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Contributions of Endothermy to Huddling Behavior in Infant Norway Rats (*Rattus norvegicus*) and Syrian Golden Hamsters (*Mesocricetus auratus*)

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Infant Syrian golden hamsters (*Mesocricetus auratus*) do not exhibit endogenous heat production before 3 weeks of age and do not huddle effectively during cold exposure, gaining little thermoregulatory benefit from the presence of multiple littermates. In contrast, infant Norway rats (*Rattus norvegicus*) produce heat endogenously and are effective at maintaining elevated body temperatures by huddling. Therefore, the ineffective huddling of infant hamsters may be due to the absence of endogenous heat production. The huddling behavior of infants in mixed huddles of 8-day-old hamsters and weight-matched 4–5-day-old rats was observed to explore this possibility. The results indicate that hamsters, even when cold, effectively gain access to heat-producing rats, supporting the idea that endothermy contributes to the behavior of huddling by providing heat to each individual and thermal stimuli to other infants to support aggregation.

An infant's ability to maintain body temperature depends on behavioral and physiological adjustments as well as the contribution of the mother (Hull, 1973; Leon, 1986). Maternal behavior, infant behavior, and infant physiology differ from species to species, thereby resulting in a multitude of differences in infant thermoregulatory systems. For example, Syrian golden hamsters and Norway rats both produce altricial young that differ substantially in their thermoregulation across both behavioral and physiological dimensions. Specifically, infant hamsters lack endothermy during the first 2 weeks of age (Blumberg, 1997; Hissa, 1968) but exhibit rapid thermotaxic responses in the cold (Leonard, 1974; Sokoloff, Blumberg, Boline, Johnson, & Streeper, 2002). Therefore, the only means by which an infant hamster can regulate body temperature is by locating and moving toward a source of heat, whether the source of heat is its mother or not (Leonard, 1974).

Infant rats also show thermotaxic behavior but are less sensitive to thermal stimuli in the environment than infant hamsters (Johanson, 1979; Kleitman & Satinoff, 1982; Sokoloff et al., 2002). Infant rats, however, produce heat endogenously using brown adipose tissue (BAT) and exhibit huddling behavior during cold exposure (Alberts, 1978a; Sokoloff, Blumberg, & Adams, 2000). In fact, the heat production of infant rats has been shown to be a necessary resource for the maintenance of huddle temperature (T_{huddle}; Sokoloff & Blumberg, 2001; Sokoloff et al., 2000). Therefore, when air temperatures decrease, infant rats clump together and pile on top of each other, conserving heat by reducing the exposed surface area of each individual (Alberts, 1978a; Sokoloff & Blumberg, 2001; Sokoloff et al., 2000). During the 1st week postpartum, the mother reduces the amount of time she spends in the nest (Grota & Ader, 1969; Leon, Croskerry, & Smith, 1978) as the infants' physiological and behavioral responses provide them with increasingly adequate means of independent thermoregulation.

The origin of the behavioral differences exhibited by infant rats and hamsters, described earlier, still requires clarification. For example, the presence or absence of BAT thermogenesis may shape the different behavioral capabilities of altricial infants. In infant rats, BAT thermogenesis may interfere with thermotaxis by making them less sensitive to changes in ambient temperature (Sokoloff et al., 2002). In contrast, in infant hamsters, the absence of BAT thermogenesis may prevent effective huddling by removing the thermal stimulus that facilitates aggregation (Sokoloff et al., 2000).

Previous studies have suggested that huddling behaviors mature during the early postnatal period (Alberts, 1978b; Leonard, 1982; Sokoloff & Blumberg, 2001). Specifically, infant hamsters show very active and unstable aggregation during the 1st postnatal week (Leonard, 1982; Sokoloff et al., 2000). By the end of the 2nd postnatal week, however, hamster huddling becomes more stable (Leonard, 1982). Interesting to note, this period corresponds with the onset of BAT thermogenesis in infant hamsters (Blumberg, 1997; Hissa, 1968). Similarly, by Postnatal Day 2, infant rats do not show effective huddling behavior as air temperatures decrease; by Postnatal Day 8 (PD8), however, huddling is elicited by even modest decreases in temperature (Sokoloff et al., 2000).

