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Huddling by Rat Pups: Ontogeny of Individual and Group Behavior

ABSTRACT: *A full account of behavioral development in rats must include the ontogeny of both individual and group behavior. Most of our accumulated knowledge, however, pertains to individual ontogenesis. Group behavior and its development are readily seen in the huddling behavior of rat pups. A rat huddle is an entity with characteristics and capabilities distinct from those of the individuals that comprise it. The huddle is a natural context for acquiring olfactory preferences for species odors. Olfactory learning in a huddle involves thermal and tactile stimulation from the mother's body but, surprisingly, not the rewards of suckling or of milk transfer. Although there is complete developmental continuity of huddling behavior, the sensory controls of huddling change dramatically during the first 2 weeks of postnatal life. Huddling behavior is initially controlled by thermal cues (''physiological huddling'') and then becomes dominated by olfactory stimuli (''filial huddling''). The complex group behavior of huddling was modeled successfully with computational methods. Group behavior emerges from individual interactions, guided entirely by rules of individual behavior (no rules for group behavior). Three simple rules of autonomous activity/inactivity can spawn the patterns of aggregon formation displayed by groups of 7-day-old pups, but not by 10-day-olds. The developmental change evident by Day 10 requires adding a rule by which each individual is affected by the activity state of adjacent pups. Group behavior responded to manipulations of central oxytocin on Day 10, but not on Day 7.* © *2006 Wiley-Periodicals, Inc.* Dev Psychobiol 49: 22–32, 2007.

Keywords: *early experience; infant; motor; neonatal; orientation*

INTRODUCTION

The present article is a contribution to the archival record of a symposium celebrating Jay S. Rosenblatt, who has long contributed to the scientific study of maternal behavior and to the analysis of behavioral development. Among his earlier, integrative essays, were analyses that described the ''synchrony between maternal behavior and offspring development'' (e.g., Rosenblatt, 1965). Here he painted a picture of the ways in which the phased sequence of daily changes in a mother rat's behavior fit the rapidly changing needs and capabilities of the offspring. With beautiful experiments in which offspring age was varied while the behavior of dams at a constant postpartum stage was studied, or the offspring's stage was held constant (by daily substitutions) and the course of the maternal cycle was measured, Jay and his associates demonstrated that offspring continually stimulate their mother in ways that change the dam. They change her internal state, sometimes via hormones (Rosenblatt, 2002) and sometimes without hormonal involvement (Rosenblatt, 1967; Rosenblatt & Siegel, 1981). The mother's stimulation (milk, heat, licking, brooding, protection) of the infants, in turn, fuels and affords offspring growth and development, and the offspring change accordingly. As the offspring change, so does their stimulation of the mother, and thus the dam is altered dynamically (Alberts & Cramer, 1988; Alberts & Gubernick, 1983).

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Plainly (and paradoxically), the offspring are both individual and not. That is, *rat pups exist both in a litter and as a litter.* Similarly, they develop both as individuals and as a group. These two domains and levels of development are related but not identical. The group is a real, biological entity. But it is an ‘‘emergent’’ entity, and it emerges from individual interactions within the group.

Consistent with the theme of the symposium, the research described in the forthcoming account is mostly from my laboratory. Jay Rosenblatt’s writing, his teaching, and his research have greatly influenced mine; I am happy to attribute its best qualities to Jay and any of its shortcomings to me.

HUDDLING BEHAVIOR

The Norway rat (*Rattus norvegicus*) is a highly gregarious animal, often labeled a ‘‘contact species’’ because much of its life is spent in physical contact with other rats. The rats’ contact behavior, or huddling, starts at birth when the mother gathers the 10 or so newborns into a clump and settles upon them in a nest. The littermates remain together in the natal nest for 2 weeks or more, often in contact with the mother.

During the first few days after birth, the dam may be with the pups nearly constantly (Grota & Ader, 1969; Leon, Croskerry, & Smith, 1978), either brooding, nursing, licking, or maintaining the nest. The mother does leave the group, of course, and these excursions become more frequent and lengthier as lactation progresses (Cramer, Thiels, & Alberts, 1990; Grota & Ader, 1969; Leon et al., 1978). When the dam is absent, pups remain huddled together. The litter does not just lie passively in a heap. They move frequently and the coherence of the group is maintained by their rooting, pushing, and orienting. Should a pup be displaced from the nest, it is likely that it will be observed to orient toward the group and return to it.

After 2 or 3 weeks, the pups are furred, sensorily replete, motorically ept, and are increasingly likely to make excursions from the nest. Their behavioral repertoire expands to include playfighting and other social behaviors, but they nonetheless reliably aggregate and huddle together (Alberts & Leimbach, 1980; Thiels, Alberts, & Cramer, 1990).

ENERGETIC CONSEQUENCES OF HUDDLING

A newborn rat’s dramatic immaturity and rapid postnatal development has been repeatedly and thoroughly documented (e.g., Adolf, 1968; Alberts, 1985, 2005; Bolles & Woods, 1964; Small, 1899). Although the rat pup’s thermal fragility is now well-known (Alberts, 1978a; Blumberg, 2001; Leon, 1986), when Jay Rosenblatt initially described the rat dam’s pup-directed behavior (e.g., Rosenblatt & Lehrman, 1963), the ‘‘traditional wisdom’’ concerning the infant’s body temperature regulation still needed correction. Around that time it was unexpected to find that infant rat pups in huddles lose heat more slowly than do singletons (Alberts, 1978a; Blumberg, 2001).

