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Effects of Warmth on Newborn Rats' Motor Activity and Oral Responsiveness to an Artificial Nipple

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Temperature is a powerful regulator of the behavior and physiology of newborn altricial animals. The effects of warmth on newborn rats' oral responsiveness to suckling stimuli and spontaneous motor activity in a thermoneutral environment were investigated. Newborn rat pups' oral grasp responses to an artificial nipple and overall motor activity were recorded for 18 min. Near-term pups were delivered by cesarean section so that their 1st experiences with suckling stimuli could be observed. Experimental pups were warmed for 15 s every 2 min; control pups were not warmed. Warmed pups grasped the nipple fewer times than the not-warmed pups. However, oral grasp durations became longer for the warmed pups but not for the not-warmed pups. Warmth increased pups' motor activity but only while the heat was applied. Warmth in a thermoneutral environment may promote longer nipple attachment during newborns' early feeding experiences.

Newborn rat pups naive to maternal experience will respond orally to an artificial nipple (AN) with mouthing, licking, and oral grasps (Koffman, Petrov, Varlinskaya, & Smotherman, 1998; Smotherman, Goffman, Petrov, & Varlinskaya, 1997). These oral responses to an AN are temporally associated with fluctuations in motor activity in the newborn and late-gestation fetal rat (Bacher, Robertson, & Smotherman, 2000; MacLennan, Smotherman, & Robertson, 1998; Reilly, Robertson, MacLennan, & Smotherman, 1997). Furthermore, in newborns, oral grasp responses become more frequent across consecutive minutes of exposure to an AN, and more nipple experience is positively related to the expression of longer grasps (Bacher et al., 2000).

Warmth is a powerful regulator of the behavior of infant rat pups (Alberts, 1978; Blumberg & Sokoloff, 1998; Hoffman, Flory & Alberts, 1999a). When the mother rat is at the nest, her body provides warmth and other cues that increase pups' motor activity, eliciting nipple search and attachment (Eilam & Smotherman, 1998). When the mother rat is away from the nest, pups' behavior in the huddle corresponds to demands of thermoregulation (Alberts, 1978; Alberts & Brunjes, 1978). Infant rat pups' preference for relatively warm temperatures is strongest after birth and wanes during the 1st postnatal week (Hoffman, Flory, & Alberts, 1999b; Johanson, 1979). For example, 1-day-old pups prefer a warmer region (36–40 °C) of a thermocline than older pups, even when ambient temperature is high (40 °C; Hoffman et al., 1999b). Additionally, warmth is reinforcing in young pups; 1-day-old pups will acquire an operant response to receive warmth (Flory, Langley, Pfister, & Alberts, 1997; Hoffman et al., 1999a).

Given the critical role of warmth for the infant rat, we investigated the effects of warmth on newborn rats' oral responsiveness to suckling stimuli. Newborn rats will orally grasp a warmed nipple more often than a not-warmed nipple (Koffman et al., 1998), but the effects of environmental warming on oral grasping behavior are not known. The main objective of the present experiment was to examine the effects of warmth on oral grasping and overall motor activity. To meet this objective, oral grasp responses to continuous AN presentation and concurrent overall motor activity were recorded in 28 newborn rat pups delivered by cesarean section. Cesarean section permits testing before pups have any suckling experience and, therefore, permits observation of newborns' first experiences with suckling stimuli (Smotherman, Goffman, et al., 1997; Smotherman, Petrov, & Varlinskaya, 1997). During the 18-min observation period, experimental pups were exposed to a heat source for 15 s every 2 min while an AN was presented continuously to the pup. Control pups were not warmed but were also presented continuously with an AN. Investigation of the effects of warming on newborn rats' oral responsiveness to feeding cues and overall motor activity may reveal new information about the role of temperature in the newborn's initial suckling experiences. The results also might reveal whether warmth facilitates certain aspects of suckling. If warmth does promote some aspects of suckling, then it might be an important variable to consider when promoting feeding in human infants who are not feeding well. Also, the results of this study have implications for greater understanding of behavior during newborn pups' first suckling episode, because the oral grasp response is an important

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component of the suckling sequence (Smotherman, Goffman, et al., 1997).

