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Repeated exposure to social stress alters the development of agonistic behavior in male golden hamsters

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Abstract

In male golden hamsters, exposure to social stress during puberty alters aggressive behavior. Interestingly, agonistic behavior undergoes two major transitions during puberty: a decline in attack frequency and a shift from play fighting to adult-like aggression. Based on previous observations, we developed an approach for characterizing offensive responses as play fighting or adult-like. The present studies had two aims. First, we validated our approach by looking at the development of attack types during puberty. Second, we looked at the effects of repeated social stress on the development of agonistic behavior by repeatedly exposing individuals to aggressive adults during puberty. In the first phase of the study, our results point to three different developmental periods. Initially, animals engage in agonistic behavior though attacks targeted at the face and cheeks. This period lasts from Postnatal Day 20 (P-20) to P-40 (early puberty). This phase corresponding to play fighting is followed by a transitional period characterized by attacks focused on the flanks (from P-40 to P-50, mid-puberty). Afterward, animals perform adult-like aggression characterized by attacks focused on the belly and rear. Our data also show that repeated exposure to aggressive adults has two separate effects on the development of agonistic behavior. Repeated social stress accelerated the onset of adult-like agonistic responses. Furthermore, attack frequency, while decreasing during puberty, remained at a higher level in early adulthood in stressed animals. These results show that repeated exposure to social stress during puberty alters the development of agonistic behavior both qualitatively and quantitatively.

Keywords: Adolescence; Aggression; Play fighting; Puberty; Chronic stress; Flank marking

Introduction

Aggressive behavior can be described as either defensive or offensive. In defensive aggression, animals fight back in response to an attack, while initiating attacks in offensive aggression (Adams, 1979; Blanchard and Blanchard, 1977, 1988). Offensive aggression can be tested in a laboratory using a resident/intruder paradigm in which a smaller and younger conspecific intruder is placed into the home cage of an experimental animal (Miczek, 1979). Male golden hamsters are ideal for studying offensive aggression as they readily attack intruders placed into their home cage. In addition, hamsters start to engage in agonistic behavior with their littermates as soon as they develop motor coordination around Postnatal Day 20 (P-20) (Goldman and Swanson, 1975; Siegel, 1985). As such, hamsters can be useful for studying factors capable of influencing the development of agonistic behavior.

During puberty, offensive responding in male golden hamsters undergoes both quantitative and qualitative transitions. The quantitative transition is best described as a decline in frequency of attacks which peaks early in puberty (P-30 to P-35) and steadily declines until stabilizing during early adulthood (circa P-70) (Goldman and Swanson, 1975; Pellis and Pellis, 1988a). The qualitative change is best described as a transition from play fighting in juveniles to aggression in adults. Play-fighting attacks and bites are focused on the head and cheeks of the intruder (Pellis and Pellis, 1988a,b). In contrast, attacks and bites in adults are

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directed toward the lower belly and rump of the intruder (Pellis and Pellis, 1988a,b). Thus, play fighting in juveniles and aggression in adults have been considered as distinct forms of agonistic behavior.

Previous studies have examined environmental factors capable of influencing the development of offensive aggression in hamsters (Delville, 1999; Delville et al., 1998; Ferris et al., 1998; Harrison et al., 2000; Melloni et al., 1997). For example, repeated exposure to aggressive adults during puberty alters aggressive behavior in a context-dependent manner (Delville et al., 1998). Previously subjugated males are more likely to attack younger and smaller intruders, yet are more likely to avoid their equals. Interestingly, this context-dependent effect occurs only with animals exposed to stress during puberty. Male golden hamsters chronically subjugated during adulthood display conditioned defeat marked by submissive behavior and lack of aggression in the presence on any intruder regardless of size or age (Jasnow et al., 1999; Potegal et al., 1993). These observations point to the existence of a critical developmental period during which stress can enhance offensive aggression.