Particularly noteworthy was the demonstration that metabolic expenditure (oxygen consumption) by pups decreased with increasing numbers of bodies huddling together (Alberts, 1978a). Litters of pups were arranged as eight singletons, then four pairs, then as two huddles of four, and in a single aggregate of eight. (This was done both in ascending and descending sequences, of course.) Oxygen consumption by each combination was measured. Figure 1 shows that oxygen consumption (ml/gm/time) was less in the larger, that is, warmer, groups. The descending slope of oxygen consumption rate with increasing warmth conforms to the metabolic profile of an endotherm. This was the surprise, because there were many who considered the infant rat to be both immature and even primitive, that is, nonregulatory and ectothermic in means of temperature balance (see Alberts, 1978a; Blumberg, 2001; Blumberg, 2001).

The huddle thus earned significance as a kind of physiological entity. Under conditions in which individual

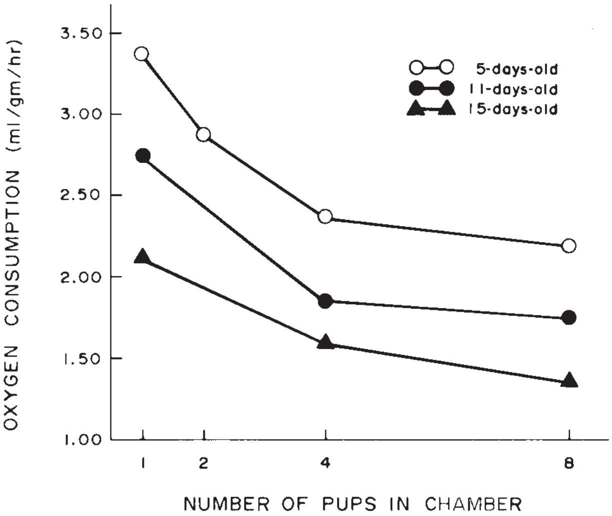


FIGURE 1 Metabolic effort (rate of oxygen consumption) by squads of eight pups separated in individul stalls or in (four) clumps of two, (two) clumps of four, or as a single huddle. Heat loss is attenuated as a function of group size (Alberts, 1978a): Body temperatures are lowest in the singletons and highest in pups huddled as eight. Metabolic energy is conserved as a function of group size by huddling pups at 5-, 10-, and 15-days of age. From Alberts (1978a).

pups perform as ectotherms, a group of them displays an endothermic pattern. Thus, the group was shown to be different than the individuals comprising it (Alberts, 1978a).

STIMULUS CONTROL OF CONTACT BEHAVIOR

Experimental results and observational data such as those described in the previous sections demonstrated the significance of huddling behavior. It was relevant to ask, ''what are the cues that elicit and maintain contact among rat pups?''

To answer basic questions of stimulus control of huddling, rat pups, 5-, 10-, 15- or 20-days of age were tested individually in arenas scaled approximately to their size and locomotor ability. Normally, huddling behavior among littermates is interactive. When two or more animals are in contact, each huddles with the other(s), and there is no control over which animal moves or when or how much it does. Therefore, for better control in these experiments, the test stimuli were stationary so that the behavioral dynamics were always attributable to the subject. Frequency and duration of contact during 4-hr-long tests was measured. We obtained robust levels of huddling (>3 hr/session).

A variety of stimuli were used. An anesthetized agemate elicited huddling, as did a euthanized pup that had been cooled to room temperature (Alberts, 1978b). Other stimuli were inanimate models. Intranasal zinc sulphate was used to render pups anosmic as a means of examining olfactory controls of huddling. From these various experiments, it was concluded that huddling by rat pups is under ''multisensory control.'' That is, the results indicated that any of a variety of cues can elicit and maintain pups' contact behavior. The important cues include heat, attenuation of light, contour, texture, odor, and inertia.

EMERGENCE OF SPECIES-SPECIFIC PREFERENCE

Is there a hierarchy of preference or are all the cues sufficient to elicit huddling equally potent? Peter Brunjes, then a graduate student, and I found that by 15 days of age, a pup prefers to huddle with a like-aged rat rather than with a similarly sized (and thermally similar) gerbil. To younger rats, however, gerbils and rats are equally attractive, whether presented singly or simultaneously (Alberts & Brunjes, 1978). Interestingly, gerbils do not become less attractive to 15-day-old rats. It is just that 15-day-old rats prefer to huddle with other rats. This basic finding enabled us to document a developmental transition in the salience of some of the cues that affect huddling by rat pups.

For the infant rat, heat is the salient cue for eliciting and maintaining huddling (Alberts, 1978b; Alberts & Brunjes, 1978; Sokoloff & Blumberg, 2001). Heat is also the physiological commodity conserved by contact behavior (Alberts, 1978a; Alberts & Gubernick, 1983). Thus, heat is both cue and commodity in huddling. We, therefore, dubbed infant huddling to thermal cues, *physiological huddling*. Upon this thermal foundation, and with continuing development, the contributions from other senses become increasingly influential. At about 2 weeks of age, conspecific odors emerge as an especially potent cue for huddling. Rosenblatt (1976) outlines some basic aspects of such sensory-based transitions.