We have previously hypothesized that differences in huddling behavior between infant hamsters and infant rats during the 1st postnatal week as well as differences in the huddling behavior of

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infant rats within the 1st postnatal week arise from two mechanisms (Sokoloff & Blumberg, 2001). First, endogenous heat production is necessary for the maintenance of elevated T_{huddle}s. Second, the heat produced by BAT acts as a thermal stimulus to other rats, directing aggregation via thermotaxis. Because of the strong thermotaxic behavior of infant hamsters, it is predicted that hamsters will thermoregulate more successfully in the huddle if they are provided access to heat-producing infant rats.

In the present experiment, four-pup huddles of 8-day-old hamsters and/or 4- to 5-day-old rats were sequentially exposed to three subthermoneutral air temperatures. In the first group (hamster), huddles were composed of four 8-day-old hamsters. In the second group (rat), huddles were composed of four weight-matched infant rats (4- to 5-day-old rats). In the third group (mixed), huddles were composed of two 8-day-old hamsters and two 4- to 5-day-old rats. The behavior of representative focal pups in each huddle was videotaped and scored, and infrared (IR) thermography was used to measure T_{huddle}.

Method

Subjects

Forty-eight 8-day-old Syrian golden hamsters (*Mesocricetus auratus*; PD8 hamsters) and 48 weight matched 4- to 5-day-old Norway rats (*Rattus norvegicus*; Postnatal Day 4–5 [PD4–5] rats; $n = 24$ of each age) were used. Hamster infants were from 16 litters born to Syrian golden hamsters, and rat infants were from 16 litters born to Sprague-Dawley Norway rats. Adult hamsters and rats were housed in standard laboratory cages (48 × 20 × 26 cm) in the animal colony at the University of Iowa. Food and water were available ad libitum. Body weights ranged from 7.7 to 14.3 g for the PD8 hamsters and 8.5 to 14.7 g for the PD4–5 rats. All litters were culled to 8 infants by 3 days after birth (day of birth = Day 0). The animal colony was maintained on a 14:10-hr light–dark cycle for the hamsters and a 12-hr light–dark cycle for the rats (lights on at 0600).

Test Environment

The test environment has been previously described in detail (Sokoloff et al., 2000). Briefly, huddles of infants were tested in a double-walled glass chamber (17 cm in height; i.d. = 12.5 cm). Air temperature inside the chamber was controlled by circulating temperature-controlled water through the chamber's walls. Access holes in the side of the chamber allowed for the connection of thermocouples and the passage of air through the chamber at a rate of 1,200 ml/min (300 ml/min/pup; Alberts, 1978a). A round polyethylene mesh platform allowed the infants to move freely within the chamber.

Temperature Measurements

The temperature of the chamber ($T_{chamber}$) was measured using a calibrated chromel-constantan thermocouple (Omega, Stamford, CT) accurate to within 0.1 °C. $T_{chamber}$ was measured by attaching the thermocouple to the glass wall on the inside of the metabolic chamber. The thermocouple was connected to a digital thermometer (Omega, Stamford, CT) located outside the chamber.

IR Thermography

The IR thermography system consists of an IR camera (FLIR Systems, Portland, OR) and a Windows NT computer system that controls the camera as well as image acquisition and analysis (ThermaCAM Researcher 2000, FLIR Systems, Portland, OR). IR thermography is ideal for studies of huddling behavior because it allows for the acquisition of huddle surface temperature and huddle surface area without disturbing the infants' ongoing behavior (Sokoloff & Blumberg, 2001). The IR system has an accuracy of ± 1.0 °C and a sensitivity of 0.1 °C.

To measure surface temperature with IR thermography, we needed to derive calibration equations to obtain accurate measures of T_{huddle}. The process of deriving these calibration equations has been described in detail elsewhere (Sokoloff & Blumberg, 2001). Briefly, calibration equations and an average emissivity value were derived for PD8 hamsters and were used to correct IR temperature data acquired during the experiment. The emissivity of PD4–5 rat skin and the regression equation for correcting IR temperatures were determined from previous emissivity values and regression equations for 2-day-old and 8-day-old rats (Sokoloff & Blumberg, 2001).

Data Acquisition

Thermal data (i.e., $T_{chamber}$ and IR images) were acquired by the experimenter once every 15 min throughout the test. $T_{chamber}$ was recorded by hand and 3–5 successive IR images were saved on hard disk. A minicamera situated above the Plexiglas chamber lid was connected to an S-VHS videotape recorder (JVC, Wayne, NJ) for continuous recording of behavior throughout the test.