However, earlier studies did not fully analyze the developmental transition from play fighting in juveniles to aggression in adults. In addition, previously described differences between play fighting and adult attacks were primarily based on bite location. In the current study, we observed the initial site of the intruder targeted rather than initial bite location to differentiate between play fighting by juveniles and aggression by adults. This approach better reflects the behavior of the subjects as bites can be redirected or prevented by the defensive behaviors of the intruder. This study had two major aims. First, we validated observations of targets of attack as an approach for describing the development of offensive responding. Second, we focused on alterations in the development of agonistic behavior caused by repeated exposure to aggressive adults during puberty.

Materials and methods

Animals and treatment

All animals (golden hamsters, Aura strain) were either obtained from a breeding colony housed within the laboratory or purchased from Harlan Sprague–Dawley (Indianapolis, IN). Adult animals were mated in the laboratory. A few days after birth, litters were culled to 6 pups per litter including males and females. Male pups used in experiments (subjects and intruders) were weaned on P-25 and individually housed in Plexiglas cages ($8 \times 13 \times 5$ in). On P-27, all animals were briefly (a few seconds) screened in the presence of an adult intruder. Individuals that fled from the adult immediately (approximately 1 in 12) were classified as inherently fearful and removed from the experiment. All animals were kept under a reversed daylight cycle (14L–10D, lights on at 9:00) and received food and water ad libitum.

Experimental design

Development of aggressive behavior

To determine the normal pattern of the development of agonistic behavior, a group of male golden hamsters (n = 15) was repeatedly tested for offensive responses in the presence of smaller (circa 20%) and younger (3–10 days) conspecific intruders. All behavioral tests lasted for 10 min and were carried out weekly from P-26 to P-68. In order to prevent the establishment of dominant/subordinate relationships, no individual was exposed to the same intruder more than once. During all behavioral tests, the offensive responses of the experimental animal were recorded with a Sony digital video camera for later review using iMovie software. All behavioral tests were performed under dim red light illumination. Body weights were recorded for each animal twice a week.

Social stress

Repeated exposure to social subjugation was performed according to a previously described protocol (Delville et al., 1998; Wommack and Delville, 2002). On P-28 animals were separated into two groups (Subjugated, $n = 19$, and Control, $n = 16$). Attention was taken to ensure that the groups were balanced for litter, body weight, and offensive responses (as screened for on P-28). Animals in the experimental group were placed in the home cage of an aggressive adult male daily for 20 min. All experimental animals were observed during this time to confirm that they were all equally exposed to social subjugation. All subjugated animals were repeatedly chased and bitten by the resident adult hamster, receiving an average of 6.5 bites per day. In addition, each animal displayed about 3 submissive postures daily. Social subjugation was carried out between P-28 and P-42. This developmental period corresponds to the first half of puberty in golden hamsters (Vomachka and Greenwald, 1979). Control animals were placed into empty clean cages for 20 min daily during this same time period. Subjugated and control animals were tested for offensive responses in the presence of smaller (circa 20%) and younger intruders on P-28, P-35, P-45, and P-70. Behavioral testing was conducted prior to any behavior manipulation scheduled for the day in order to prevent any effect of stress exposure on the performance of offensive responses. All animals were weighed twice a week. All behavioral manipulations and tests were performed during the latter portion of the dark phase.

Description of behaviors

During tests and video playbacks, a number of behaviors were observed and recorded including targets of attack, contact time, numbers of attacks, flank marks, bites, retreats,