Generally, odors are not considered to be a physiological stimulus in the same way that heat is. An odor may, by association or by some other mechanism, represent species identity; or odor may simply be associated with a source of heat. Either way, the organizational basis of huddling changes with the addition of olfactory guidance and the behavior becomes *filial*. This, then, is the transition from ''physiological to filial huddling.''

THE FILIAL PREFERENCE IS LEARNED

The preference for huddling with conspecifics displayed by Day 15 rats provides a noteworthy developmental milestone but it does not inform us about the basis of this preference. Is it a ''predetermined,'' species-typical characteristic of a rat's development, a sensory/perceptual fixation awaiting the necessary neural maturation? Or, alternatively, is the rat's preference guided by experience? We examined these possibilities.

The logic was to alter the olfactory characteristics of the dam and thus create a distinct maternal odor that would be naturally associated with certain experiences of the pups. We altered a mother's odor by anointing her ventrum with an ''arbitrary'' and nonbiological odor. Everyday from Postnatal Day 1 to Day 14, one of two different odorants was applied to the ventral fur of the mother of each test litter. These family units were otherwise left undisturbed until Day 15, the previously identified age for seeing olfactory-guided ''filial huddling'' (Alberts & Brunjes, 1978).

Pups (15-day-old) reared by scented dams spent more time huddling with a similarly scented, anesthetized rat than with an equally accessible, naturally smelling anesthetized rat (Brunjes & Alberts, 1979). We had reassigned the Norway rats species-typical, filial huddling preference. The altered preference was specific to the odor placed on the dam. We had not simply disrupted normal development or observed contact with any strong, unusual odor. To use terminology proffered by Gottlieb (1976), the pups' experience with an artificially scented mother had *induced* a filial preference for the artificially scented rat smell. Such induction was seen not in the expression of contact behavior, but rather in the perceptual preferences that guided huddling.

The basic finding that a rat's species-specific preference could be easily reassigned, led us to seek to identify the inductive experience. Sucking and the receipt of mother's milk seemed logical and likely answers. This proved to be untrue.

TITRATING THE INDUCTION OF HUDDLING PREFERENCES

We were impressed of course that relatively brief (4 hr), daily exposures to a scented foster dam induced a filial huddling preference in the 15-day-olds. But, before pursuing questions about specific mechanisms that might induce social preferences, it was important to consider a most general explanation of the phenomenon. This was the role of *familiarity.*

Odors associated with the foster dam become familiar. In previous tests of huddling preferences, we compared a familiar olfactory stimulus to a novel odor. Thus, we could not be certain that we were seeing an effect of a maternal association or, more generally, the effect of familiarization. There were already several important examples in which basic sensory registration—familiarity from mere exposure—had profound behavioral effects (cf., Galef, 1982; Hoffman, 1979; Leon, Galef, & Behse, 1977; Sluckin, 1964).

Is there a difference between the experience of familiarity (mere exposure) and the experience of receiving the attention of a lactating dam? We adapted our methods to enable *labeling experiences* with distinct odors and then tracing subsequent effects of distinct experiences on later olfactory-guided behavior. In these experiments, litters were separated from their mother once each day (for 4 hr) during which time they received either of two types of experience, each associated with a different odor. Experience with a scented foster dam was provided every other day (e.g., odd-numbered days, from Day 1 to Day 13) and on the alternate days, the litter's experience was that of ‘‘mere exposure’’ to the 2nd odor. In this case, they resided for the 4 hr in an empty container with the 2nd odorant on a gauze pad clipped to the wall above them. On Day 15, a standardized huddling test was run. The test stimuli were tubes wrapped with an artificial fur on which a small amount of a test odor had been applied. A two-choice test was used, with the dam-associated odor on one target and the odor of mere exposure on the other (Alberts & May, 1984).

The results showed that under these conditions, the dam-associated odor elicited and maintained more huddling than did the odor of mere exposure. Thus, familiarity can alter the pups' huddling behavior, but not as strongly as the experience of ‘‘milky mother love,’’ so-called because we confirmed that there was milk transfer, licking, and brooding by foster dams during the daily, 4-hr cohabitations.

Noting that suckling and milk ingestion can both be highly reinforcing stimuli to rat pups (Brake, 1981), we asked whether the suckling experience was necessary for the induction of a filial preference, one that was beyond that provided by mere exposure. To do this, we used maternally responsive virgin rats that provided the full spectrum of maternal activities to the foster pups, but did not lactate (Rosenblatt, 1967). We also monitored them to insure that their nipples remained involuted and that pups were not engaging in nonnutritive suckling. Again, we labeled their maternal behavior with one odor and mere familiarity with another scent. Nonlactating foster dams induced a filial preference stronger than that associated with familiarization. Remarkably, suckling and milk rewards are not necessary for the formation of filial preferences in the preweanling rat pup!