Method

Subjects

Newborn subjects (N = 28; 18 females) were the offspring of Sprague-Dawley rats (Charles River, Wilmington, MA) produced by time matings. For a 4-day breeding period, adult rats were housed in groups of 3 females and 1 male in plastic breeding cages (36 cm wide × 47 cm long × 20 cm high). Each day, vaginal smears were collected. The 1st day of detectable sperm was designated as Embryonic Day 0 (E0). Birth occurs on E21.5; the day of birth was designated P0. Pregnant female rats were maintained at constant room temperature (22 °C), on a 12-hr light–dark cycle (lights on at 0700) until the day of testing. Food and water were available ad libitum. Rats used in these experiments were treated in accordance with guidelines for animal care established by the National Institutes of Health (1986). To avoid potential litter effects through overrepresentation from a single litter, not more than 1 male and 1 female were tested from a given litter, and no pups from the same litter were assigned to the same experimental condition (Holson & Pearce, 1992). One or 2 pups from approximately 20 litters were used to complete the final sample of 28 pups.

Cesarean Delivery

To control the type and quantity of stimulation the pups received between delivery and testing, experimental subjects were delivered by cesarean section near term on E21 to restrict their access to suckling stimuli. Pups delivered vaginally and which have 24 hr of maternal experience behave similarly toward an AN as do those delivered by cesarean section that have no maternal experience (Petrov, Varlinskaya, & Smotherman, 1997). After brief ether anesthesia, the pregnant rat was given an injection of 100% ethanol (100 μl) between the first and second lumbar vertebrae to block neural transmission in the spinal cord. This procedure eliminates sensation in the lower part of the body. Thus, neither ether nor ethanol affects pups' behavior during the time they are tested after birth. A midline laparotomy provided direct access to the uterine horns. Fetuses were removed one at a time. Umbilical circulation was halted by ligation of the umbilical cord with 6.0 surgical suture. The umbilical cord then was cut on the placental side of the ligation. Each pup was stimulated by rolling and wiping immediately after being removed. After the whole litter was delivered (between 8 and 16 pups), pups were stimulated by rolling and misting (to keep the skin moist). Pups from an individual female were placed together in a 12-cm-wide × 12-cm-long × 6-cm high plastic container lined with a water-moistened paper towel. Pups were not positioned in the container in a specific pattern. The container with newborn pups was put in a temperature-regulated (33 °C), humid incubator. When the cesarean section procedure was completed, the donor female was killed by rapid cervical dislocation.

Procedure

Before testing, each pup was transported alone from the incubator to the testing site (therefore, pups experienced room temperature for 10–15 s). Pups were allowed to acclimate to the testing environment (M = 35.5 °C) for 5 min. Each pup was observed for 18 min during continuous AN exposure. The experimental pups were exposed to heat from a small lamp nearby, which was turned on for 15 s every 2 min (each pup received nine pulses of heat). The control pups were not exposed to the heat from the lamp (the lamp was not turned on). Pups were tested between 2.7 and 4.3 hr (M = 3.5 ± 0.5 hr) after cesarean delivery.

Presentation of the AN. The AN was sculpted from soft vinyl material so that its dimensions were approximately 16 mm in length, tapered to a diameter of 1 mm at its rounded tip (Robinson et al., 1992). A ring (7 mm in diameter) was made from the same material and secured 7 mm from the tip of the nipple. This ring provided a point of contact for the snout of the pup when the pup made an oral grasp of the nipple. The nipple was fixed to the end of a dental probe, which enabled the experimenter to position the nipple. During continuous presentation, the experimenter kept the AN in contact with the pup's perioral area. The AN contact of the perioral area was very gentle. The tip of the AN was not forced into the pup's mouth (Petrov et al., 1997; Smotherman, Goffman, et al., 1997). Presenting the AN to the pup did not produce detectable artifacts in the output of the movement sensor (Bacher et al., 2000).

Behavioral observation. Testing occurred in a transparent testing box measuring 63.5 cm wide × 50 cm long × 26 cm high. The box was constructed with two holes in one side for the experimenter to present the AN. Each pup was placed on a movement sensor that was surrounded by a fixed circular border (1.5 cm high × 7 cm in diameter) to keep the pup on the sensor. A humidifier was used to add moisture to the testing box. So that subjects tested later could not detect signs (odors, fluids) of previously tested pups, the film covering the movement sensor (discussed next) was changed between pups, and the circular border was cleaned with a solution of 20% hydrogen peroxide between each pup's use.