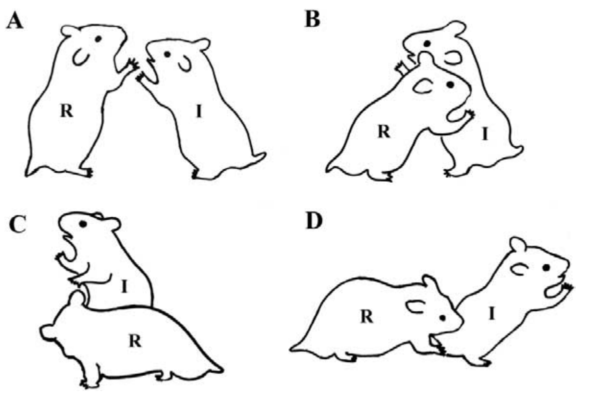

Fig. 1. Drawing representing different types of attacks by a resident (R) on an intruder (I). These different types of attacks are based on the initial target on the body of the intruder: the face and cheeks (A), the side and flanks (B), the lower belly (C), or the rump and rear (D). These attacks were classified as Frontal Attacks (A), Side Attacks (B), and Belly/Rear Attacks (C,D).

and reversals. Contact time was defined as the total duration of the test period during which the resident initiated and maintained contact with the intruder. Attacks were defined as a combination of an approach followed immediately by an attempt to bite. The portion of the intruder initially targeted by the resident during an attack was divided along the anterior/posterior axis of the intruder and placed into several categories: *frontal* (head and cheeks), *side* (including flank glands), and *belly/rear*. The categories of target were inspired by previous studies (Pellis and Pellis, 1988a,b).

Attacks in which the experimental animal initially targeted the face or cheeks of the intruder were scored as *frontal attacks.* During frontal attacks, resident animals attacked the residents straight at their face (Fig. 1A).

Side attacks were defined as attacks in which the experimental animal initially targeted the dorsolateral areas of the intruder's trunk (including the flank glands). The resident would either approach the intruder's trunk from the side (Fig. 1B) or deflect its head sideways and downward while approaching an animal from the front and target the flank glands.

Attacks in which the resident initially targeted the lower belly and rear of the intruder were defined as *belly/rear attacks.* The resident would approach the intruder sideways and roll onto its side or back to target the intruder's lower belly (Fig. 1C). Alternatively, the resident would chase the intruder from behind and target its rump (Fig. 1D).

An additional type of attack was called the *walk-in attack.* Walk-in attacks were typically observed while the intruder was holding a submissive posture on its back as a result of a previous attack. The resident would then walk on top of the intruder and bite it repeatedly anywhere.

Following each test for offensive aggression, the percentage of attacks directed at a specific target (e.g., frontal, side, and belly/rear) was calculated by dividing the number of a specific type of attack by the total number of attacks. For example, the percentage of frontal attacks performed by an individual on a specific test day was calculated by dividing the number of frontal attacks by the total number of attacks performed by an individual on that day [frontal/(frontal + side + belly/rear)]. Walk-in attacks were not used to calculate attack percentages because no specific area of the intruder was consistently targeted by the resident during these attacks. The average of each type of attack was compared between groups.

Data analysis

Parametric data (percentage of attacks, body weights, latencies, and contact times) were analyzed through repeated measure ANOVAs followed by post hoc tests or as contingency tables followed by χ^2 tests (for comparing frequency distributions). In addition, Student's t tests were also used for group comparisons on specific days. Nonparametric data (frequency of behaviors) were analyzed by Mann–Whitney tests (for group comparisons at specific days) and Friedman tests followed by Wilcoxon tests (for time comparisons inside each group). Statistical values were calculated as two-tailed when appropriate.

Results

Development

The frequency of attacks peaked during early puberty (P-33) and steadily declined until stabilizing during the second half of puberty (starting around P-47) (Fig. 2A). This gradual decline was statistically significant [$\chi^2(6) = 42.6$, $P < 0.001$, Friedman]. Post hoc tests showed a significantly higher frequency of attacks on P-33 as compared to P-40 ($P < 0.05$, Wilcoxon), P-47 ($P < 0.01$, Wilcoxon), P-26, P-54, P-61, and P-68 ($P < 0.001$, Wilcoxon). Contact time followed a similar developmental pattern. The highest duration of contact time was observed on P-33. As animals matured, contact time gradually declined after P-33 (Fig. 2B). Changes in contact time during development were statistically significant [$F(6,66) = 5.8$, $P < 0.001$, repeated measure ANOVA]. Post hoc tests showed that the duration of contact time on P-33 was statistically greater than P-26, P-47, P-54, and P-68 ($P < 0.001$, Bonferroni).

