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Sensory Modulation of Juvenile Play in Rats

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Sensory Modulation of Juvenile Play in Rats

Abstract

A series of experiments was conducted to determine the extent to which somatosensory stimulation is necessary for the elaboration of juvenile play in rats. Anesthetization of the dorsal body surface of juvenile rats with xylocaine reduced the frequency of pinning, an indicator variable for play, by 35% to 70%, while motivation to play, measured by dorsal contacts, an index of play solicitation, remained largely intact. These data suggest that dorsal body surface anesthetization impairs the ability of juvenile rats to perceive and/or respond to playful gestures. When untreated animals were paired with xylocaine-treated animals, the xylocaine-treated animals consistently pinned the untreated pups more than vice versa, further suggesting that somatosensation may be involved in the establishment and/or maintenance of play dominance relations. A preliminary examination assessing potential involvement of other modalities in the play of rats was also conducted, with the data suggesting a possible role for audition in the play of this species.

Keywords

Xylocaine, Play, Somatosensory Stimulation, Motivation

Disciplines

Behavioral Neurobiology | Molecular and Cellular Neuroscience | Psychology

Sensory Modulation of Juvenile Play in Rats

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A series of experiments was conducted to determine the extent to which somatosensory stimulation is necessary for the elaboration of juvenile play in rats. Anesthetization of the dorsal body surface of juvenile rats with xylocaine reduced the frequency of pinning, an indicator variable for play, by 35% to 70%, while motivation to play, as measured by dorsal contacts, an index of play solicitation, remained largely intact. These data suggest that dorsal body surface anesthetization impairs the ability of juvenile rats to perceive and/or respond to playful gestures. When untreated animals were paired with xylocaine-treated animals, the xylocaine-treated animals consistently pinned the untreated pups more than vice versa, further suggesting that somatosensation may be involved in the establishment and/or maintenance of play dominance relations. A preliminary examination assessing potential involvement of other modalities in the play of rats was also conducted, with the data suggesting a possible role for audition in the play of this species.

Rough-and-tumble play is prevalent among the juveniles of most mammalian species (e.g., Fagen, 1981; Panksepp, Siviy, & Normansell, 1984; Thor & Holloway, 1984). However, little is known concerning the external stimuli which elicit play. In the rat, rough-and-tumble play is characterized by rapidly fluctuating periods of body contact between the two participants, usually resulting in one animal pinning the other (Panksepp & Beatty, 1980; Panksepp, 1981). Given that a pin is a valid indicator variable for play (Panksepp & Beatty, 1980) and is often preceded by rough contact to the dorsal surface of the pinned animal, it seemed reasonable to suppose that somatosensory stimulation may signal playful intentions and, hence, reflect an appetitive phase of juvenile play in this species. Although this observation has been noted by others (e.g., Panksepp & Beatty, 1980; Poole & Fish, 1975; Thor & Holloway, 1983; Wemmer & Fleming, 1974), the involvement of somatosensory stimulation in play has never been empirically evaluated.

Recent work from our laboratory has helped to identify several areas of the brain which may be critical in elaborating the playful behavior of rats and, in doing so, has also provided data which suggest a possible role for somatosensation in

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juvenile play. For instance, one brain region which seems critical for the normal elaboration of play is the parafascicular area of the thalamus (PFA). Specifically, we have found that damage to the PFA results in a consistent 70–80% decrease in the frequency of pinning while having either no effect or only modest effects on other behaviors (Siviy, Panksepp, & White, 1983; Siviy & Panksepp, 1984; 1985a). Given that the PFA receives certain types of somatosensory information (Casey, 1966; Dong, Ryu, & Wagman, 1978; Kruger & Albe-Fessard, 1960) and the amount of somatosensory information which occurs during rough-and-tumble play, it was proposed that pups with PFA lesions may be unable to properly respond to incoming sensory stimuli which normally provoke pinning (Siviy & Panksepp, 1985a).

In preliminary work designed to directly assess the possibility of somatic involvement in play, we observed that when the dorsal surface of juvenile rats was anesthetized with xylocaine, frequency of pinning was significantly reduced, with measures of solicitation being unaffected (Figure 4 in Panksepp et al., 1984). The present series of experiments were designed to further evaluate this initial finding by systematically measuring the extent to which somatosensory information is necessary for the normal elaboration of juvenile play in the rat. In addition, a cursory examination of other sensory modalities was also undertaken.

Experiment 1

In our preliminary work, looking at the effects of dorsal body surface anesthetization on juvenile play, we observed that a 0.2-cc injection of 2% xylocaine to the dorsal surface resulted in a significant reduction in the frequency of pinning in this species. In order to confirm and extend that preliminary finding, the present experiment assessed the effects of a wider range of xylocaine concentrations on play.