Though the rewards of suckling may be unnecessary for forming filial attachments, it was nonetheless relevant to ask whether suckling augments the pups' experience and produces a stronger preference. Apparently, it does not. ‘‘Milky mother love’’ (exposure to a lactating foster mother) was labeled with one odor and nonlactating foster dam was labeled with the other. After the standard 14 days of alternating exposures, we tested the pups on Day 15. The two forms of experience induced equivalent preferences. Suckling and milk transfer appear to be unnecessary and nonadditive in the induction of filial huddling preferences.

After discovering that suckling and milk rewards were neither necessary nor additive in the induction of filial huddling, we asked further about what forms of maternal stimulation might be sufficient to induce the olfactory preference. The next likely candidate was the thermotactile stimulation derived from contact with the dam's warm, furry, body. For the pups, the dam is a mobile feast of experiences, for the dam's body approaches and settles upon them, often encircling the entire litter, and it remains in place while they root, squirm, shift, probe, and push. It undulates with each breath. Throughout such contact, conductive heat exchange is maintained (also see discussion accompanying Figs. 5 and 6).

To test the inductive power of thermotactile experiences, we simplified matters and presented pups with an olfactorily tagged warm, furry tube. The ‘‘mere exposure’’ control was again employed. Not surprisingly, pups huddled avidly with the warm cylinder during the daily exposures. Although inanimate and motionless, the heated tube was an effective inductor.

One of the more surprising findings came from the final experiment in this series, in which we used labeled experiences to assay the relative strengths of ‘‘milky-mother love’’ and basic thermotactile experiences. In other words, we provided pups with 14 daily experiences alternating between a scented, lactating foster dam and the warm, furry tube bearing a 2nd odor. The standardized huddling preference test was conducted on Day 15 with two, simultaneously present fur-wrapped tubes. We found, under these conditions, that the two stimuli were equally effective. It was stunning and definitely not sentimental with respect to mother love, to see that the inanimate stimulus was as effective as the fully active, nursing dam (Alberts & May, 1984).

Recently, graduate student Sayuri Kojima and I have revisited the induction of filial huddling with a series of studies designed to specify when the key inductive events may engage the pups’ filial huddling and whether such experiences are remembered well. Interestingly, pairing odor and foster mother care during the first 5 days does not induce filial preference. Beginning around Day 5, the pups show preferences for maternally associated odors. These associations are retained well at ages when infant rats are notorious for rapidly forgetting other associations (Kojima & Alberts, 2005, 2006).

GROUP AND INDIVIDUAL REGULATORY BEHAVIOR

Not only does a group have physiological characteristics that differ from the individual pup, but also it is possible to recognize ways in which the group actually behaves in ways not seen in the individual. Specifically, when a litter is viewed as a single entity, we can see *group regulatory behavior*, which had previously not been recognized.

Figure 2 depicts four, 10-day-old rat pups. On the right hand side, the drawing is translated into a depiction of the pups as a single entity, essentially by outlining the group ignoring lines of separation where their bodies are in contact and are not separate. I used this approach to characterize and to measure the size (perimeter) of groups of pups under cyclic temperature conditions.

Figure 3 summarizes the results of a series of measures that revealed group regulatory behavior in rat pups. The pups’ ambient temperature is shown on the horizontal axis. Over about 2 hr, the initially cool ambient temperature increased gradually to as much as 40°C and then declined gradually back to the cool, 20°C ambience. Every 10 min during this thermal cycle, a photograph was taken of the litter and a measurement based on a view of the pups as depicted in Figure 3 was made. Using these methods, tightly packed aggregations with parts of bodies touching or partly overlapping subtended as little as 1.4 ‘‘pup units’’ (which was the average circumference of a single pup at each age, correcting for differences in both pup and image sizes) or as much as four pup units, which occurs when all four bodies were positioned without contact.

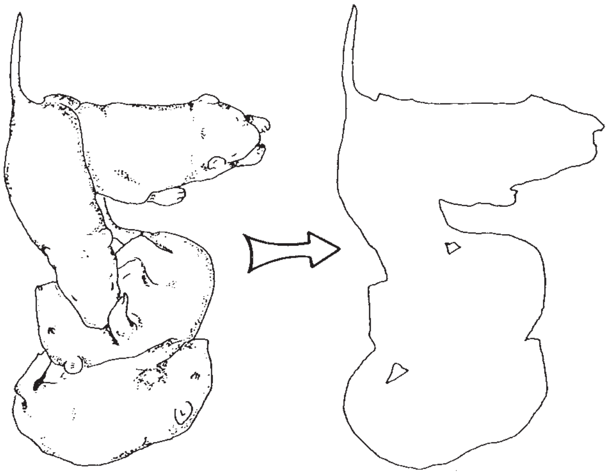


FIGURE 2 Converting a view of four individual pups into one of a single mass with a quantifiable, 2-dimensional surface area. Circumferences of pups as individuals were measured from a fixed distance to yield an average *pup unit* (surface area). Four pups not touching one another = 4 pup units; contact behavior thus yields smaller areas (Alberts, 1978a).