The proportion of each attack type followed a distinct pattern of development (Fig. 3). On P-26 and P-33, the majority of attacks were frontal. The proportion of frontal attacks declined steadily until P-54, after which very few were observed. The developmental pattern of belly/rear attacks was opposite to that of frontal attacks. On P-26 and P-33, no belly/rear attacks were observed. Individuals began to direct their attacks toward the belly and rear of the intruders around P-40. The proportion of belly/rear attacks steadily increased until early adulthood. By P-54, most

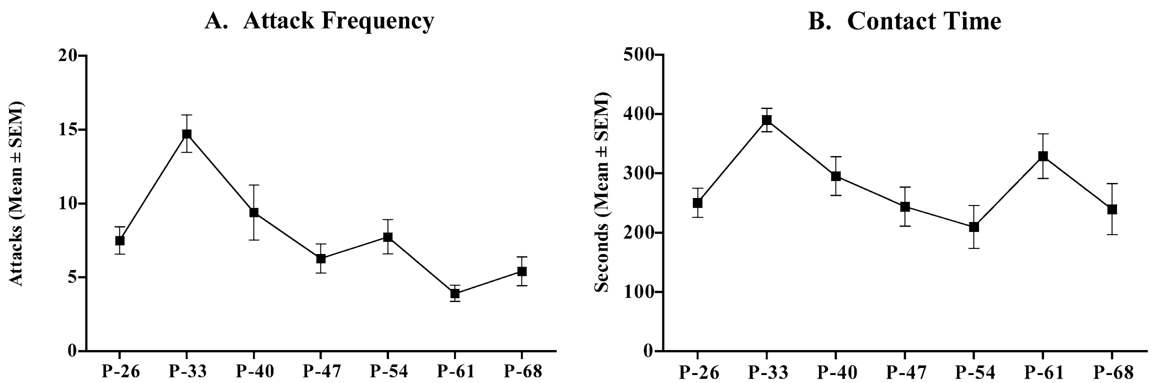

Fig. 2. Developmental changes in Attack Frequency (A) and Contact Time (B) during weekly encounters with an intruder on different postnatal days (P-26, P-33, P-40, P-47, P-54, P-61, and P-68).

attacks were targeted at the belly and rear of the intruder. Side attacks began increasing early during puberty (around P-33). The highest proportions of side attacks were observed on P-40 and P-47. Throughout the remainder of development, the proportion of side attacks decreased. Very few side attacks were observed on P-68. Frequency distributions for each attack type were compared using a contingency table followed by χ^2 analyses. The results from these tests showed that the frequency distributions statistically differed between attack types over time [$\chi^2(12) = 561.5$, $P < 0.001$, Contingency], with each type of attack having a specific frequency distribution ($P < 0.001$, χ^2). These same data were also analyzed using a repeated measure ANOVA. Results from this statistical test showed significant differences between attack types [$F(2,23) = 25.2$, $P < 0.001$, repeated measure ANOVA] and a significant interaction between attack types over time [$F(12,138) = 41.0$, $P < 0.001$), repeated measure ANOVA].

Finally, we also observed flank-marking activity on each day of testing. In particular, flank marking was observed following successful attacks by the residents. However, this behavior was performed with a great deal of variability. Therefore, these data were not analyzed.

Social stress

Prior to any behavioral manipulations (P-28), the average body weight was 56.2 and 56.6 g in the subjugated and control groups, respectively. By P-70, subjugated animals were slightly heavier (5%) than their controls (respectively, 115.7 ± 10.5 and 109.3 ± 11.0 g). The difference was not statistically significant [$t(33) = 0.89$, $P > 0.1$]. A similar difference was previously observed in chronically subjugated hamsters (Delville et al., 1998; Wommack and Delville, 2002).