Procedure

On the day of testing, 4 infants (hamsters and/or rats), all with visible milk bands, were removed from their home cage(s) and weighed. Huddles had equal numbers of male and female infants, and each infant was marked for identification. Pups were placed in the metabolic chamber maintained at 35 °C and were allowed to acclimate to the chamber for at least 45 min. Three experimental groups were tested. The hamster group consisted of four-pup huddles of PD8 hamsters. The rat group consisted of four-pup huddles of PD4–5 rats. Finally, the mixed group consisted of four-pup huddles of 2 PD8 hamsters and 2 PD4–5 rats.

At the end of the 45-min acclimation period, videotaping began, and a 15-min period of behavioral data was acquired at a thermoneutral air temperature (35 °C). After 15 min, the lid of the chamber was removed and the first set of IR images was acquired. The chamber lid was replaced within 10 s, and the temperature was decreased to 30 °C. For the next 60 min, IR images were acquired at 15-min intervals. This procedure was repeated for the subsequent changes in chamber temperature to 25 °C and 20 °C. After the test, the infants were removed from the chamber and returned to their home cage.

Behavioral Data

Behavioral data were analyzed as described by Sokoloff et al. (2000). Briefly, for each huddle, data were analyzed for only 1 infant of each species (i.e., 1 hamster and/or 1 rat). For overall comparisons of behavioral data, a focal pup was randomly selected from each species. For hamster and rat huddles, 1 focal pup was selected (i.e., 1 hamster or 1 rat), and for mixed huddles, 2 focal pups were selected (i.e., 1 hamster and 1 rat).

Two measures of huddling were scored: three-dimensional (3-D) huddling and contact. We scored 3-D huddling by determining when the focal pup was situated on top of, underneath, or between the other littermates in the huddle. Contact behavior was scored by determining the number of littermates with which the focal pup was in direct contact at any given time during the period of observation. In addition, active sleep (e.g., myoclonic twitching), stationary awake (e.g., yawning and stretching), and translational awake (e.g., forward locomotion and righting) behaviors were scored.

Data Analysis

For the analysis of behavioral data, the test was divided into a 15-min baseline period at thermoneutrality (35 °C) and successive 60-min periods

at 3 subthermoneutral air temperatures (i.e., 30 °C, 25 °C, and 20 °C). For each 60-min period, the fourth 15-min period, designated the *stability* period (Min 45–60), was scored.

The behaviors of the focal pups were coded by an experienced observer during video playback and were recorded using an event recorder program written in HyperCard (HyperCard, 1991) for the Macintosh. HyperCard programs were also used to calculate the duration of each behavior for each 15-min period. Converted data were then imported into StatView 5 (StatView, 1998) for statistical analysis.

To assess inter- and intrarater reliability, we performed simple regression analyses on randomly chosen segments of behavioral data for stability periods at each of the values of $T_{chamber}$ for infants from both species. For all behaviors scored, tests of interrater reliability yielded rs $\geq$ .89. Intrarater reliability tests for the same measures were even higher with rs $\geq$ .91.

At each temperature, a mean value for $T_{chamber}$ was calculated from two data points acquired just prior to the appropriate 15-min period corresponding to the acquisition of behavioral data. T_{huddle} was analyzed as described by Sokoloff and Blumberg (2001). Briefly, the temperature value (in degrees Celsius) of each pixel that consisted of the exposed surface of the huddle was selected and imported into StatView 5 to obtain the average T_{huddle}.

IR images also provided a means of assessing the exposed surface area of the huddle. To do this, we analyzed IR images of the huddle using NIH Image (v. 1.62; National Institutes of Health, Washington, DC, available at http://rsb.info.nih.gov/nih-image/). An outline of the huddle was created by tracing a silhouette of the exposed surface of the infants using a drawing tablet (Wacom Technology Corporation, Vancouver, WA). Percentage change in huddle surface area (ΔHuddle Spread) was obtained by subtracting the baseline (i.e., 35 °C) huddle surface area from its value at each time point during the experiment and multiplying this value by 100.

Physiological and behavioral data were analyzed using repeated measures analysis of variance (ANOVA). Single factor ANOVAs and Fisher's protected least squared difference were used as post hoc tests when significant main effects or interactions were obtained. Alpha was set at .05. For missing data, values were interpolated from the average of individual values immediately preceding and following the missing value (T_{huddle} and ΔHuddle Spread). These instances of interpolation were rare (< 0.6% of all cells). When appropriate, the degrees of freedom for statistical analyses were adjusted.