Methods

The subjects were 20 male and female juvenile, Long-Evans derived rats bred and born at the BGSU animal facility. Within the first week following birth, the litters were culled to 8 pups each. Animals were housed in a colony room maintained at 25–27°C, with a 12:12 hr light: dark cycle (lights on from 0800 hours to 2000 hours). From birth to the beginning of play testing the rats were group housed with their littermates and mother in $24 \times 40 \times 19$ cm suspended, solidbottom cages with bedding on the floor. Pups were weaned on day 21. During play testing, the pups were housed individually in suspended wire-bottom cages (23 × 10 × 13 cm), with food and water available ad libitum.

Behavioral testing for play was conducted in a $31 \times 31 \times 32$ cm test cage with Lucite walls and approximately 2 to 5 cm of wood shavings on the floor. The test cage is contained within a soundproofed chamber illuminated by a single 25-W red light bulb mounted to one side. The pups were observed through an observation window in the front door of the chamber. All behavioral testing occurred during the light phase of the light : dark cycle.

When the rats were approximately 35 days of age, testing for the effects of xylocaine began. Prior to this time, the animals were allowed to play for 5 min

daily over a period of about a week. Pairings remained the same throughout testing, with pups being tested in same-sex, like-treatment pairs. Four concentrations of xylocaine, in addition to the vehicle (0.9% saline), were tested: 0.5, 1.0, 2.0, and 4.0% (w/v). Order of treatment was counterbalanced in a Latin-square fashion with testing occurring over 5 consecutive days. On each day of testing, animals were injected subcutaneously with 0.2 cc of their assigned concentration for that day, 15 min before a 5-min play session. Four injections, 0.05 cc each, were given, 2 on the dorsal surface just posterior to the ears (approximately 0.5 cm from midline), and 2 at the level of the clavicle (approximately 1.0 cm from midline).

The number of times each animal pinned the other was recorded by means of a digital counter. A pin is defined as occurring when one pup is on its dorsal surface with the other pup on top. The frequency of dorsal contacts for each animal was also recorded. A dorsal contact is defined as occurring when one animal makes contact with any portion of its ventral surface (e.g., mouth, paws) onto the dorsal surface of its partner (tails being excluded). In order to exclude investigatory responses, contacts in the anogenital region were not included in this category. This measure is essentially a composite of the three measures of play solicitation suggested by Thor and Holloway (1983). These were combined since attempting to make similar distinctions on-line during the fury of rough-and-tumble play proved difficult and threatened to impair overall accuracy of measurements. Therefore, frequency of dorsal contacts was taken as an overall index of solicitive behavior.

Results and Discussion

Treatment of the dorsal body surface of juvenile rats with xylocaine resulted in a concentration-dependent reduction in the frequency of pinning (Fig. 1). The effect of xylocaine was not dependent upon gender, so all subsequent data were analyzed irrespective of sex (also see Panksepp et al., 1984). Analysis of these data yielded an F(4,76) = 40.34 (p < .001), with frequency of pinning at the 2 higher concentrations differing reliably from control (p < .05, Newman-Keuls test). Frequency of pinning following treatment with the two lower concentrations of xylocaine (0.5 and 1.0%) did not differ reliably from control. Frequency of dorsal contacts also varied as a function of xylocaine concentration (F(4,76) =11.45, p < .001). However, only the highest concentration (4.0%) was found to differ reliably from control values, resulting in a 35% decrease in dorsal contacts. Although not differing reliably from control, there was a slight trend for the lower three concentrations of xylocaine to increase dorsal contacts.

These data confirm our preliminary findings, which demonstrated a reduction in the frequency of pinning following dorsal body surface anesthetization with xylocaine. Furthermore, these data demonstrate that the minimally effective concentration of xylocaine, based on the dose range and injection procedure currently employed, lies somewhere between 1.0 and 2.0%. In addition, the marked decrease in both pinning and dorsal contacts seen following the highest concentration (4.0%) suggests that this concentration is perhaps resulting in some non-specific impairment (perhaps of motor functions), in addition to resulting in local anesthesia. Although no systematic evaluation was made of their motoric abilities, the animals did seem somewhat sluggish following 4% xylocaine.

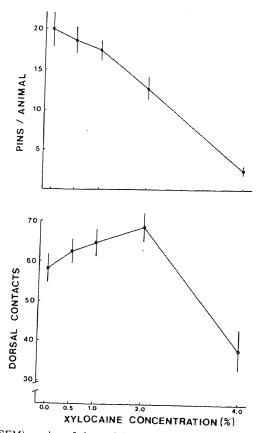


Fig. 1. Mean (\pm SEM) number of pins and dorsal contacts during a 5-min test session following various concentrations of xylocaine.

Experiment 2

In the previous experiment, most of the anterior dorsal surface of the pups was presumably anesthetized. The present experiment was designed to determine whether the effect of xylocaine on pinning could be localized to a relatively specific body region. Accordingly, xylocaine was administered at anterior and posterior dorsal sites, anterior and posterior ventral sites, and also intraperitoneally.