In both subjugated and control animals, attack frequency steadily declined from its peak at P-35 (Fig. 4A). On P-35 and P-45, there was no statistical difference in attack fre-

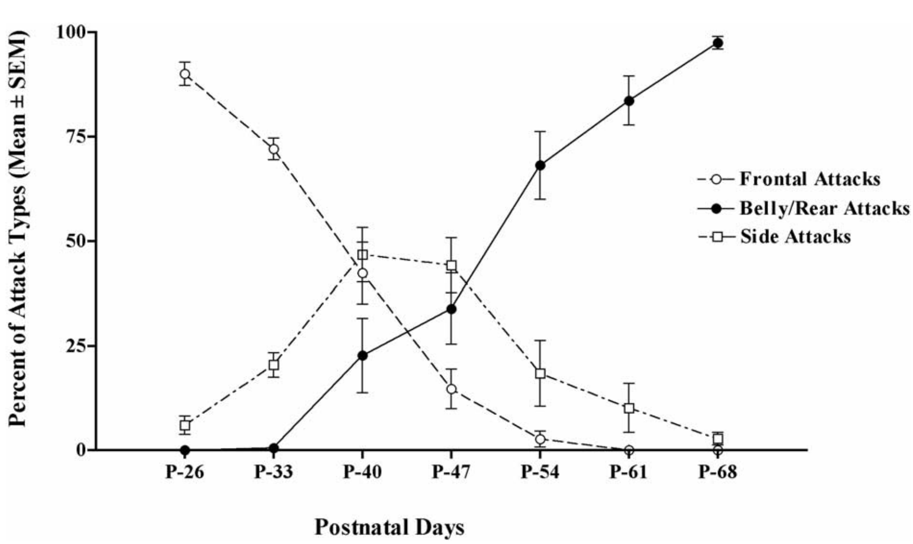

Fig. 3. Developmental changes in percentage of each attack type (Frontal Attacks, Side Attacks, and Belly/Rear Attacks) performed during weekly encounters with an intruder on different postnatal days (P-26, P-33, P-40, P-47, P-54, P-61, and P-68).

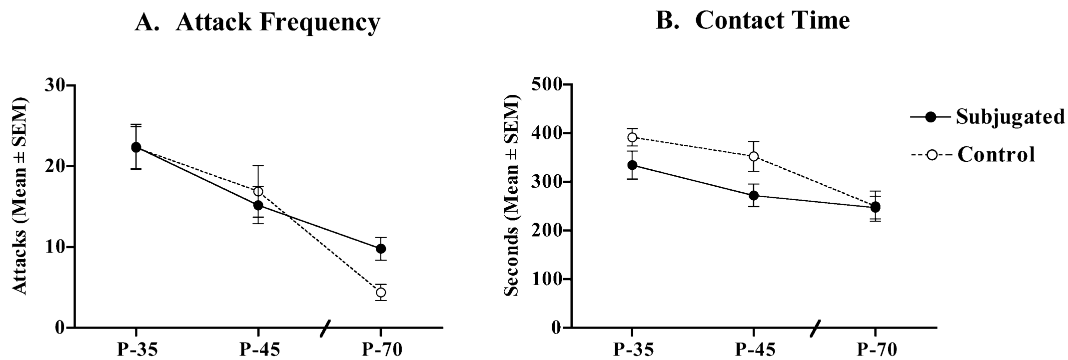

Fig. 4. Effect of repeated exposure to aggressive adults on Attack Frequency (A) and Contact Time (B) during encounters with an intruder on postnatal days 35, 45, and 70. Subjugated animals (Subjugated) were exposed daily to aggressive adults for 20-min periods between Postnatal Days 28 and 42. Control animals (Controls) were placed in an empty clean cage during the same periods.

quency between groups. However, attack frequency remained at a statistically higher level in subjugated animals by P-70 ($U = 65$, $U' = 175$, $P < 0.05$, Mann–Whitney).