Results

Huddles composed partially or entirely of infant hamsters exhibited significantly reduced T_{huddle}s during cold exposure. Figure 1A presents T_{huddle} for all huddles of infants at each of the three levels of cold exposure. A single factor ANOVA indicated that at 35 °C, T_{huddle} for hamster huddles was already significantly lower than T_{huddle} for rat and mixed huddles, $F(2, 21) = 13.9$, $p < .01$. As $T_{chamber}$ decreased below 35 °C, T_{huddle} differed between all three groups, $F(2, 21) = 90.8$, $p < .01$. Although all groups showed significant decreases in T_{huddle} with each decrease in $T_{chamber}$ (ps $< .01$), T_{huddle} for the rat group was significantly higher than T_{huddle} for the mixed and hamster groups throughout the test (ps $< .01$).

Figure 1B presents the ΔHuddle Spread for all huddles of infants at each of the three levels of cold exposure. A single factor ANOVA indicated that there was no significant difference in the exposed huddle surface area at 35 °C between the three groups. As $T_{chamber}$ was decreased below 35 °C, huddle surface area decreased, although the magnitude of decrease began to differ between groups: temperature, $F(2, 40) = 19.9$, $p < .01$; Temperature × Group, $F(4, 40) = 2.9$, $p < .05$. Specifically, at 20 °C, both

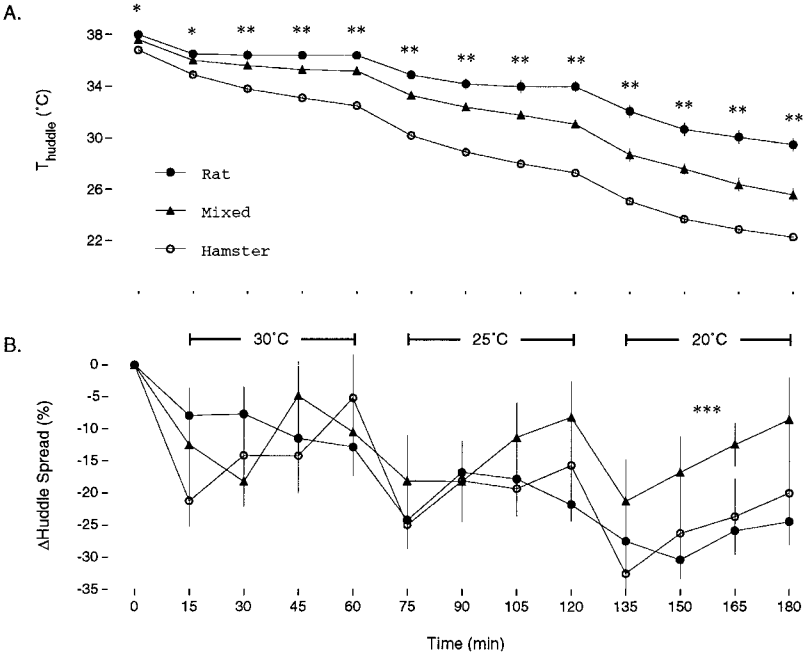

Figure 1. (A) Huddle temperature (T_{huddle}) and (B) percentage change in huddle surface area (ΔHuddle Spread) for four-pup huddles of PD8 hamsters and PD4–5 rats. Rat huddles were always warmer than mixed and hamster huddles. The largest and most sustained ΔHuddle Spreads were shown by rat and hamster huddles. * = rat and mixed huddles were warmer than hamster huddles; ** = all three groups were significantly different from each other; *** = mixed huddles were significantly different from the other two groups.

hamster and rat huddles showed significantly larger reductions in surface area than mixed huddles ($ps < .01$).

Figure 2 presents the 3-D huddling of infant rat and hamster focal pups in the three huddle groups. As the temperature decreased below 35 °C, 3-D huddling increased for all focal pups, regardless of huddle group, $F(3, 84) = 59.0$, $p < .01$. Repeated measures ANOVA also revealed a significant effect of focal pup species as well as an interaction between focal pup species and huddle condition, $Fs(1, 28) > 6.0$, $ps < .05$. Focal pups from rat huddles significantly increased 3-D huddling at 30 °C and spent significantly more time exhibiting 3-D huddling at 30 °C and 25 °C as compared with all other focal pups from the remaining huddle conditions ($ps < .05$). Finally, in contrast to focal pups from rat huddles, the other focal pups did not show maximal amounts of 3-D huddling until $T_{chamber}$ reached 20 °C ($ps < .05$).