Methods

Twenty-four juvenile rats served as subjects. Animals were housed individually beginning on postnatal day 24 and given a 5-min daily opportunity to play, as described in Experiment 1. Days 25, 26, and 27 served as adaptation days, with no behavior being recorded. On days 28, 29, and 30, animals were tested for play following three dorsal treatment conditions (i) 0.9% saline, (ii) 2% xylocaine injected subcutaneously via 2 punctures (0.1 cc each, each placed approximately 1 cm from midline) between the clavicle and ears (anterior injection), and (iii) 2% xylocaine injected via 2 comparable punctures in the animals' hindquarters (poste-

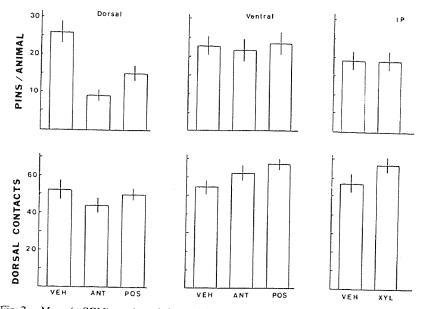


Fig. 2. Mean (\pm SEM) number of pins and dorsal contacts following 2% xylocaine when injected on either the dorsal body surface, ventral body surface, or injected intraperitoneally (IP). Abbreviations: VEH = vehicle, 0.9% saline; ANT = anterior injection site; POS = posterior injection site.

rior injections). Order of treatment was counterbalanced in a Latin-square fashion. On days 31 and 32, no injections were given prior to the 5-min play session. On days 33, 34, and 35, animals were tested for play following 3 ventral treatment conditions: (i) 0.9% saline, (ii) 2% xylocaine injected subcutaneously via two punctures (0.1 cc each) on either side of the rib cage at the level of the sternum, and (iii) 2% xylocaine injected via two punctures in the pelvic/peritoneal region. On days 36 and 37, no injections were given prior to the 5-min play session. Finally, to evaluate whether any of the observed effects may be due to some central rather than local anesthetic properties of xylocaine, the effects of xylocaine (0.2 cc of 2% solution) administered intraperitoneally (IP) were compared to vehicle on days 38 and 39 (counterbalanced). As before, all tests were done on same-sex and like-treatment pairs.

Results and Discussion

As shown in Figure 2, injections of xylocaine to anterior- or posterior-dorsal sites significantly reduced pinning by 66% and 42%, respectively (F(2,30) = 15.68, p < .001). While both treatment conditions differed significantly from control (p < 05, Newman-Keuls test), they did not differ reliably from each other. Dorsal njections of xylocaine did not reliably affect frequency of dorsal contacts. Ventral njections were without effect on frequency of pinning or dorsal contacts F's(2,30) < 1.2). IP injections had no effect on pinning (t(15) < 1.0), but did yield 1 reliable 17% increase in dorsal contacts (t(15) = 2.19, p < .05).

As before, subcutaneous injections of xylocaine to the dorsal body surface educed frequency of pinning. Although number of pins following anterior-dorsal ind posterior-dorsal injections did not differ significantly from each other, it does

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seem that the anterior injections were slightly more effective in reducing pinning than posterior ones.

None of the SC injections reduced dorsal contacts, indicating that the appetitive component of rough-and-tumble play remained intact following anesthetization of the body surface. Therefore, the effect of xylocaine on pinning, when administered subcutaneously, is behaviorally specific. The significant increase in dorsal contacts following IP administration remains to be explained but may be reflective of central excitatory effects associated with xylocaine (e.g., Covino, 1972).

Experiment 3

The previous 2 experiments demonstrated that treatment of the dorsal body surface of juvenile rats with xylocaine can disrupt a consummatory component of rough-and-tumble play, i.e., pinning. However, as these were acute studies, the observed effect may have been due to factors other than a specific modulatory effect on play processes. For example, the numbing sensation produced by xylocaine may represent a competing sensation which is incompatible with normal play. If this is the case, then one may expect this nonspecific effect to diminish as animals become accustomed to the abnormal sensations. The present experiment addressed this possibility by evaluating tolerance to repeated administrations of xylocaine to the anterior dorsal body surface.

Methods

Fifty-six rats served as subjects and were housed individually beginning at 24 days of age. Animals were divided into 4 treatment groups (n = 14/group), and tested for play in like-treatment pairs during 5-min observation sessions every other day beginning on postnatal day 25 and ending on postnatal day 39, following SC injections as administered in Experiment 1. The control group (Group C) received 0.9% saline 15 minutes before each play session. Animals assigned to Group 25+ received 2% xylocaine on all test days. Groups 31+ and 37+ served as tolerance probes, with animals from Group 31+ receiving saline on days 25, 27, and 29, and then xylocaine on days 31 to 39. Animals in Group 37+ received saline on days 25 to 35, and then xylocaine on days 37 and 39. As before, number of dorsal contacts and pins was recorded for each animal.