Following P-35, contact time steadily declined in both subjugated and control animals (Fig. 4B). The decline in contact time was statistically significant over days [$F(2,58) = 9.2$, $P < 0.001$, repeated measure ANOVA]. However, there was no statistically significant difference between subjugated and control animals, and there was no statistically significant interaction between groups over time [respectively, $F(1,29) = 3.1$, $P > 0.05$; $F(2,58) = 2.0$, $P > 0.1$, repeated measure ANOVA].

In addition, the development of the attack types differed between groups (Fig. 5). The decline in the proportion of frontal attacks started earlier in subjugated animals. Overall, subjugated animals performed a lower proportion of frontal attacks than controls [$F(1,33) = 21.2$, $P < 0.001$, repeated measure ANOVA]. A statistically significant interaction between groups over time was also observed with regards to frontal attack [$F(2,66) = 8.2$, $P < 0.001$, repeated measure ANOVA], as frontal attacks declined faster in subjugated hamsters. Moreover, the onset of belly/rear attacks also started earlier in subjugated animals. Overall, subjugated animals performed a greater proportion of belly/rear attacks than controls [$F(1,33) = 22.2$, $P < 0.001$, repeated measure ANOVA]. The interaction between groups over time was also statistically significant [$F(2,66) = 3.8$, $P < 0.001$, repeated measure ANOVA], as subjugated animals started belly/rear attacks at earlier periods.

Differences in proportions of attack types were analyzed between groups on specific test days using Student's t tests (Fig. 5). On P-35, subjugated animals performed a significantly lower proportion of frontal attacks than controls [$t(33) = 3.09$, $P < 0.01$]. On the same day, subjugated

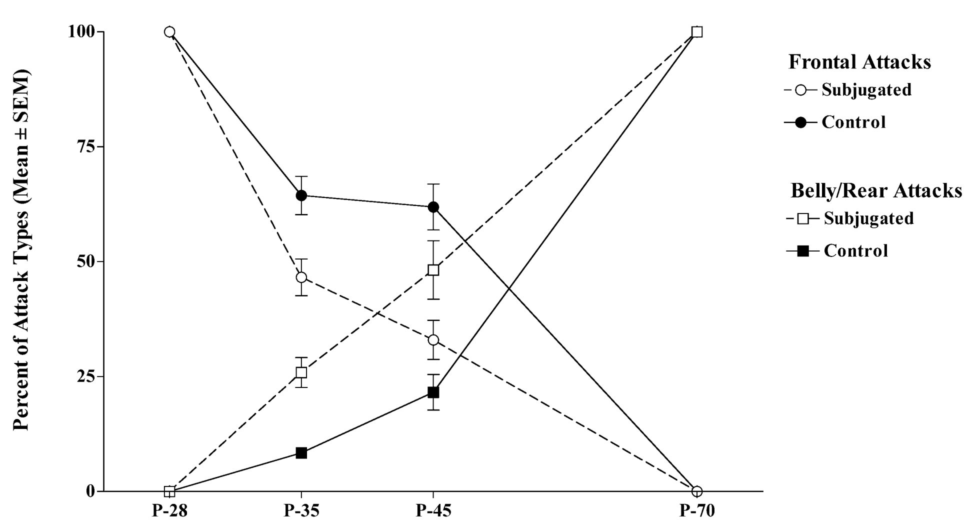

Fig. 5. Effect of repeated exposure to aggressive adults on the proportion of Frontal Attacks and Belly/Rear Attacks performed during encounters with an intruder on Postnatal Days 35 and 45. Subjugated animals (Subjugated) were exposed daily to aggressive adults for 20-min periods between Postnatal Days 28 and 42. Control animals (Controls) were placed in an empty clean cage during the same periods. ***$P < 0.001$, Student's t test.

animals also performed a significantly higher proportion of belly/rear attacks compared to controls on P-35 [$t(33) = 4.56$, $P < 0.001$]. The acceleration of the development of agonistic behaviors caused by repeated stress persisted through puberty (Fig. 5). On P-45, subjugated animals again performed a lower proportion of frontal attacks compared to controls [$t(33) = 3.99$, $P < 0.001$]. The same day, the proportions of belly/rear attacks performed by subjugated individuals was significantly greater than in controls [$t(33) = 3.70$, $P < 0.001$]. No difference was observed between groups with respect to the proportion of side attacks. Furthermore, differences in targets of attack between groups were not analyzed on P-70 as the proportions of belly/rear attacks performed by both subjugated and control animals were near 100%.