As shown in Figure 3, three-pup contact (i.e., the amount of time spent by the focal pup in contact with the 3 other infants in the huddle) increased for all focal pups as the temperature decreased below 35 °C, regardless of huddle group, $F(3, 84) = 14.7$, $p < .01$. Repeated measures ANOVA again indicated a significant interaction between focal pup species and huddle condition, $F(1, 28) = 5.4$, $p < .05$. Post hoc analyses revealed significant differences at 30 °C in the amount of three-pup contact of focal pups from rat huddles when compared with focal pups in the other three conditions ($ps < .01$). Finally, as with 3-D huddling, focal pups from rat huddles increased three-pup contact at 30 °C, whereas the other focal pups did not increase three-pup contact until $T_{chamber}$ decreased to 25 °C or 20 °C ($ps < .05$).

Because the behavior of rat focal pups from rat-only huddles and from mixed huddles differed, we performed a more detailed analysis of contact behavior within mixed huddles to see why infant rats in this huddle composition huddled less effectively. Specifically, we observed hamster and rat focal pups during one-pup and two-pup contact (i.e., focal pup contact with only 1 or 2 infants in the huddle). Figure 4A shows the proportion of time

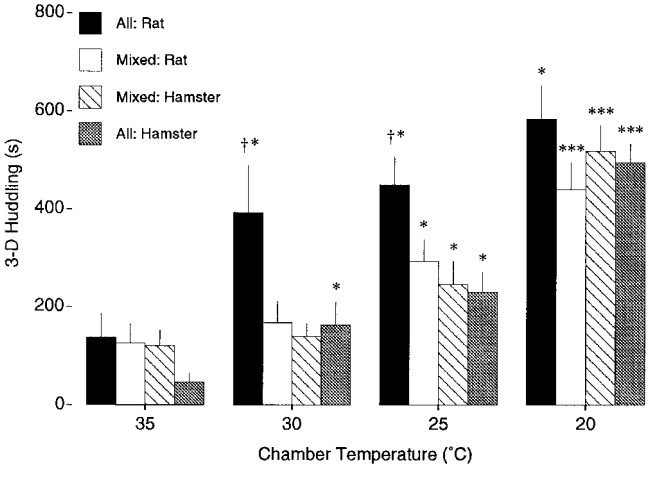

Figure 2. Mean (± *SEM*) duration of three-dimensional (3-D) huddling for all focal pups throughout the test. Only focal pups from rat huddles exhibited immediate increases in 3-D huddling when the chamber temperature ($T_{chamber}$) decreased below 35 °C. † = significantly different from all other focal pups at that particular $T_{chamber}$; * = significantly different from 35 °C; *** = significantly different from all other $T_{chamber}$.

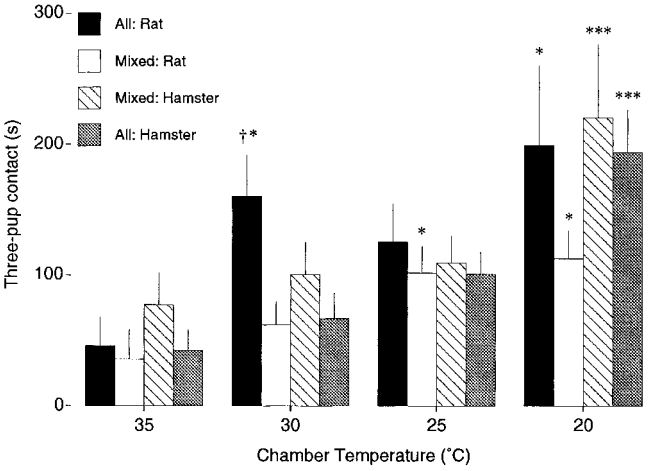

Figure 3. Mean (± *SEM*) duration of three-pup contact for all focal pups throughout the test. Only focal pups from rat huddles exhibited increases in three-pup contact as soon as the chamber temperature ($T_{chamber}$) decreased below 35 °C. Rat focal pups from mixed huddles exhibited smaller increases in the duration of three-pup contact than the other focal pups. † = significantly different from rat focal pups from mixed huddles and hamster focal pups from hamster huddles at that particular $T_{chamber}$; * = significantly different from 35 °C; *** = significantly different from all other $T_{chamber}$.

hamster focal pups spent in contact with only 1 hamster or 1 rat throughout the entire test. The one-pup contact of hamster focal pups changed as $T_{chamber}$ was decreased, $F(3, 42) = 4.2$, $p = .01$. Specifically, at 35 °C, hamster focal pups spent more time in contact with the other hamster than with a rat ($p = .01$). As $T_{chamber}$ decreased, however, the amount of contact between the hamster focal pup and a hamster or a rat did not differ. Figure 4B shows the proportion of time rat focal pups spent in contact with only 1 hamster or 1 rat. As cooling progressed, rat focal pups spent more time in contact with a hamster than with the other rat, $F(1, 14) = 9.1$, $p < .01$. Specifically, at 25 °C and 20 °C, the amount of contact with a hamster was greater than focal pup contact with the other rat ($ps < .05$).