Measurement of gross motor activity. Motor activity was measured at 60 Hz by using a piezoelectric speaker element as a movement sensor (Archer Model 273-091, Radio Shack, Ithaca, NY). When the element (a 4-cm-diameter thin metal disk) was deformed by the pup's movement, small voltages were generated. The movement sensor was covered with a thin plastic film to protect the sensor. Thresholds were applied to the raw movement signal to remove low-amplitude background activity resulting from respiration, heartbeat, or electrical noise. A single threshold was selected and used for all pups. The movement data were rectified and integrated to create movement time series of 1 or 60 Hz, depending on the analysis. These techniques have been used reliably in previous studies of motor activity in infant and fetal rat pups (Bacher et al., 2000; MacLennan et al., 1998; Reilly, Robertson, MacLennan, & Smotherman, 1997).

Application of heat. Heat was provided by a small, incandescent lamp (15 W) positioned next to the movement sensor on which the pup lay. An aluminum cone was used to direct the heat toward the pup. The lamp was 3 cm above the horizontal plane of the sensor, and its tip was 5.5 cm from the center of the sensor (Figure 1). The location of the temperature probe used

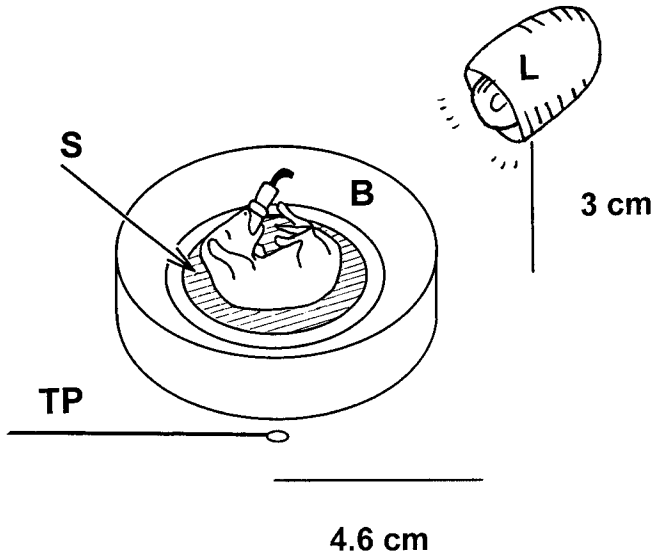

Figure 1. Positions of pup performing an oral grasp of the artificial nipple. S = sensor; L = lamp; B = border; TP = temperature probe.

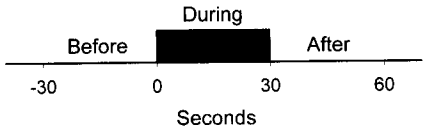

Figure 2. Three 30-s segments of motor activity were selected before, during, and after heat was applied to the pups. The lamp was turned on at Time 0 and turned off at 15 s. The temperature started to decrease at 15 s and returned to baseline at approximately 60–90 s after the lamp was turned on.

to monitor the air temperature near the pup was 5 cm from the center of the sensor and 3 cm from the tip of the lamp. Prior testing showed that after the lamp was turned on the air temperature measured near the movement sensor increased 3.5 °C at 15 s. The temperature returned to baseline by approximately 90 s after the lamp was turned on.

The ambient air temperature of the testing box was measured at the center of the box, approximately 9 cm above the sensor and 7 cm to the rear of the box. The ambient temperature was monitored continuously and kept between 34 °C and 37 °C by adjusting heating (e.g., heating pads) and cooling sources (e.g., fan). The ambient temperature was sampled five times during the testing session just before the lamp was turned on (when the temperature at the sensor had returned to baseline). The samples taken from the control data were not different from those taken from the experimental data, $t(8) = -1.1$, $p = .31$.

Oral grasping of the AN. Oral grasping of the AN by the newborn rat is a highly stereotyped, easily identifiable behavior. The pup's head moves quickly toward the AN, its mouth opens and then closes around the tip of the AN, pressure is applied on the AN by the jaws, a seal is formed around the tip of the nipple, and negative pressure is exerted (Robinson et al., 1992; Smotherman, Goffman, et al., 1997). In the present experiment, the experimenter marked oral grasp responses by depressing a switch at the onset of the grasp and releasing the switch at the offset of the grasp. This signal from the switch marking the grasps was sampled concurrently with the movement signal. To correct for the reaction time associated with the use of a manual switch, the signal marking the onset and offset of the grasp was adjusted 0.33 s earlier. This estimate of reaction time for moving a manual switch was based on reaction times from pilot testing of a similar task and reaction times published in research using similar manual tasks (Chelazi et al., 1995; Gomez et al., 1998).