Pups in all of the age groups interacted in a manner that produced group surface areas that varied directly with ambient temperature. Thus, the pups display *group*

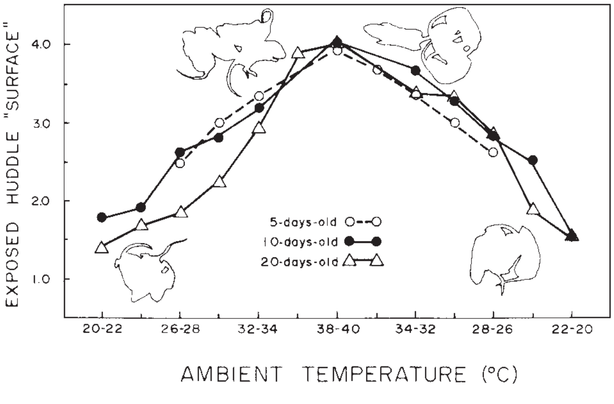


FIGURE 3 Group regulatory behavior by huddles of rat pups at 5-, 10-, and 15-days of age. This summary graph (cf., Alberts, 1978a) shows the surface area of huddles (expressed in size-corrected ‘‘pup units’’). Huddles of pups exposed to a 2-hr-long cycle of ambient temperatures that begin cool (20°C), increase to as much as 40°C, and then decrease to 20°C show a corresponding increase and decrease in exposed surface area.

regulatory behavior. They form more compact aggregations at cool temperatures and looser ones at warm temperatures. In doing so, they regulate the group's surface:mass ratio—the very parameter by which they gain and lose heat.

We had purposively simplified the group regulatory behavior in the studies depicted by Figure 3, by studying small ($n = 4$ pups) huddles and by observing pups on a flat surface without the 3-dimensional geometry of a nest and without the presence of the mother. Additional analyses were conducted, however, and these revealed some of the intricacies of the behavior. Figure 4, for instance, depicts the movements of pups when the huddle is observed within a slope-sided, nestlike container. The arrows superimposed on the pups in Figure 4 show the direction of their movements. The graph within Figure 4 shows the time that specific, marked, ''focal pups'' were visible on the surface of the huddle. This figure shows that a huddle of pups is an active, seething mass of bodies. The movements of the pups create ''convection currents'' of bodies through the huddle, as pups dive down into its depths and displace other pups that rise to the surface (see Alberts, 1978a for more detailed experiments on the directionality and the bases of pup flow).

Do group regulatory behavior and pup flow occur under more naturalistic conditions? Yes, they do. Rat dams and litters resided in an artificial ''burrow,'' consisting of three darkened (but infrared illuminated) interconnected chambers that opened onto a large ''field'' with a normal light/dark cycle. The dams' behavior resembled that observed in feral *R. norvegicus* living in seminatural, outdoor habitats (e.g., Calhoun, 1963) where lactating dams maintain a cache of hordage in a burrow chamber separate from the one used to brood and nurse the pups. From infrared video recordings of the nests, we measured the surface areas of litters immediately after undisturbed departures of the dam and minutes before an undisturbed return to the nest. As predicted from the laboratory experiments in which ambient temperature was manipulated, group surface expanded after pups received conductive heat from the dam's body. Pups subsequently reduced group surface area in the timeframe and more modest conditions of convective heat loss that occurred in their nest (Addison & Alberts, 1980).

In another set of experiments, we (Alberts & White, 1985, unpublished) observed litters of pups and their mother through the glass floor of a maternity chamber. For purposes of these observations, there was no nesting material. Two pups in a litter were marked distinctively and served as the ''focal'' subjects. The absence of nesting material provided an opportunity to observe the complex behavior of a litter of pups beneath the body of a mother rat during undisturbed brooding, nursing, and other nest-typical interactions.