Results and Discussion

Xylocaine was effective in reducing frequency of pinning regardless of when treatment began, although the relative reductions did differ (Fig. 3). When given throughout testing (Group 25+), xylocaine reduced pinning by an average of 64% (F(1,26) = 27.18, p < .001). On day 25, pinning was totally abolished, followed by a steady increase until day 33, at which time frequency stabilized at approximately 12 pins/5 min. However, a significant treatment by days interaction (F(7,182) = 3.55, p < .002) would seem to suggest that xylocaine was acting differentially across days of testing. Given that control animals began to exhibit fewer pins toward the end of testing, it is difficult to assess the major contributing factor responsible for this interaction. However, it does seem safe to say that while some tolerance may have occurred to xylocaine's ability to reduce pinning, this was by

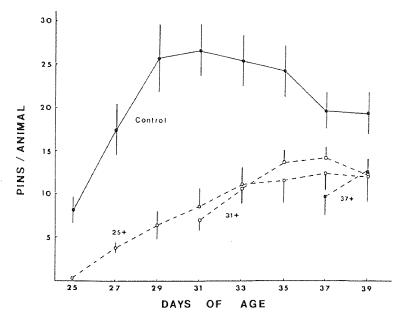


Fig. 3. The effects of 2% xylocaine on pinning when injected over repeated test days. Control animals received saline throughout, Group 25+ received xylocaine on all test days, Group 31+ received xylocaine on days 31 to 39, and Group 37+ received xylocaine only on days 37 and 39. Frequency of pins or dorsal contacts for Groups 31+ and 37+ did not differ from controls prior to treatment with xylocaine.

no means complete. Even after 6 days of exposure, xylocaine was still capable of reducing frequency of pinning to 46% of control levels. Mean pins for the 2 tolerance probes (Groups 31+ and 37+) essentially overlapped those of the group which received xylocaine throughout, further emphasizing the relative lack of tolerance development.

With dorsal contacts (Fig. 4), a differential effect of xylocaine with repeated testing was quite apparent. Although treatment condition was not a reliable source of variance when comparing the control group to either Group 25+ or Group 31+ (F's(1,26) < 1.3, p's > .05), the treatment × days interaction was significant when considering Group 25+ (F(7,182) = 8.49, p < .001) and Group 31+ (F(4,104) = 2.76, p < .05). Post-hoc analyses of these data using Fisher's modified lsd method (Winer, 1971) revealed that dorsal contacts were reduced following xylocaine treatment on days 25 and 27 (p < .05). No significant differences were found on any of the other days.

These data suggest little tolerance developed to xylocaine's ability to reduce frequency of pinning. However, the data also show that under certain conditions, xylocaine is capable of resulting in an expressive deficit (i.e., interfering with dorsal contacts). For instance, the xylocaine effect was markedly enhanced when treatment began at 25 days of age, in terms of both pinning and dorsal contacts. Furthermore, the deficit seen for dorsal contacts did show signs of developing tolerance with repeated exposure. It is possible that the more potent effect of xylocaine seen at this earlier age was due more to an increased susceptibility at this younger age (perhaps because of the animals' overall weaker urge to play as indicated by the ascending limb of the ontogeny curve). That animals beginning

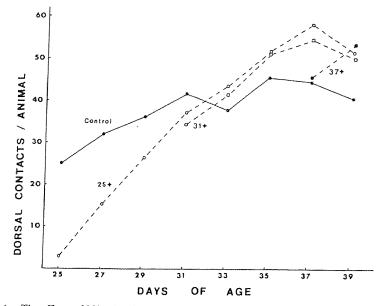


Fig. 4. The effects of 2% xylocaine on frequency of dorsal contacts when injected over repeated days. Groups are the same as those described in Figure 3.

xylocaine treatment on day 31 did not show a similar susceptibility, with respect to dorsal contacts, supports this contention.

Experiment 4

The previous experiments suggest that xylocaine is having a meaningful effect on disrupting consummatory aspects of play. It would be useful, however, to have independent assignments of the extent of the behavioral specificity of this effect. Therefore, the present experiment examined the effects of xylocaine on 2 additional dependent measures, one of which isolates an appetitive component of play, while the other assesses general behavior competence.

Methods

Play Solicitation

Seventeen rats served as subjects to analyze the effects of xylocaine on play solicitation. The animals were individually housed beginning on day 21. Postnatal days 23, 25, and 27 served as acquisition days, on which the animals were given a 5-min opportunity to play with a partner of the same sex. On days 29 and 31, the animals were tested for play solicitation. On each of these days the subjects were tested for a 5-min observation period with a stimulus animal of the same age that had been made unresponsive to playful gestures with 5 mg/kg of scopolamine (Thor & Holloway, 1983). The advantage of using scopolamine over other agents is that while these animals are as active as untreated animals, they simply will not respond to the playful overtures of another animal. Within such a design, the frequency of certain discrete behaviors, indicative of play solicitation, can be easily recorded.