Analysis I: Effects of Warmth on Motor Activity

The first set of analyses investigated the effects of warmth on motor activity. The levels of motor activity were measured during three consecutive 30-s intervals around the increase in temperature. These three intervals began 30 s before the lamp was turned on, at the onset of the lamp (during), and 30 s after the lamp was turned on (Figure 2).

For the first analysis, the 60-Hz movement time series for each pup were integrated to 1-Hz series, and the 30-s segments of motor activity were then extracted for each heat presentation and averaged for that pup. Effects of warmth on the level of motor activity were analyzed in a three-factor analysis of variance (ANOVA; condition [experimental, control]; warmth; time in session) with warmth (before, during, after) and time (first, second, and last 6 min) treated as repeated measures factors. Because the heat was applied at regular intervals, the same temporal intervals were selected for comparison from the movement data of the pups that were not warmed (control). Periodic stimulation with heat might also affect cyclic organization in motor activity. Therefore, spectral analysis was conducted on movement time series to identify and quantify cyclic organization. Given the minimum amount of data required for spectral analysis, each motor activity time series was divided into two equal parts of 9 min. This division also permits the testing for change in cyclic organization over time. The 60-Hz movement time series were first integrated to 1 Hz. Each motor activity time series was detrended, and the Fourier transform of the autocorrelation function was calculated using an algorithm by Jenkins and Watts (1968). When calculated this way, the movement spectrum represents stable estimates of the relative strength of periodic fluctuations occurring at different frequencies. The area under the movement spectrum in a given frequency band represents the proportion of movement variance between the two frequencies that define that band. Cyclic organization was inferred from a peak in the movement spectrum that exceeded the upper 99% confidence limit of white noise. This analysis has been used in previous investigations of cyclic organization of spontaneous motor activity (Bacher et al., 2000; MacLennan et al., 1998; Reilly et al., 1997; Robertson, 1985; Smotherman, Robinson, & Robertson, 1988). Three measures of cyclic organization were calculated for each spectrum that contained a significant peak: frequency of the largest peak in the spectrum, height of the largest peak in the spectrum, and width of the largest peak in the spectrum. The frequency indicates the dominant rate of oscillation in motor activity, the height measures the strength of the dominant oscillation, and the width indicates the irregularity of the dominant oscillation. The three measures of cyclic organization were compared in a two-factor, Condition × Half (first half and second half of session), ANOVA with repeated measures on half.

Results

Level of motor activity. A three-factor ANOVA of the level of motor activity by condition (experimental, control), warmth (before, during, after the heat), and time (first, second, and last 6 min) was conducted with repeated measures on warmth and time. Results indicated main effects of warmth, $F(2, 52) = 15.00$, $p < .001$, and time, $F(2, 52) = 8.60$, $p = .001$. Also, an interaction between warmth and condition was found, $F(2, 52) = 8.10$, $p = .001$ (Figure 3). No sex differences were found.

To further characterize the differences in motor activity before, during, and after warmth, a one-way repeated measures ANOVA for warmth (collapsing time) was performed for each condition. For the experimental group, motor activity showed a significant change, $F(2, 26) = 14.80$, $p < .001$. Post hoc paired comparisons

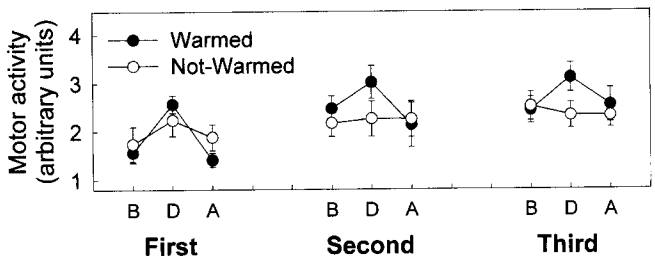

Figure 3. Mean (± *SEM*) levels of motor activity 30 s before (B), during (D), and after (A) heat for the first, second, and third 6 min of testing for both experimental (Warmed) and control (Not-Warmed) pups.

(Fisher's planned least significant difference [PLSD]) of the motor activity before, during, and after warming indicated that motor activity during warming was greater than both before and after warming ($p < .05$). The levels of motor activity before and after warming were not different from each other. For the control (not-warmed) group, no significant change in motor activity was observed, $F(2, 26) = 1.10$, $p = .33$.