Figure 5A shows the proportion of time hamster focal pups spent in contact with a mixed pair (i.e., a hamster and a rat) or a pair of rats. Hamster focal pups spent a significantly larger proportion of time in contact with a mixed pair, $F(1, 14) = 37.0$, $p < .01$. Figure 5B shows the proportion of time rat focal pups spent in contact with a mixed pair or the pair of hamsters. During cooling, rat focal pups spent more time in contact with the pair of hamsters, although this difference was not significant, $F(1, 14) = 4.5$, $p = .05$. At 25 °C and 20 °C, however, it is apparent that rat focal pups showed more two-pup contact with the pair of hamsters than with a mixed pair.

Infant hamsters exhibited less active sleep and more stationary awake behavior than infant rats, $Fs(1, 28) > 31.0$, $ps < .01$. Infant hamsters also exhibited more translational awake behavior than infant rats, $F(1, 28) = 31.9$, $p < .01$. In fact, as shown in Figure 6, infant hamsters, regardless of huddle condition, showed significantly higher levels of translational awake behavior than infant rats at each temperature ($ps < .01$). If infant hamsters are sleeping less and moving more, they could be more effective at establishing

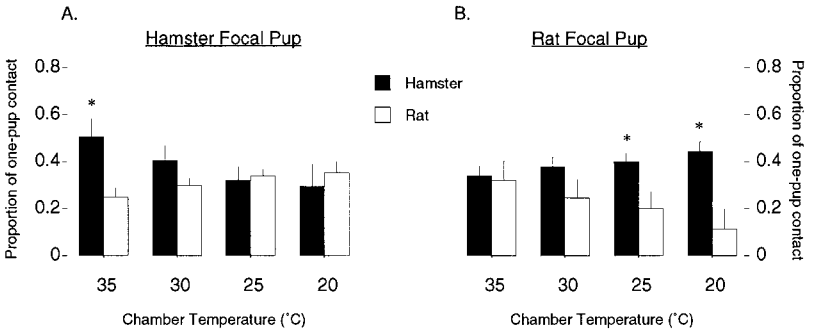

Figure 4. Proportion of one-pup contact hamster (A) and rat (B) focal pups from mixed huddles spent with either a hamster or a rat. For hamster focal pups, the proportion of time spent in contact with a hamster or a rat did not differ during cold exposure. For rat focal pups, the proportion of time spent in contact with a hamster increased as cold exposure progressed. *$p < .05$.

contact with infant rats, thereby, improving their thermoregulatory success.

Discussion

The present study is the third in a series examining the contribution of BAT thermogenesis to the effectiveness of huddling by altricial infants. In the first study (Sokoloff et al., 2000), a comparative approach was adopted in which different-sized huddles of infant rats or infant hamsters were observed during cold exposure to determine whether BAT thermogenesis was necessary for group thermoregulatory success. In that study, infant rats more successfully defended T_{huddle}, whereas huddles of infant hamsters, regardless of huddle size, did not. In the second study (Sokoloff & Blumberg, 2001), a pharmacological approach was adopted to examine whether the huddling of infant rats was affected by the inhibition of BAT thermogenesis. That study indicated once again that BAT thermogenesis is a necessary resource for group regulatory success—huddles of heat-producing rats showed higher T_{huddle}s than huddles of infant rats that lacked heat production. In the present study, again using a comparative approach, we have once more shown that BAT thermogenesis is a necessary resource for effective huddling during cold exposure. Specifically, huddles composed entirely of infant rats more effectively defended elevated T_{huddle}s during cold exposure. Mixed huddles of infant rats and hamsters, as well as huddles of infant hamsters, exhibited significantly lower T_{huddle}s throughout the test.

In our first comparative study on huddling, we found that infant hamsters did not aggregate as effectively as infant rats. Furthermore, infant hamsters showed more locomotor behavior within the huddle at all temperatures tested (Sokoloff et al., 2000). In the present study, these same behavioral differences between infant hamsters and infant rats within the huddle were observed. Specifically, infant hamsters did not exhibit substantial increases in 3-D huddling or three-pup contact until they were exposed to 20 °C, whereas huddles of infant rats showed significant increases in huddling behavior on exposure to 30 °C.