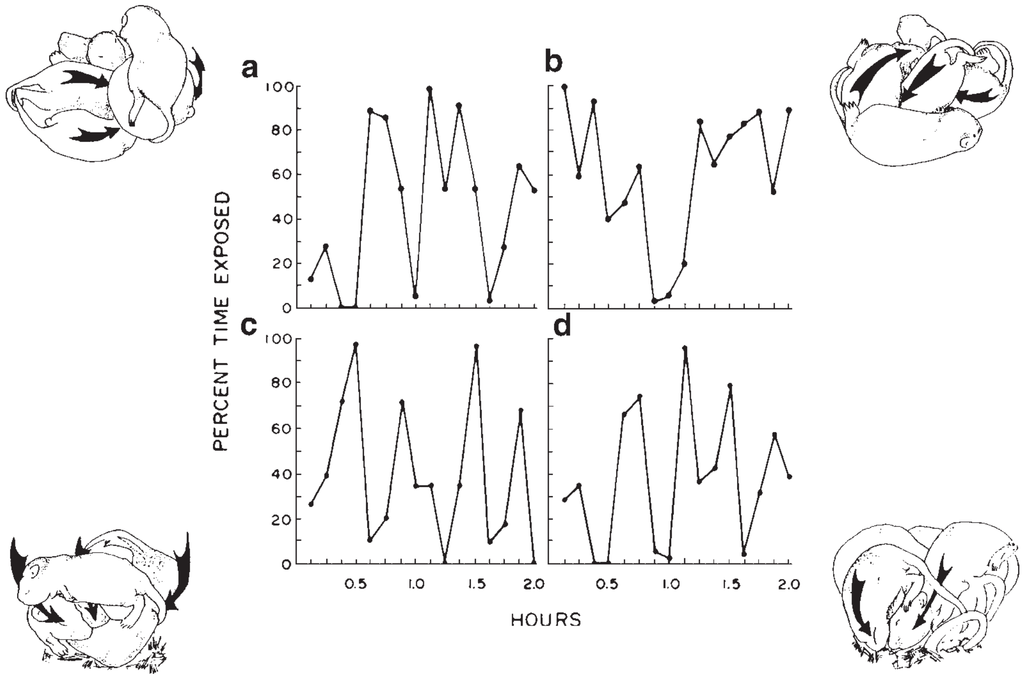


FIGURE 4 Figurative and quantitative depictions of ''pup flow''within a huddle of rat pups. The arrows superimposed on the drawings of pups in a funnel-shaped nest depict the movements in a cool nest—one in which pups dive into its depths for warmth. The graphs depict exposures of marked, focal pups on the surface of a huddle during sequential, 8 min intervals (see Alberts, 1978a).

Figure 5 summarizes one set of results of this study, showing that individual pups under the dam's body exhibit at least two distinct movement patterns. One pattern involves pups shifting their positions on the dam's ventrum, which for purposes of the present experiment was divided into quadrants (labeled A–D in Fig. 5). The second pattern is that the same pups vary the surface of their body (dorsal, ventral, lateral) that is in direct contact with the dams. This can be seen in the rectangles that represent sequential time samples in Figure 5 (in each row, left to right). Thus, Pup #1 initially is in dorsal contact with Quadrant A on the mother's ventrum, then it is against her Quadrant C with its lateral surface, and then returning to Quadrant A with its dorsum, and changing back to Quadrant C in the same orientation. The central row of cells containing a rat icon depicts the orientation of the dam, which can be seen to change once during the first five observations, after which there is a brief break in contact, and two more intervals of contact in a new orientation. This ''horizontal'' form of pup flow varies the surfaces of the mother's and pups' bodies that are in contact, thus maintaining thermal flux between the bodies.

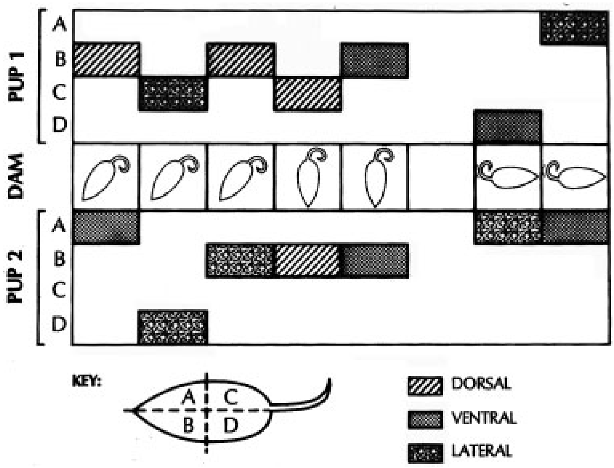
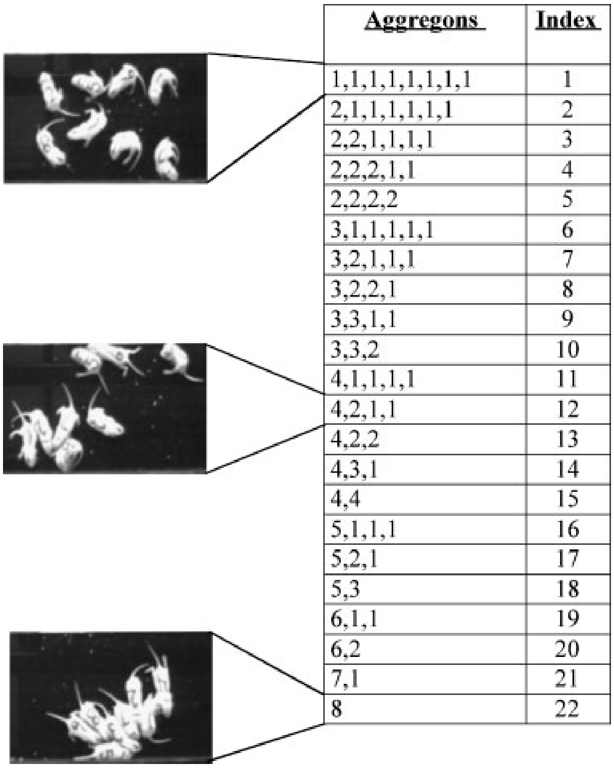


FIGURE 5 Movements and orientations of rat dam and two focal pups, as encoded from observations made through a glass bottom cage. Each row of cells depicts (from left to right), sequential, 5-min samples from continuously videotaped observations of mother–litter interactions in a glass-bottom nest. The upper four rows indicate the locations of Focal Pup 1 in relation to labeled quadrants of the dam's ventral surface, while the dam is naturally positioned over the litter. The pattern within each cell indicates which aspect of the pup's surface (dorsal, lateral, ventral) is in contact with the dam's body. Focal Pup #2′s locations and orientations are displayed in the lower four rows. The middle row of cells represents whether the dam is present in the nest with the pups, the dam's orientation in relation to the nest; changes in axis direction reflects dam-initiated changes in orientation and, hence, body contact with the litter.