Cyclic organization in motor activity. Evidence of cyclic organization in motor activity was present in both movement time series of each pup. Two-way ANOVAs of condition (experimental, control) and half (first half, second half) were used to analyze the frequency, strength, and irregularity of the dominant peak (see Table 1). For all three measures of cyclic organization, no main effects for condition or half (nor interactions) were found. The means and standard deviations for the each measure of cyclic organization for both the experimental and control subjects (first half and second half) are depicted in Table 1.

Discussion

Warmth had immediate effects on the level of motor activity. While the air temperature was elevated, pups became more active. As the temperature returned to prewarmth levels, so did the level of motor activity. Additionally, for both experimental and control subjects, motor activity increased over the 18-min testing period. This increase over many minutes may reflect a general trend for pups to become more active over the first 5 hr after delivery (Smotherman, Goffman, et al., 1997), or it could reflect effects of continuous nipple presentation (or both).

All pups showed evidence of cyclic organization both early and late in the testing session. However, measures of cyclic organization (frequency, strength, and width of the dominant peak) were not different between experimental and control pups and did not change over time. This pattern of results suggests that warmth's effects on motor activity were concurrent with the brief increase in temperature and that brief, intermittent warming may not have long-term effects on the cyclic organization of motor activity.

Analysis II: Effects of Warmth on Oral Grasp Responses

In this set of analyses, the number of oral grasp responses and the duration of oral grasp responses were compared in accordance with experimental condition and time in the session. All oral grasp responses were included in the analyses. Males performed more oral grasp responses ($M = 18.9$, $SD = 4.6$) than females ($M = 13.7$, $SD = 5.3$) during the 18-min testing session, $t(26) = 2.75$, $p = .011$. Therefore, a three-way ANOVA was used to compare the number of oral grasp responses by condition (experimental, control), time (first, second, third 6-min interval), and sex. Sex differences were found only for the number of oral grasps. The mean duration of oral grasps was calculated for each pup in the three consecutive 6-min segments of the 18-min observation. A two-way repeated measures ANOVA of condition and time was used to analyze the duration of oral grasp responses.

Results

Number of oral grasp responses. Every pup grasped the AN. The mean number of oral grasp responses per pup was 16.3 ($SD = 5.5$). Results of the three-way ANOVA for number of oral grasp responses revealed main effects of condition, $F(1, 24) = 4.90$, $p = .04$, and sex, $F(1, 24) = 8.60$, $p = .007$. More grasps were performed by control than experimental pups and by male than female pups. Also, an interaction of time and sex was found, $F(2, 48) = 3.40$, $p = .04$; males and females performed similar numbers of grasps initially, but by the end of the observation males performed more grasps than females (Table 2). No Condition × Sex interaction was detected, $F(1, 24) = 0.13$, $p = .72$.

Duration of oral grasp responses. No main effects were observed for condition, $F(1, 23) = 1.73$, $p = .20$, or time, $F(2, 46) = 1.94$, $p = .15$. However, an interaction of condition and time was found, $F(2, 46) = 3.51$, $p = .04$ (Figure 4). To further explore the differences within conditions, separate one-way ANOVAs were conducted for each condition. For the experimental group, an effect of change over time was found, $F(2, 22) = 6.00$, $p = .009$. Post hoc paired comparisons (Fisher's PLSD) indicated that grasp duration for both the first 6 min and second 6 min of the testing session was shorter compared with that of the last 6 min ($p < .05$). For the control group, no change over time was found, $F(2, 24) = 0.28$, $p = .76$.

Discussion

Pups that received pulses of warmth (experimental condition) grasped the AN fewer times than those that did not receive warmth (control). Previous research using newborn rats indicated that the level of motor activity before oral grasp responses tended to be low (Bacher et al., 2000). Therefore, one possible explanation of this decrease in oral responsiveness during warming is that the periodic increases in motor activity may have disrupted the initiation of oral

Table 1
Means (±SD) for Measures of Cyclic Organization in Motor Activity and Results of Condition × Half Analysis of Variance