The 3 measures of play solicitation were number of crossovers, dorsal grooms, and darts. A crossover was recorded when the subject broke the median plane of the stimulus animal. A dorsal groom was recorded when the subject either groomed or pulled at the stimulus animal's fur. Duration (in seconds) of grooms was also measured. A dart was recorded when the subject ran toward or away from the stimulus. Half of the animals received xylocaine on day 29 and saline on day 31, while the remaining half received these injections in the opposite order.

Foraging

An independent group of 16 animals (40-50 days old) was used to assess the ability of xylocaine-treated animals to negotiate a foraging field. Animals (who were 23-hr food deprived at the time of testing) were placed individually in an open field (60×60 cm) which has 36 recessed walls (2.5 cm in diameter and 2.0 cm deep) in the floor. The holes are equally spaced from one another, so as to form a 6×6 matrix. The floor of the field is marked into a 3×3 grid, to facilitate recording of activity (in grid crossings). A Froot Loop was placed in 4 of the holes (1 in each of the 4 quadrants of the field) and latency to locate and remove from the well, and consume each Loop was recorded. A 10-min time limit was imposed on each trial. During the first 5 min, activity (measured by grid crossings), nose pokes, rears, and grooms were also recorded.

On the first 3 days of testing, all animals received 4 subcutaneous injections of 0.9% saline (0.05 cc each), as in the previous experiment, 15 min prior to being blaced in the foraging field. No behavior was recorded on these days. Animals were given 1 hr of access to food in their home cage after each test session. On the 4th day of testing, 8 animals received xylocaine (four injections of 0.05 cc each to he anterior dorsal surface as in Experiment 1), while 8 received saline. On the 5th lay, those animals previously receiving xylocaine received saline and vice versa.

Results and Discussion

Xylocaine had no effect on frequency on either crossovers or darts in the play solicitation paradigm (Table 1). On the other hand, both frequency and duration of lorsal grooms were reliably reduced by xylocaine (t(16) = 4.11, p < .01 for fre-

	Crossovers ^a	Darts ^a	Play Grooms	
			Frequency ^a	Duration ^b
Saline	21.3	4.0	19.5	43.1
	(2.1)	(0.9)	(2.4)	(6.0)
Xylocaine	21.4	3.1	11.8*	24.3*
	(2.3)	(1.0)	(1.5)	(4.5)

TABLE 1. Effects of Xylocaine on Measures of Play Solicitation.

^a Numbers indicate mean frequency of occurrence, with numbers in parentheses indicating standard error of the mean.

^b Numbers indicate total duration in seconds, with numbers in parentheses indicating standard error of the mean.

* p < .05, 2-sample *t*-test compared to saline.

TABLE 2.	Effects of Xylocaine on
Measures c	of Foraging Competence.

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	Saline	Xylocaine	
Latencya			
1	62.5 ± 23.8	22.6 ± 9.0	
2	148.8 ± 48.3	175.4 ± 54.8	
3	213.4 ± 56.5	237.1 ± 56.9	
4 .	266.3 ± 55.8	316.1 ± 55.7	
Activity ^b	46.4 ± 6.9	$39.1 \pm 8.2^{*}$	
Exploration ^c	42.5 ± 4.9	52.4 ± 9.5	
Rears	13.3 ± 2.6	$5.2 \pm 1.0^{*}$	

^a Cumulative latency (in seconds) \pm SEM to locate each of the four pellets.

^b Mean ± SEM number of grid crossings.

^c Mean ± SEM number of nose pokes.

* p < .01, 2-sample *t*-test compared to saline.

quency and t(16) = 2.74, p < .05 for duration). Based on these data, it appears that while xylocaine did not affect overall activity levels in the play situation, as perhaps best measured by crossovers and darts, this treatment did seem to impair the ability, or motivation, to direct a specific play signal, viz., dorsal grooming, toward a stimulus animal.

The effects of xylocaine on foraging are presented in Table 2. With the exception of a slight reduction in latency to locate the first pellet following xylocaine, performance was comparable under both conditions. However, while number of nose pokes and grooms were unaffected by xylocaine, grid crossings and rears were reduced by 16% (t(15) = 3.00, p < .01) and 61% (t(15) = 3.72, p < .01), respectively. Although this may suggest that xylocaine slightly depressed general activity, it may also have been largely due to the slight (20%) increase in amount of exploration (nose pokes) which would have reduced time available for general locomotion. That the apparent lack of effect in this testing situation may have been due, perhaps at least in part, to an age-related decrease in sensitivity to xylocaine also cannot be discounted at present. In any event, the overall pattern suggests that foraging competence remained almost completely intact following a xylocaine treatment identical to that which has been shown previously to mark-

The results of this experiment indicate once again that xylocaine may produce a modest behavioral impairment. However, the manifestation of this impairment is not consistent between tests. For instance, an apparent goal directed activity (dorsal grooming) was moderately impaired in the play solicitation design while crossovers and darts remained normal. When placed in the foraging task, however, nose pokes (a goal directed activity) were not affected by xylocaine while activity was slightly depressed. Although these effects point out limitations in the specificity of xylocaine's effect on play, they do not distract from the import of the overall findings. Any external manipulation should be expected to have more than one behavioral manifestation. However, as long as these manifestations are modest in comparison to the main effect of the manipulation, we can conclude with some certainty that the manipulation is reasonably specific. We believe this to be the case with xylocaine, i.e., the extraneous impairments being observed do not ppear to be of large enough magnitude to result in the marked impairments seen n pinning.