COMPUTATIONAL MODELING REVEALS RULES OF INDIVIDUAL BEHAVIOR

In an ongoing series of studies, Dr. Jeffrey Schank and I combine observational and computational methods to probe further into the structure of the rat pups' group behavior. The observational component is aided by computer technology. From videorecordings of litters placed in an arena with warm ambient temperature and a warm floor, digitized measurements of the location of each individual are captured every 5 sec. The digital files were used to construct timelimes for a variety of parameters: Which pups are in contact with (a) walls, (b) corners, (c) and/or other pups, or (d) no contact. In addition, by analyzing overlayed, sequential frames, it is possible to discern pups that are in active and nonactive states.

These observational methods yield a variety of group characterizations. One of the richest is an overview of the frequency of each possible combination of numbers of bodies in contact. Each possibility is an *aggregon*; Figure 6 lists the 22 aggregons that can be formed by eight individuals. The upper photograph within the Figure



Aggregons	Index
1,1,1,1,1,1,1,1	1
2,1,1,1,1,1,1	2
2,2,1,1,1,1	3
2,2,2,1,1	4
2,2,2,2	5
3,1,1,1,1,1	6
3,2,1,1,1	7
3,2,2,1	8
3,3,1,1	9
3,3,2	10
4,1,1,1,1	11
4,2,1,1	12
4,2,2	13
4,3,1	14
4,4	15
5,1,1,1	16
5,2,1	17
5,3	18
6,1,1	19
6,2	20
7,1	21
8	22

FIGURE 6 Aggregon Index for eight rats. Eight bodies can express 22 aggregons by moving in and out of contact with one another. The photographs depict three of the aggregons. The right hand column defines each aggregon in terms of the sub group size.

shows Aggregon #1, in which the eight pups are all physically separated (this was roughly the initial condition for the trials). The middle photograph is an aggregon comprising masses of 4, 3, plus 2 single bodies (#12). The lower photo is an Aggregon #22, in which all eight pups are in contact as a single mass. If eight pups are initially arranged in two rows of four and allowed to "run," they usually display all 22 aggregons within 15 min. The dynamics and frequency of each aggregon provides a summary of the group's behavior.

Jeff Schank devised and tested computer programs that generate the behavior of "computational pups." Like their biological counterparts, the computational pups were initially arranged in two rows of four and then allowed to "run" freely. In these computer programs, the behavior of each pup was governed entirely by rules that dictate the behavior of individuals. There were no rules concerning group behavior. Nevertheless, group behavior emerged from litters of computational pups.

A small number of simple rules proved sufficient to replicate the behavior of the real, 7-day-old rats (Schank & Alberts, 1997)! These rules and their derivations, described in detail elsewhere (Schank & Alberts, 1997; 2000), involved simple probabilities of a pup being active or not, contingent on whether it was active or inactive in the preceding 5 sec period. Then, there were probabilities of moving if the pup was in contact with another pup, a wall, or a corner. Again, all this was done with realistic probabilities, decisions by random numbers tables, and each pup behaving completely autonomously.

Figure 7 depicts the aggregon distributions of real, 7-day-old rat pups and the nicely matched aggregon frequencies of computational pups governed by rules of individual behavior. This is a significant and impressive concordance. The matching dynamics of the real and computational pups is testimony to the power of the model and suggests that the real, biological phenomenon is dictated according to such rules of individual behavior.

We then tested the model with 10-day-old rat pups and confronted a rather colossal failure! This proved to be opportunity rather than calamity. Between Days 7 and 10, the pups' behavior had obviously changed. If we could restore the model's efficacy, we might have an insight into what had developed in the pups. We asked, what additional rule(s) must be added to account for the development of pup behavior? An elegantly simple addition to the model proved successful.

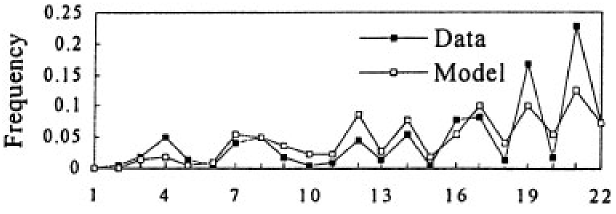


FIGURE 7 Aggregon frequencies for a litter ($n = 8$) of 10-day-old Sprague–Dawley rats and for an agent-based model expressing only rules of individual behavior.

To restore the model's efficacy, another rule was needed. A rule was added by which each pup's behavior was affected by the activity state of the pup(s) that it contacted. If in contact with an active pup, the focal animal was more likely to be active (still determined stochastically each 5 sec) whereas inactive neighbors favored subsequent inactivity. The addition of this single rule restored the model's efficacy.

Besides being rewarded with a parsimonious solution to a potentially complex problem, it seemed possible that this computational approach had revealed an important developmental milestone, namely the onset of sociality—albeit in elementary form. This type of modeling encourages pursuit of parsimonious explanations, because the pups are agents that operate exclusively by individual rules. Moreover, each parameter can be validated by measuring real pups. We can test the importance and the specificity of a rule by deleting it, or by altering its value and then running the model and performing the same tests applied to observations of real pups. Computational methods have even altered our perception of the group, helping draw attention to activation and detailed aspects of the pups' responses to proximal cues (see Alberts, Motz, and Schank (2004) for an example of this).

