opposite strain partners in Experiments 2 and 3 would be more consistent with a modified brain hypothesis – prior experience with the play of the opposite strain modifies how rats defend against strain discordant partners. Thus, defending in a strain-typical way with same strain partners and in non-strain typical ways with opposite strain partners could be consistent with both hypotheses. Yet the changes in defense seen in Experiments 2 and 3 were not predicted by any version of the two hypotheses.

In Experiments 2 and 3, the rats had eight days of cohabitation experience with both same and opposite strain partners before being tested, so providing them with experience of the differences in play typical of the two strains. Yet, while SD rats maintained the higher frequency of attacks and probability of defense compared to LE rats as was seen in same strain reared animals, rats from neither strain maintained their strain-typical patterns of defense. When playing with an LE or SD partner, LE rats displayed lower frequencies of complete rotation and higher frequencies of evasion than seen in LE rats from Experiment 1 and from the previous studies (B. T. Himmler et al., 2013b; Kamitakahara et al., 2007; Pellis & Pellis, 1987). Similarly, when playing with either a LE or SD partner, SD rats displayed higher frequencies of complete rotation and lower frequencies of evasive tactics than SD rats from Experiment 1 and from a previous study (S. M. Himmler et al., 2014).

For Experiments 2 and 3, defensive behavior patterns in both same-strain and different-strain pairings were not strain-typical, but rather, the playful defense of both LE and SD subjects converged at a level intermediate between the two strains (Experiment 1; B. T. Himmler et al., 2013b, S. M. Himmler et al., 2014). This convergence was present whether the rats were tested with familiar (Experiment 2) or unfamiliar (Experiment 3) partners, increasing the likelihood that the difference with the results from Experiment 1 and from previous studies (B. T. Himmler et al., 2013b; S. M. Himmler et al., 2014) was due to the effects of being housed with partners of both strains. These findings suggest that the strain-typical biases for using particular tactics can be modified by social experiences in the first week of the juvenile period.

For LE and SD rats, the strain typical pattern of defense emerges whether housed in same sex pairs, quads or whole, mixed sex litters (e.g., Experiment 1 in this study; B. T. Himmler et al., 2013b, S. M. Himmler 2014; Pellis & Pellis, 1987, 1990, 1997). The critical difference between the rats in Experiments 2 and 3 compared to Experiment 1 appears to be that those rats experienced living with and interacting with rats of both strains from 24-31 days of age. Play fighting begins to emerge in the week preceding weaning at about 16-17 days of age (Bolles & Wood, 1964; Pellis & Pellis, 1997) and reaches its peak frequency of occurrence between 30-35 days of age (Meaney & Stewart, 1981; Panksepp, 1981; Pellis & Pellis, 1990; Thor & Holloway, 1984). Even though playful interactions begin as early as 16 days of age, they do not reach the fully strain-typical pattern until about 30 days of age. In LE rats, patterns of facing defense leading to supine are favored, with the strain-typical pattern of infrequent evasion and highly frequent complete rotation gradually maturing through the weaning to the early juvenile period (Pellis & Pellis, 1997). The early post-weaning period, when the rats were formed in mixed strain quads for Experiments 2 and 3, represents an age when the juvenile-typical pattern of play is still maturing and so may be susceptible to novel social experiences.

The juvenile period is critical for brain and behavioral development, making animals in this stage of life particularly sensitive to a variety of experiences, especially social ones (e.g., Baarendse, Countotte, O'Donnell & Vanderschuren, 2013; Eimon & Morgan, 1977; Eimon, Morgan, & Kibbler, 1978; Hall, 1998; Van den Berg, Hol, Van Ree, Spruijt, Everts, & Koolhaas, 1999; Von Frijtag, Schot, van den Bos, & Spruijt, 2002). A series of studies on the effects of social isolation at different times during post-weaning development not only supports the view that the juvenile period is critical for neurobehavioral development, but that the first week of post-weaning is particularly critical for the development of social behavior (Arakawa, 2002, 2003, 2007a,b). In addition, Meaney and Stewart (1981) compared the play behavior of adult rats reared in mixed sex social groups compared to same sex groups as juveniles. The behavior of the females remained relatively

consistent across rearing conditions, whereas that of the males differed. The males reared in mixed sex groups had a bigger age-related decrease in play than did those reared in same sex groups. In combination, these studies suggest that the type of partners experienced during the juvenile period can affect the development of social behavior and that the early phase of post-weaning is likely a highly critical time for these experiences to affect brain and behavior.

Conclusions

Strain differences in play behavior appear to be determined by brain mechanisms that control preferences for particular patterns of defense, as animals that have been reared with animals of the same strain will exhibit their strain-typical patterns of play regardless of the strain of the partner (Experiment 1). However, brain mechanisms regulating strain differences appear to be vulnerable to change during the early juvenile period - indeed, so much so, that living with a different strain during the early juvenile period produces atypical strain behavior during play (Experiments 2 and 3), further supporting that, during the juvenile period, behavior is modifiable by novel social experiences. Thus, while it can be concluded that strain differences in playful defense do not arise from biomechanical differences but from brain mechanisms regulating biases in tactics used, it is possible that playful experience with same strain partners is necessary for those brain biases to be established.

Acknowledgments

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