It is also important to note that flank marking was observed (usually following a successful attack) in both subjugated and control animals on P-35, P-45, and P-70. However, the variability in this behavior was particularly high and no statistical comparisons were performed between groups.

Discussion

Before testing the effects of repeated social stress on aggression, we first established the normal developmental pattern of this behavior. Our descriptions of the development of agonistic behavior were based on initial target location rather than initial bite location. This approach was validated, as developmental patterns of both attack frequency and attack target corresponded to previous reports (Pellis and Pellis, 1988a). Attack frequency peaked around P-33 and steadily declined until P-47 (Fig. 2A). From P-47 until the end of the study (P-68), levels of attack frequency remained stable. We also observed a gradual shift from frontal attacks to side to belly/rear attacks. This transition from frontal to belly/rear attacks is also consistent with previous observations (Pellis and Pellis, 1988a,b). Previous research in hamsters has identified two periods characterized as either play fighting behavior or adult aggression (Goldman and Swanson, 1975; Pellis and Pellis, 1998a). These two periods were clearly present in our data. However, it could be argued that a third (transitional) period is also present. This period was characterized by an increased proportion of side attacks, as well as reduced play fighting and increasing adult attacks.

As such, the development of offensive responses could be described as follows. First, early in puberty (P-26–P-33), animals perform predominantly frontal attacks. This period of development is recognized by a predominance of frontal attacks and can be characterized as a play fighting period. The second period in the development of agonistic behavior (P-40–P-47) is characterized by a decreasing proportion of frontal attacks, an increasing proportion of belly/rear attacks, and a peak in the proportion of side attacks. This period can best be described as a transitional period as side attacks are characteristic of neither play fighting nor adult-like aggression. It is important to note that the proportion of side attacks is never truly predominant in this phase of development as both frontal attacks and, occasionally, belly/rear attacks are observed during this time. Interestingly, this period of development coincides with rising plasma testosterone levels (Vomachka and Greenwald, 1979). Thus, it could be argued that this behavioral shift is somehow influenced by the many physiological changes associated with puberty and occurring during this transitional period. Finally, during the third period in the development of agonistic behavior (P-54–adulthood), individuals perform mostly belly/rear attacks. Belly/rear of an intruder are the predominant targets of attack in adults (Pellis and Pellis, 1988a,b). This third period could be characterized as the adult period of agonistic behavior. Therefore, it is reasonable to conclude that the development of agonistic behavior is complete by this point. Overall, our observations show that during peripubertal development hamsters change the focus of their attacks from the face and cheeks to the lower belly and rump. This change is gradual, and follows an evolution along the rostrocaudal axis on the opponent's body.

Previous studies on the development of agonistic behavior in golden hamsters have reported a decline in attack frequency from its peak in early puberty (Pellis and Pellis, 1988a). Observations from the current study confirm these reports. Interestingly, a slightly higher attack frequency was observed during the social stress experiment than during the study describing the development of aggression. The causes of these differences are unclear. However, it is important to note that similar patterns of development were observed in both studies. In addition, the duration of contact time initiated and maintained by the resident followed a similar pattern of development. The duration of contact time peaks around P-33 and then declines throughout the remainder of development. This decline in contact time is not a result of habituation, as residents were never exposed to the same intruder more than once. Moreover, the observed decrease in contact time following P-33 is closely associated with puberty in hamsters (Vomachka and Greenwald, 1979). The identification of factors actually causing this effect will be addressed in the future by examining the temporal sequence of agonistic and olfactory behaviors during behavioral testing.