	Experimental		Control		Condition		Half		Interaction	
Measure	First half	Second half	First half	Second half	$F(1, 26)$	p	$F(1, 26)$	p	$F(1, 26)$	p
Pups with CM (%)	100	100	100	100						
Frequency	0.87 (0.40)	0.96 (0.46)	0.76 (0.39)	1.0 (0.56)	0.02	.89	2.00	.17	0.50	.49
Strength	0.38 (0.12)	0.36 (0.14)	0.33 (0.10)	0.31 (0.10)	0.29	.60	2.10	.16	0.75	.40
Irregularity	0.68 (0.19)	0.67 (0.15)	0.70 (0.20)	0.61 (0.12)	0.18	.19	0.44	.52	0.02	.88

Note. Theoretical range of strength values is 0.00–2.67, theoretical range of irregularity values is 0.38–30.00. CM = cyclic motor activity.

Table 2
Mean (±SD) Number of Grasps for Males and Females for Each 6-Min Interval

Sex	First	Second	Third	Overall
Male	4.79 (2.90)	6.71 (2.90)	7.36 (3.20)	6.286
Female	4.79 (3.10)	5.14 (2.30)	3.71 (1.30)	4.548

grasping, perhaps by interfering with the motor sequencing that leads to oral grasping.

Another possibility is that the effects of warmth on oral grasping are mediated not by motor activity, but by other physiological changes that accompany warmth. For example, perhaps pups' sensitivity to the stimulation of the AN was reduced and, therefore, grasps were not initiated as readily. Because warmth is reinforcing for infant rats (Hoffman et al., 1999a), cutaneous sensitivity might be reduced as a consequence of the reinforcing properties of stimuli (e.g., milk) that activate the kappa opioid system (Robinson, Moody, Spear, & Smotherman, 1993). Additionally, it is unlikely that nipple temperature explains these differences in the frequency of oral grasping, because previous work (Koffman et al., 1998) indicates that a warmed nipple increases, not decreases, the frequency of oral grasping.

Female pups grasped the AN fewer times than male pups, and changes in grasp frequency over the testing session were different for males and females. Body weights of males and females were compared as a possible explanation for the sex difference in number of grasps, but no differences were found, $t(26) = -0.35$, $p = .73$. This sex difference is difficult to explain because no sex differences have been found in numerous previous studies of oral grasping behavior in newborn rats.

The duration of oral grasps increased over the 18 min observation for warmed pups. Because pups that were not warmed did not show an increase in grasp duration in this time period, it is improbable that nutritional deprivation produced the increase in grasp duration over time. One possible explanation is that the pulses of warmth may have altered pups' core body temperature, which, in turn, may have affected their likelihood to sustain nipple attachment.

Analysis III: Temporal Relationship Between Oral Grasping and Motor Activity

Previous research indicates that motor activity is lower than baseline before an oral grasp and higher than baseline after a grasp (Bacher et al., 2000). Analysis II in this report indicated that the average duration of oral grasps increased over time for the warmed pups but not for the not-warmed pups. To test whether changes in motor activity were related to the observed increase in oral grasp duration, we examined the pattern of motor activity before, during, and after oral grasps to determine whether warming disrupted the pattern. Because the effects of warmth on grasp duration were apparent only in the last 6-min interval of the observation, we focused our analysis on behavior during that last 6-min interval. For both the warmed and not-warmed pups, the longest three grasps were selected from the last 6 min of the testing session. The longest grasps were selected to maximize the amount of motor activity data analyzed during the oral grasps.

Selected grasps were at least 10 s apart so that motor activity in the 5 s before and after each grasp could be analyzed. Grasps from 2 subjects were omitted from the analysis because three grasps were not available during the last 6 min. Therefore, the number of subjects used was 26, with 13 pups in each condition. Movement data for the three grasps were averaged for each pup. Then the average levels of motor activity before (5 s), during, and after (5 s) oral grasps were compared in separate one-way ANOVAs of time (before, during, after) for the experimental and control conditions to model the analysis used in Bacher et al. (2000).

Additionally, motor activity in the 5 s before oral grasps was analyzed to determine whether there were systematic changes in level of activity immediately preceding an oral grasp. The existence of a pattern might lead to further understanding of the initiation of oral grasp responses. The 5-s movement time series preceding each grasp was integrated to 1 Hz (from 60 Hz), yielding a series of five data points for each grasp. Then 1-Hz data were differentiated, which produced four difference scores representing the successive changes in movement in the last few seconds before the grasp was initiated. Data from the three grasps were averaged for each pup. The group means for each of the four values were then compared with zero (the expected value if no consistent differences in level of motor activity occurred before the grasp was expressed).