Experiment 5

Juvenile rats, when tested in the paired encounter design over several days, end to establish a relatively stable "dominance-submission" relationship, with one animal accounting for approximately 60% to 70% of total pins (Panksepp, 981). Such a relationship is especially relevant in that establishment of domiiance has been proposed to represent one function of juvenile play (e.g., Adams & Boice, 1983; Einon, Morgan & Kibbler, 1978; Normansell, 1984; Panksepp et il., 1984). Given the results of the previous experiments implicating somatosenory stimulation in play, we sought to determine the extent to which somatosenory stimulation is important for the development of dominance relationships luring play. Furthermore, a nonspecific behavioral impairment hypothesis should oredict that the xylocaine treated animals would tend to be submissive.

Methods

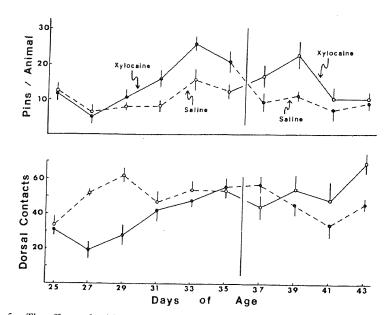
Sixteen rats were used to examine how xylocaine-treated animals react when paired with an untreated partner over several test sessions. Animals were isolated on day 24, with a single baseline day being conducted on postnatal day 25. One nember of each play dyad was then assigned to receive xylocaine 15 min prior to he 5-min test session on days 27, 29, 31, 33, and 35, while the other member eceived saline. Animals were assigned to treatment groups based on number of pins for day 25, so as to balance performance for each group prior to any treatment. The degree to which any asymmetry could be reversed was also assessed by switching treatment conditions and continuing testing on days 37, 39, 41, and 43.

Results and Discussion

Prior to any treatment (day 25), the 2 groups did not differ from one another with respect to either pins or dorsal contacts, as designed. However, a clear pattern of differential responding emerged shortly after treatment began (Fig. 5). Essentially, those animals receiving xylocaine prior to play accounted for approxmately 59% of total pins (F(1,14) = 6.16, p < .05), although this asymmetry was tot fully apparent until after several days of testing, being clearly apparent by day 11. By day 35, xylocaine-treated animals accounted for 65% of total pins. This gradual development of asymmetry was supported by a significant treatment by lays of testing interaction (F(4,56) = 2.93, p < .05). Although there was an initial "eversal of roles upon reversal of treatment, pins for the two treatment groups collapsed by the end of testing. Body weights, which have been shown to be a "actor in development of dominance (e.g., Panksepp et al., 1984), were identical "or both groups throughout testing, never diverging by more than 2%.

A different pattern emerged with dorsal contacts. A clear asymmetry appeared on the first 2 days of treatment, with those animals treated with saline accounting for approximately 71% of total dorsal contacts. By the 3rd day of esting (day 31), this asymmetry was no longer apparent, as supported through a eliable treatment × days of testing interaction (F(4,56) = 8.99, p < .01). No clear reversal occurred when treatment conditions were reversed. In fact, those ani-

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Fig. 5. The effects of pairing a xylocaine-treated animal with one treated with saline on both pins and dorsal contacts, when tested over repeated test days. Treatment began on Day 27 and was reversed on Day 37.

mals which had more dorsal contacts early on were once again soliciting more by the end of testing (F(3,42) = 3.02, p < .05 for the treatment × days of testing interaction on the reversal days).

Several aspects of these data are worthy of further discussion. It is particularly significant that xylocaine-treated animals consistently pinned their untreated partners more than vice versa. This is especially relevant since xylocaine, in previous experiments, always had the effect of reducing the occurrence of this measure. However, in the previous experiments, both animals were treated with xylocaine and the net result of this manipulation was an overall reduction in pinning. With only one animal of a pair being treated with xylocaine, it becomes clear that the ability to pin is not being impaired by xylocaine, but rather the ability to be pinned is compromised. As a result, xylocaine-treated animals seem less sensitive to dorsal contacts than controls are, as reflected in their apparent dominance.

In addition to diminished sensitivity of xylocaine-treated subjects, it is also possible that the observed effects may be attributable to a gradual diminution of responding by the control subjects, i.e., extinction. Unfortunately, the extent to which any response extinction may be occurring cannot be adequately assessed from the present data. In any event, it is important to emphasize that had xylocaine been having its primary effect via some nonspecific debilitatory action, one would not have predicted this pattern of results.