OXYTOCIN MANIPULATIONS AFFECT 10-DAY-OLDS BUT NOT 7-DAY-OLDS

There is now a body of research highlighting the roles of the neuropeptides, oxytocin and vasopressinin in the expression of social behaviors that involve proximity, preference, positive valence, parental and sexual contact (e.g., Ferguson, Young, & Insel, 2002; Keverne & Curley, 2004). Most of the supporting research was done with adult animals. We have made an initial inquiry into a possible early role for oxytocin in the huddling and group behavior (Odya, Sokoloff, & Alberts, 2002).

We manipulated central oxytocin in rat pups and measured group behavior, using a variant of the "group size" metric that first validated the concept of regulatory huddling (Alberts, 1978a). We measured the overall circumference of aggregations (all the pups, whether in contact or not). In the present study, tests were conducted in a uniformly warm (32°C) ambience to minimize the thermal controls of huddling. There were three treatment groups: Control (saline injected), Oxytocin, and pups

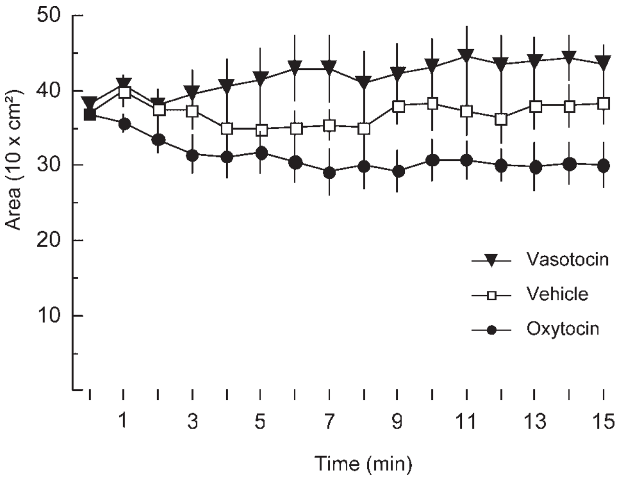


FIGURE 8 Oxytocin/Vasopressin/Saline. Total area (cm^2) subtended by litters of 10-day-old rat pups. The open circles show the relatively compact spacing of the pups over the 15 min observation, following a control injection of saline into the ventricles. Oxytocin administered intracisternally stimulated more cohesive and compact arrangements, whereas 10-day-olds treated with the oxytocin antagonist, Vasotocin, were the least cohesive.

receiving Vasotocin, an oxytocin antagonist. The injections were intracisternal, likely bathing all systems around the ventricles. Pups were injected while anesthetized with a short-acting inhalant (isoflurane) and tested for 1 hr.

Figure 8 shows the results for huddles of 10-day-olds. Average huddle circumference was the same for all three groups at the beginning of the test. By the 2nd or 3rd min, however, oxytocin-treated pups were in closer proximity than were the Controls. Oxytocin facilitated proximity and coherence by the group in relation to the saline controls. In contrast, when oxytocin receptors were blocked by the antagonist, groups became more diffuse, in relation to both the Oxytocin and to the Control condition. These results were not explainable by thermal effects of oxytocin or by differences in activity.

The same manipulations did not alter the 7-day-olds! Thus, oxytocin affected the behavior of pups at an age when we hypothesized the pups become social. In contrast, oxytocin had no discernible effect just a few days prior, when we hypothesized them to be autonomous and asocial. We shall pursue this further.

CONCLUSIONS

1) Group behavior adaptively regulates physical parameters such as the group's exposed surface: body heat is conserved and metabolic expenditure is reduced in relation to ambient temperature.
2) A few simple rules of individual behavior are sufficient to produce the complex patterns of aggregation (aggregon frequency) that define the dynamics of a behaving huddle of pups. Computational modeling yielded an agent-based solution without information pertinent to group behavior. Information contained in the interactions of individuals produces orderly group activity that, in nose-to-nose comparisons, matched that of rat pups. A self-regulating whole emerges from the sum total of the individual interactions. *The huddle, as an emergent entity regulates "downward" to the level of the individual*, as seen by the expression of an endothermic metabolic response from pups that would otherwise perform with the opposite, ectothermic pattern. It is the properties of the whole (the huddle) that produces microenvironments for the parts (the individual pups).
3) The behavior of the group itself develops. Rules of individual behavior are added during development—as a result of growth, new motoric abilities, and sensory and physiological maturation—and the behavioral properties of the emergent group develop dynamically.
4) Sought and tested here were various "essential elements" of behavior—the cues that elicit it, the experiences that canalize it, the functional consequences that derive from it (and the stimuli that are produced), and the behavioral structures that emerge. I have reflected on the power and appropriateness of such "essentialism" versus pure "reductionism" (Alberts, 2002) and hope to see a greater appreciation for the analyses that seek primary explanations on behavioral levels, prior to departing to "lower," and more molecular correlates of untested behavioral elements.

NOTES

Jay Rosenblatt's many and varied contributions to our science is distinct, I think, in the primacy given to behavior. Among his many gifts to us is the obvious love and respect he holds for behavior and for focus on organismal levels of analysis. I join with many others, such as those contributing to the present collection of articles, in acknowledging with deep appreciation, Jay's guidance, inspiration, and wisdom.

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