Results

The average duration of the three longest oral grasps did not differ between experimental ($M = 29.9$, $SD = 32.4$) and control ($M = 17.5$, $SD = 13.1$) groups, $t(24) = 1.27$, $p = .21$.

A main effect for time was observed for the experimental group, $F(2, 24) = 6.80$, $p = .005$ (Figure 5). Post hoc paired comparisons indicated that motor activity before the grasp was lower than activity during and after the grasp, $t(12) = -2.90$, $p = .01$ and $t(12) = -3.60$, $p = .003$, respectively. Motor activity during the grasp was not different from activity level after the grasp, $t(12) = -0.18$, $p = .86$. No sex differences were found.

A main effect for time was observed for the control group also, $F(2, 24) = 9.90$, $p < .001$. Post hoc paired comparisons indicated that motor activity before the grasp was lower than activity during

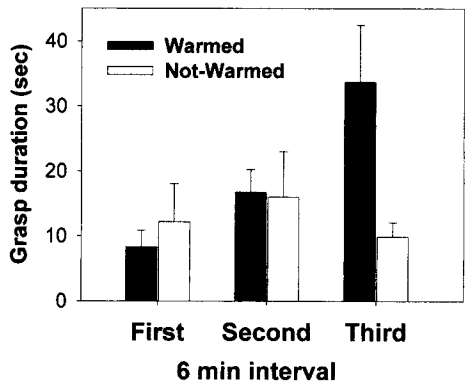

Figure 4. Mean (± *SEM*) grasp duration (in seconds) for grasps from the first, second, and third 6-min intervals of testing for the experimental (Warmed) and control (Not-Warmed) pups.

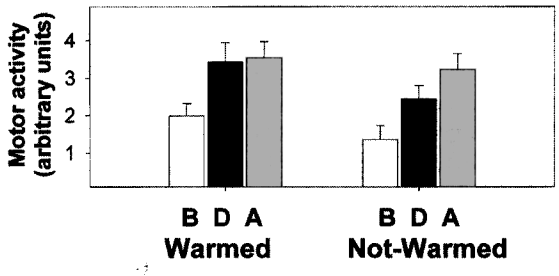

Figure 5. Mean (± *SEM*) level of motor activity 5 s before (B), during (D), and 5 s after (A) the three longest oral grasp responses from the last 6 min of testing for the experimental (Warmed) and control (Not-Warmed) pups.

and after the grasp, $t(12) = -2.30$, $p = .04$, and $t(12) = -2.4$, $p = .03$, respectively. Also, motor activity during the grasp was lower than that after the grasp, $t(12) = -2.40$, $p = .03$.

The change in motor activity in the 1–2 s before the oral grasp responses was greater than zero for both the experimental and the control groups, $t(24) = 2.97$, $p = .007$, and $t(24) = 2.50$, $p = .02$, respectively. None of the other changes (2–3 s, 3–4 s, or 4–5 s) in motor activity were different from zero. The results for the experimental group were as follows: 2–3 s, $t(24) = 0.09$, $p = .93$; 3–4 s, $t(24) = -0.98$, $p = .34$; 4–5 s, $t(24) = -0.82$, $p = .42$. The results for the control group were as follows: 2–3 s, $t(24) = -0.81$, $p = .42$; 3–4 s, $t(24) = -0.09$, $p = .93$; 4–5 s, $t(24) = -1.70$, $p = .11$.

Discussion

The pattern of motor activity around oral grasp responses in the not-warmed pups during the last minutes of the observation was the same as that observed in previous work with a directly comparable design (Bacher et al., 2000). That is, motor activity was lower before the grasp than during the grasp, and activity during the grasp was lower than activity after the grasp. That the control pups in the present experiment exhibited the same pattern of motor activity before, during, and after oral grasps that was observed in the previous study is significant in that it suggests that the relatively long exposure to the AN did not introduce a systematic change in this behavior.

However, warmed pups' motor activity during the oral grasp was as high during the grasp as it was after the grasp. This suggests that warmed pups (which showed longer oral grasps as testing proceeded) behaved differently while attached to the nipple than not-warmed pups during the last 6 min of the testing session. Increased activity during grasping may reflect warmed (or "activated") pups' ability to maintain nipple attachment despite higher levels of spontaneous activity. Alternatively, warmed pups may be interacting with the nipple differently. For example, warmed pups might show more movements directed toward the AN (e.g., mouth movements, pushing on the AN with forepaws).