The lowered sensitivity of xylocaine-treated animals to dorsal contacts can perhaps best be demonstrated by evaluating dorsal contact/pin ratios (i.e., the number of dorsal contacts required, on average, to be pinned once). On day 31, for example, the dorsal contact/pin ratio for controls was 2.6 to 1, whereas for xylocaine-treated animals this ratio was 5.8 to 1. Thus, approximately twice as

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many dorsal contacts were required for an equal number of pins of xylocainetreated subjects by controls than of controls by xylocaine-treated subjects. Based on these data, it is possible that an animal's sensitivity to somatic stimuli may help determine the relative status of that animal in a playful dominance hierarchy.

Experiment 6

During juvenile play, a multitude of sensory information is impinging upon the animal. Therefore, one may expect other sensory modalities to be involved in the elaboration of juvenile play. Given that rats have highly developed olfactory senses and depend upon this modality in other social encounters, it seemed that olfaction may be important for play in this species. However, the published data do not support this contention. Play in the rat is largely unaffected by either zinc-sulfate induced anosmia (Thor & Holloway, 1982) or bilateral olfactory bulbectomy (Beatty & Costello, 1983). A recent study by Bierley, Hughes, and Beatty (1986) has also shown that blindness has no effect on levels of play in rats. In the present study, we sought to assess the relative contribution of audition, as well as vision, on rough-and-tumble play. In addition, one group of animals was also tested for the effects of vibrissae removal on play.

Methods

Forty-four juvenile rats served as subjects. On postnatal day 21 the animals were weaned. On postnatal day 22, animals were assigned to 1 of 4 treatment groups: (1) control, (2) blind, (3) deaf, and (4) vibrissae removal. All animals were anesthetized with Nembutal (25 mg/kg) and chloral hydrate (50 mg/kg). Those animals assigned to the blind group had their eyelids carefully sealed with a cyanoacrylate adhesive, avoiding contact of the adhesive with the eyeball. Those animals to be deafened had their tympanic membranes punctured by a stereotaxic ear bar, followed by the insertion of Bone Wax into the ear canal. The pinna of the ear was folded over the ear opening and sealed with a cyanoacrylate adhesive. Vibrissae were removed by plucking each vibrissa from the entire snout region. Animals from the control group were lightly anesthetized and allowed to recover. Animals were pair housed in solid bottom cages with those animals that they would be paired with during the play tests (i.e., animals from the same group).

On postnatal day 24, all animals were moved to individual housing On days 25 and 27, the animals were observed in like-treatment pairs during the 5-min observation periods, with number of pins and dorsal contacts being recorded. Although it was originally hoped to follow the play of the animals for a longer period of time, the treatments did not remain patent much longer than day 27. The success of the deafening manipulation was assessed after each of the test sessions by looking for a startle response following a loud hand clap. Although the efficacy of the blinding procedure was not empirically evaluated, only those animals whose eyes remained shut were used for subsequent analyses.

Results and Discussion

As summarized in Table 3, frequency of pinning varied as a function of treatment (F(3,40) = 5.53, p < .01). Pinning in the deaf animals was reduced significantly by an average of 54% over the 2 days of testing (p < .05, Newman-Keuls test).

	Pins		Dorsal Contacts	
	Day 25	Day 27	Day 25	Day 27
Control	16.1	24.1	44.9	63.9
(n = 12)	(2.8)	(2.5)	(4.9)	(5.4)
Deaf	4.7*	15.4*	45.8	67.3
(n = 12)	(0.9)	(2.5)	(4.9)	(4.9)
VBX ^a	8.3	18.7	41.5	54.7
(n = 12)	(1.2)	(2.9)	(3.9)	(3.6)
Blind	8.5	19.0	47.4	58.5
(n = 8)	(1.0)	(3.4)	(4.7)	(6.0)

TABLE 3. Mean (± SEM) Number of Pins and Dorsal Contacts for Animals with Impairments of Various Modalities.

* VBX = vibrissectomized group.

* p < .05, compared to control.

Although pinning in the blind animals and vibrissectomized animals was reduced by an average of 35%, neither reduction reached significance. Dorsal contacts were not affected by any of the manipulations.

Our finding that blindness had minimal effects on play confirm the findings of Bierley et al. (1986), and could be expected on several grounds. First, since our play tests are conducted in an enclosed chamber, illuminated only by a red light, the animals are close to functionally blind. Furthermore, tests have shown that juvenile rats tend to play more when tested under red light than when tested under white light (Panksepp et al., 1984).

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The tentative finding that deafness impairs pinning leaves open the possibility that an intact auditory system may be necessary for the full elaboration of play in the rat. As was the case with xylocaine, dorsal contacts were unaffected by deafness, implying that these animals were motivationally competent. However, the tentative nature of these data must be stressed and, hence, any conclusions drawn from these data should be viewed with caution. Also, the extent to which an interaction between deafness and functional blindness (the rats were tested under red light conditions) may have accounted for the observed effects cannot be presently assessed and needs to be pursued further.