Repeated exposure to social stress during puberty produced both qualitative and quantitative alterations in the development of agonistic behavior. Subjugated male hamsters underwent an accelerated transition from play fighting to adult aggression (Fig. 6). After 1 week of subjugation (P-35) and 10 days thereafter (P-45), the proportion of play-fighting attacks performed by subjugated individuals was lower than that of controls. Also on P-35 and P-45, subjugated animals were more likely than controls to perform adult-like attacks. Interestingly, no differences in attack frequency were observed until P-70. On P-70, previ-

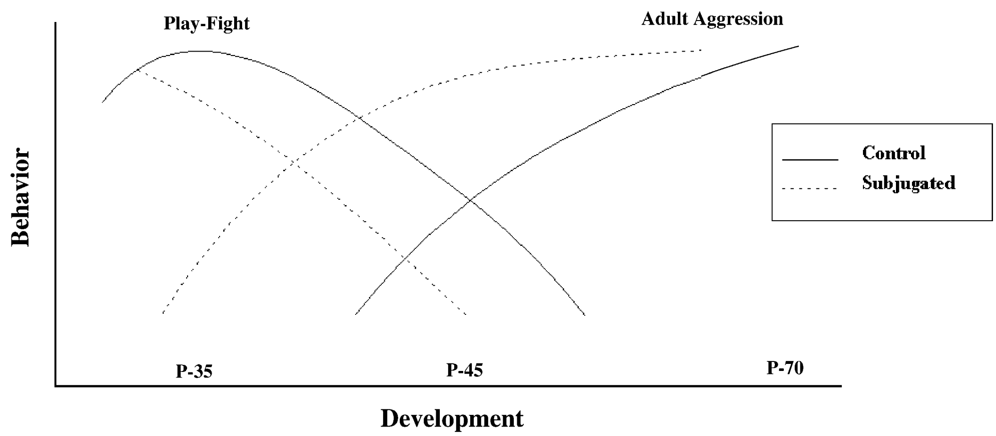

Fig. 6. Schematic model of the developmental transition of agonistic behavior from play fighting to adult-like aggression. Daily exposure (in Subjugated animals) to aggressive adults from P-28 accelerates the development of agonistic behavior in golden hamsters.

ously subjugated individuals were more likely than controls to attack the intruder. This difference can be viewed as a maintenance of higher levels of offensive responding. Future studies will focus on the biological factors responsible for these behavioral alterations.

In the present study, we did not determine the exact nature of the stressor causing these behavioral changes. The behavioral alterations could result from physical stress caused by the repeated attacks and bites. Alternatively, our observations could be related to olfactory stimulation from the cage of the aggressive individuals. These possibilities will be tested in future experiments. Nevertheless, it is likely that the behavioral alterations in subjugated animals were caused by repeated physical stress. We determined the importance of the aggressive adults in pilot studies. Animals exposed to less responsive adults did not differ from their controls (Wommack and Delville, unpublished data). In addition, pilot data show elevated plasma cortisol levels on P-28 for animals in both the subjugated and the control groups (Wommack and Delville, unpublished data). On P-42, however, elevated plasma cortisol levels were only observed in subjugated animals (Wommack and Delville, unpublished data). These findings suggest that somehow (possibly due to physical stress) subjugation is a stressful experience to which an individual is incapable of habituating.

In conclusion, our data validate the use of attack types to characterize the development of agonistic behavior in golden hamsters. In addition, our data show that repeated exposure to aggressive adults during the play-fighting period alters the development of agonistic behavior. We observed an accelerated transition from play fighting to adult aggression. We also observed a maintenance of a higher level of aggression into adulthood. This alteration in the development of agonistic behavior in animals subjugated during puberty may be relevant to human studies on bullying. We would hypothesize that bullying alters the development of concepts of violence in children, resulting in enhanced use of extreme violence by bullied children.

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