Although differences exist between infant hamsters and infant rats with respect to their behavior within the huddle, one prediction of the present study was that infant hamsters would huddle more effectively if allowed to huddle with heat-producing infant rats. Even though infant hamsters did not show increases in those behaviors exhibited by infant rats within the huddle (i.e., 3-D huddling and three-pup con-

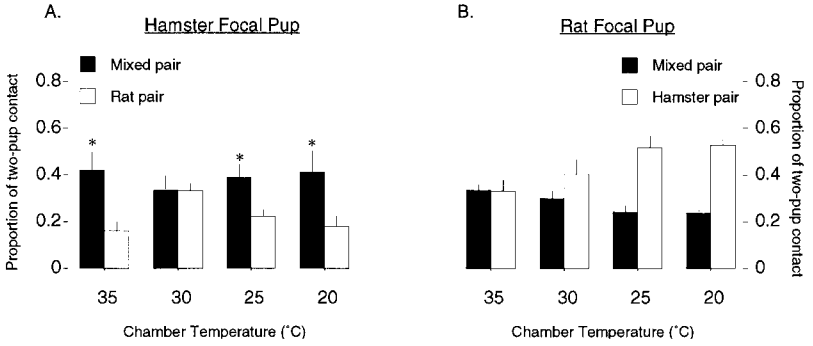

Figure 5. Proportion of two-pup contact hamster (A) and rat (B) focal pups from mixed huddles spent with specific pairs of pups during the last 15 min of exposure to each chamber temperature. For hamster focal pups, the proportion of two-pup contact spent with a mixed pair (i.e., 1 hamster and 1 rat) was greater than the proportion of two-pup contact spent with a pair of rats. For rat focal pups, the proportion of two-pup contact spent with a pair of hamsters increased as cold exposure progressed. *$p < .05$.

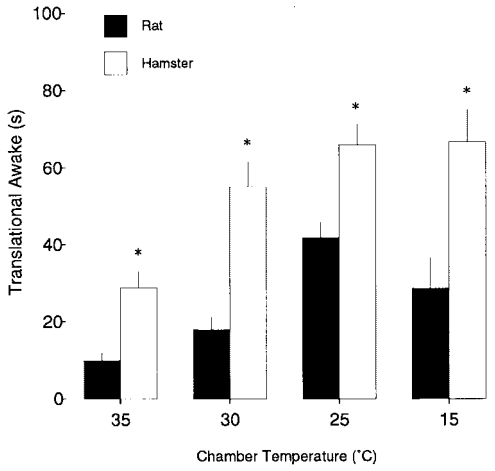

Figure 6. Mean (± *SEM*) translational awake behavior (in seconds) for hamster and rat focal pups. Hamster focal pups exhibited more translational awake behavior than rat focal pups at all chamber temperatures. $*p < .05$.

tact), infant hamsters did show effective behavioral thermoregulation within the huddle by initiating and maintaining contact with 1 or more heat-producing rat pups as the air temperature decreased.

As stated earlier, besides differences in the ability to produce heat endogenously, infant hamsters and rats exhibit differences in the behaviors they show within the context of the huddle. These differences in behavior exhibited by infant hamsters and rats could arise from nonthermoregulatory differences between these two species. Specifically, even though gestation length is 16 days for hamsters and 21 days for rats, hamsters are more motorically active during the early postnatal period (Kleitman & Satinoff, 1982; Sokoloff et al., 2000; Sokoloff et al., 2002). In fact, these differences in motor behavior may facilitate the differences in thermoregulatory behavior shown by infant hamsters and infant rats. Unfortunately, it is difficult to control for all developmental differences between infant hamsters and infant rats, especially during the early postnatal period when stimulus control of huddling behavior is changing rapidly (Alberts, 1978b; Alberts & Brunjes, 1978; Brunjes & Alberts, 1979; Leonard, 1974).

Huddling has long been considered an effective form of group thermoregulation, although the behavior of huddling emerges, in large part, from infants satisfying their individual needs (Alberts, 1978a; Schank & Alberts, 1997). Because infant hamsters exhibit more rapid thermotaxis than infant rats (Kleitman & Satinoff, 1982; Leonard, 1974; Sokoloff et al., 2002) and are motorically active even when cold (Sokoloff & Blumberg, 1998; Sokoloff et al., 2000), the opportunity to huddle with infant rats would provide the infant hamster with a unique means of thermoregulation within the context of the huddle. Therefore, the finding that infant rats in mixed huddles spent more time in contact with infant hamsters as cold exposure progressed (see Figures 4 and 5) was most likely driven by the behavior of the infant hamsters. Specifically, the heat produced by infant rats provided the infant hamsters with a thermal stimulus toward which they could orient and approach, thereby improving their thermoregulatory success.