For both warmed and not-warmed pups, motor activity increased during the 1 s before oral grasps. This probably reflects pups' orienting to the location of the AN as the grasp is initiated. Pregrasping movements likely include head movements and may include trunk and forelimb movements.

General Discussion

In the newborn rat, brief, intermittent warming altered the level of general motor activity and pups' oral grasp responses to an AN. Short-term effects on motor activity were observed: Pups became more active during the warming. Changes were also observed in the oral grasping behavior of warmed pups compared with not-warmed pups. Overall, warmed pups grasped the AN less frequently than not-warmed pups. However, over the testing period, pups' grasps became longer in duration. An additional result was that, during the last 6 min of the observation, warmed pups showed equally high levels of motor activity during long oral grasps as after the long grasps, but control pups did not.

One possible explanation of the effects of warmth on oral grasping behavior is that the effects were mediated by the changes in motor activity during warming. For example, repeated increases in motor activity during warming might inhibit oral grasp responses, because oral grasps tend to begin when movement is low (Bacher et al., 2000). However, the results of the present study indicate that, although motor activity increased over the testing session, a systematic reduction in the number of oral grasps across the session was not found across subjects. Additionally, higher levels of motor activity might be thought to disrupt sustained nipple attachment, yet warmed pups showed increased levels of motor activity during long grasps. These patterns suggest that the changes in oral responses to the AN were not mediated by changes in the level of motor activity. However, repeated motor activation by the pulses of heat may produce central changes that may have affected other systems.

Warmth affected two aspects of oral grasping behavior, and these effects occurred on different time scales. The frequency of oral grasping was reduced throughout the observation, and yet the duration of oral grasps increased but only after many minutes of exposure to warmth. The differences in the behavioral effects over time may give clues to the mechanisms that produced the effects. First, the observed dissociation between the frequency of grasp initiation and sustained nipple attachment is consistent with research that indicates that the neural mechanisms of feeding preparation and consumption are separable (Blackburn, Phillips, Jakubovic, & Fibiger, 1989; Hall, 1990; Hall & Williams, 1983). Furthermore, the observed sex difference for the number of grasps over time, but not the duration of grasps, further supports that these behavioral responses are separable.

Second, the more slowly emerging effects of warmth on grasp duration suggest that the systems affected are slower changing ones. For example, the observed behavioral changes could reflect accumulated experience (Bacher et al., 2000). Another possibility is that repeated warming over time changed the pups' core body temperature. However, it is unlikely that the brief exposures to moderate heat that these pups experienced would change core body temperature.

That warmth promotes sustained nipple attachment is reasonable given the niche of the newborn rat. Pups use warmth and olfactory cues to locate their mother (Polan & Hofer, 1998, 1999). Also, newborn pups might have to remain attached to the nipple many minutes before the first milk letdown; therefore, if warmth promotes nipple attachment, then newborn pups are less likely to miss the first milk letdowns after birth. Furthermore, warmed pups' ability to express relatively high levels of motor activity

during nipple attachment may be an advantage in the maternal context when a pup competes with siblings for access to a nipple. Pups' motor activation that occurs at milk letdown (Brake, Shair, & Hofer, 1988) suggests that motor activation at the nipple might also play a role in pups' ingesting (swallowing) milk.

Warmth plays an important role in the early feeding experiences of newborn mammals by maintaining the newborns' thermoregulatory needs and guiding the newborn to the nipple (Brake et al., 1988). The results of the present research using the newborn rat suggest that warmth in a thermoneutral environment may also facilitate sustained nipple attachment, even in the absence of milk. This result may have implications for promoting feeding in human infants who are not feeding well. It is well understood that body and environmental temperatures are critical factors in the care and feeding of special needs infants, especially preterm infants (Britton, 1980; Klaus, Martin, & Fanaroff, 1992; Mok, Bass, Ducker, & McIntosh, 1991; Thomas, 1994). However, whether warmth in a thermoneutral environment promotes aspects of feeding in infants is not known. It is not assumed that any effects of warmth in infants are the same or similar to those for observed in nonhuman mammals (Hofer, 1975). However, the principle that warmth affects newborn feeding in a thermoneutral environment may guide new research to further explore mechanisms underlying early feeding experiences in infants and might also provide insights into clinical applications.

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