General Discussion

The results of the present series of experiments show that disruption of somatosensory input compromises rough-and-tumble play in the juvenile rat, as reflected in frequency of pinning. Dorsal contacts, an index of play solicitation, were not consistently affected by xylocaine, suggesting that the observed reduction in play was due primarily to an inability to perceive and/or respond to playful gestures being made by that animal's partner. The effect of xylocaine on pinning was also found to be limited to anesthetization of the dorsal body surface and did not diminish markedly with repeated administration. This overall pattern of results only held true when both play partners were treated with xylocaine. When only one animal of a play dyad was treated with xylocaine (Experiment 5), that animal pinned its untreated partner more than vice versa, again emphasizing the behavioral specificity of this manipulation.

These data also served to highlight certain limitations in the use of xylocaine in young rats. For example, xylocaine reduced locomotor activity and rearing when animals were tested in a foraging field and also reduced the frequency of dorsal grooming when a treated animal was tested with an unresponsive partner (Experiment 4). Xylocaine was also found to substantially reduce the frequency of dorsal contacts when the treatment began at 25 days of age (Experiment 3), suggesting that these animals may have been generally debilitated to some extent. Therefore, xylocaine also seems capable of affecting behavior in a manner other than would be expected, based on its peripheral anesthetic action. Although initially troubling for interpreting the specificity of xylocaine's effect on pinning, it is important to emphasize that these apparent nonspecific actions were not necessary to obtain reliable effects on pinning, as seen in Experiments 1 and 2. In addition, if xylocaine was reducing pinning solely through a nonspecific action, then one would predict xylocaine-treated animals to be at a disadvantage when paired with an untreated partner. As shown in Experiment 5, this was not found to be the case.

The present series of experiments also examined relative involvement of other modalities in play. While this analysis was only preliminary, the data point toward a possible role for audition in play. Clearly, further analysis of ultrasonic and sonic vocalizations during ongoing play is warranted. As dorsal contacts were unaffected by deafening, it is possible that a role for audition may prove similar to that of the somatic senses. We should emphasize that these results may not remain constant across species, perhaps being dependent upon the relative importance of different modalities for any particular species. Accordingly, more work will be needed to clarify the specific involvement of these other modalities on juvenile play.

With the data pointing towards a specific modulatory role of the somatosensory system in juvenile play of the rat, a ratio of dorsal contacts to pins (i.e., the number of dorsal contacts required, on average, for that animal to be pinned once) may prove to be a useful index in evaluating the receptivity of juvenile rats to playful gestures. When this measure was applied to the xylocaine dose-response data of Experiment 1, it was found that the dorsal contact to pin ratio increased from 3.2 (\pm 0.3) following saline to 6.9 (\pm 0.8) following 2% xylocaine. In other words, xylocaine-treated animals required approximately twice as many dorsal contacts to be pinned than vehicle-treated animals. This ratio may then be thought of as a rough estimate of an animal's ability to perceive, or tendency to respond to, the playful solicitations of a conspecific, with higher numbers being indicative of animals that are less sensitive to dorsal contacts. Perhaps such an index could be useful as a means of assessing whether other manipulations which affect juvenile play in the rat are doing so by altering somatic sensitivity.

The results of the present study also suggest that somatosensory sensitivity may be involved in the establishment of dominance within the context of playful encounters. For example, control animals paired with xylocaine-treated partners were pinned more often then vice versa. Perhaps the inability of the xylocainetreated animals to respond to the solicitations of their partners contributed to this pattern of dominance. However, given the complexity surrounding the construct of dominance (e.g., Bernstein, 1981), much more data will be needed before any firm conclusions can be drawn concerning somatic involvement in playful dominance.

Somatosensory acuity is clearly not the only factor which determines the

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likelihood of play occurring and the level of intensity exhibited within play bouts. For example, other determining factors would be age of the animal (e.g., Panksepp, 1981), current energy levels (e.g., Siviy & Panksepp, 1985b), familiarity of the situation and other participants, and the presence or absence of other competing motivations such as aggression or fear (Panksepp et al., 1984). All of these factors, along with somatosensory acuity, may combine to determine the probability of a pin occurring given the presence of a dorsal contact. It is also possible that the above-mentioned factors are what determine the sensory acuity of the animal, which, in turn, determine the probability of a pin occurring. Which of these proposals, if either, best describes the data must await further testing. Having identified the somatosensory system as being important for juvenile play in the rat, these other issues can now be addressed more rigorously.

Notes

These experiments were part of a dissertation submitted to the faculty of Bowling Green State University by the first author in partial fulfillment of the requirements for the Ph.D. degree. S. M. Siviy is now with the Department of Psychology, University of Sydney, Sydney 2006 N.S.W., Australia.

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