Figure 7 presents three IR images from three representative huddles recorded at the end of the 60-min period of exposure to 20 °C for mixed huddles. It is clear that infant hamsters not only establish contact with infant rats but also monopolize the infant rats in such a way that contact between the two rats is impaired. Furthermore, on the basis of the location of BAT and the success of the infant hamsters at establishing contact with infant rats, it appears that the heat produced by BAT provides an attractive stimulus to the infant hamsters.

As stated earlier, previous studies of infant hamster huddling have shown that these infants do not form organized or effective huddles until late in the 2nd week postpartum (Leonard, 1982). This increase in huddling behavior by infant hamsters corresponds to the time that these infants exhibit BAT thermogenesis (Blumberg, 1997; Hissa, 1968). Before the development of endothermy, however, huddle size has little impact on thermoregulation during cold exposure (Sokoloff et al., 2000). Therefore, the absence of huddling by infant hamsters in the early postpartum period could arise not only from the lack of heat production to combat heat loss and maintain the body temperature of each hamster, but also from the lack of a sufficient thermal stimulus to support aggregation (Leonard, 1982; Sokoloff et al., 2000).

We have proposed that experience with the heat production of littermates helps to scaffold huddling behavior during the 1st week postpartum (Sokoloff & Blumberg, 2001). Perhaps if infant hamsters exhibited BAT thermogenesis or had access to other heat-producing infants (i.e., infant rats) earlier in the postpartum period, the thermoregulatory behavior of these infants could be modified. Specifically, if infant hamsters were cross-fostered to rat dams and rat littermates, it is possible that the aggregation behavior of infant hamsters could be altered. Cross-fostering studies of mice with rats have shown that the early developmental environment can greatly impact subsequent behavioral expression. For example, it has been shown that mice are less active and less aggressive when reared with rat mothers and rat siblings (Denenberg, Hudgens, & Zarrow, 1964; Hudgens, Denenberg, & Zarrow, 1967; Hudgens, Denenberg, & Zarrow, 1968; Rosenberg, Denenberg, & Zarrow, 1970). In the present study, infant hamsters were acutely exposed to infant rats, therefore, more time spent huddling with infant rats may be necessary to determine whether infant hamster behavior could be modified.

In the present study, the thermotaxic behavior of infant hamsters allowed these infants to monopolize contact with heat-producing infant rats, thereby compensating as best as the hamsters could for their own lack of endogenous heat production. In contrast, individual infant rats effectively maintain thermal homeostasis using BAT across a range of ambient temperatures, and this range is

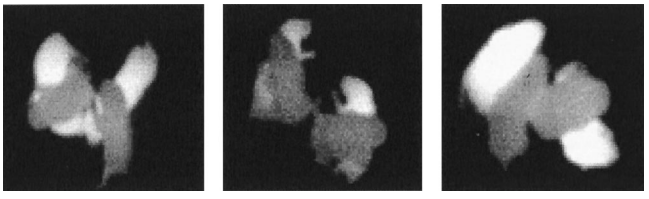

Figure 7. Infrared images at the end of the period of exposure to 20 °C for three mixed huddles. In each image, the darker bodies are the cooler infant hamsters, and the lighter bodies are the warmer infant rats. As is evident from the images, infant hamsters took advantage of the thermal opportunity afforded by contact with infant rats.

greatly extended as additional heat-producing infants are added to the huddle (Alberts, 1978a; Blumberg & Sokoloff, 1998; Sokoloff et al., 2000). Although infant rats were at a behavioral disadvantage when huddling with infant hamsters, these infant rats, nonetheless, were able to maintain elevated body temperatures using BAT. These observations highlight the notion that huddling did not arise merely as behavioral compensation for inadequate physiological capabilities but that behavior and physiology are complementary in the context of huddling. Therefore, in pursuit of an elevated and sustained body temperature, each individual rat or hamster behaves in such a way as to maximize heat gain and minimize heat loss. The end result is that the behavioral strategy used to achieve this goal is intimately tied to the individual rat or hamster's endothermic capabilities.

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