



Self-Organized Huddles of Rat Pups Modeled by Simple Rules of Individual Behavior

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Starting at infancy and continuing throughout adult life, huddling is a major component of the behavioral repertoire of Norway rats (*Rattus norvegicus*). Huddling behavior maintains the cohesion of litters throughout early life, and in adulthood, it remains a consistent feature of social behavior of *R. norvegicus*. During infancy, rats have severely limited sensorimotor capabilities, and yet they are capable of aggregating and display a form of group regulatory behavior that conserves metabolic effort and augments body temperature regulation. The functions of huddling are generally understood as group adaptations, which are beyond the capabilities of the individual infant rat. We show, however, that huddling as aggregative or cohesive behavior can emerge as a self-organizing process from autonomous individuals following simple sensorimotor rules. In our model, two sets of sensorimotor parameters characterize the topotaxic responses and the dynamics of contact in 7-day-old rats. The first set of parameters are conditional probabilities of activity and inactivity given prior activity or inactivity and the second set are preferences for objects in the infant rat's environment. We found that the behavior of the model and of actual rat pups compare very favorably, demonstrating that the aggregative feature of huddling can emerge from the local sensorimotor interactions of individuals, and that complex group regulatory behaviors in infant rats may also emerge from self-organizing processes. We discuss the model and the underlying approach as a paradigm for investigating the dynamics of social interactions, group behavior, and developmental change.

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1. Introduction

Huddles of infant rats (pups) are aggregations established by the tendency of pups to approach one another and then actively maintain contact. Pups within a huddle are observed to root and burrow between other bodies, climb on one another, crawl around the periphery and then re-enter the huddle. A multitude of sensory cues, including tactile, thermal and olfactory stimuli, govern the behavior of pups and thus control huddling (Alberts, 1978a). In addition to aggregation and maintaining the cohesion of a litter, interactions among huddling pups can serve a form of group regulatory behavior whereby

the size, or exposed surface area of the huddle conforms to ambient temperature conditions (Alberts, 1978b). The aggregative and group regulatory capacities of huddles derive from individual behavior that is essentially topotaxic (see Fraenkel & Gunn, 1961, on topotaxis as orientation and movement towards objects). In the nest, these topotaxic reactions produce a “pup flow” within the huddle, creating a downward flow into the depths of the huddle when pups are cold and an upward flow when they are hot (Alberts, 1978b). Group regulatory behavior manifested by pup flow in the nest, together with the degree of surface area exposure of the huddle, not only provide pups with a means of body temperature regulation but also energy conservation, as measured by oxygen consumption, allowing them

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to channel energy into processes of growth and maturation (Alberts, 1978b; Alberts & Gubernick, 1983). Both behaviorally and physiologically, huddles of pups display features of a larger, more mature single organism. For these reasons, huddles are sometimes viewed as a kind of "superorganism".

Huddling is aggregative and cohesive contact behavior that is modulated by the sensorimotor activity of individuals. It is observed among the young and adults of numerous and diverse species (e.g. Putaala *et al.*, 1995; Du Plessis *et al.*, 1994; Bazin & MacArthur, 1992; Hayes *et al.*, 1992; Stapp *et al.*, 1991; Frey, 1991; Yahav *et al.*, 1991; Wang & Wang, 1990; Bozinovic *et al.*, 1988; Genoud, 1985; Chaplin, 1982), often involved in functions such as thermoregulation and energy conservation (it may also be a factor in the regulation of population dynamics in some species; Madison *et al.*, 1984), and can be found at various stages of sensorimotor development (e.g., Haim *et al.*, 1992; Harri *et al.*, 1991; Carter & Hobson, 1988; Geers *et al.*, 1987; Wang *et al.*, 1985; Leonard, 1982; Hull & Hull, 1982; Alberts, 1978b). Thus, huddling is of broad biological, ecological, and developmental significance, serving essential biological functions for the individual, which either cannot be achieved or only partially achieved by an individual on its own.

The aim of the present paper is to develop a modeling framework for the initiation, maintenance, and dynamics of contact behavior in huddling. During early postnatal life the sensorimotor capacities of infant rats develop sequentially and have been experimentally investigated (Alberts, 1978a, 1984; Alberts & Cramer, 1988). These sensorimotor capacities are represented in the model by sensorimotor rules (described below). In this modeling framework, we show how simple sensorimotor rules for activity and preferences for objects in an infant rat's environment can largely explain the complex patterns of aggregation, cohesion, and dynamics of contact observed among pups.

Because huddling is observed from infancy throughout adulthood (Calhoun, 1962; Barnett, 1963), the development of a modeling framework for aggregative behavior in rat pups may also provide a starting point and baseline model for investigating the development of aggregative behavior and its dynamics in rats and perhaps in other species. In addition, by modeling huddling, we believe not only that aggregative and cohesive behavior emerges as a self-organizing process, but that group regulatory behaviors (e.g., thermoregulation and energy conservation) may also be self-organizing processes (i.e., autonomous individuals interacting locally in accord-

ance with simple rules can generate complex and group regulatory behaviors without assuming group-level regulatory mechanisms). If group regulatory behaviors in infant rats emerge from self-organizing processes, then the model presented here should be a first step towards characterizing and quantifying the sensorimotor rules of individual behavior.

Huddling by infant rats offers a promising opportunity to study both the ontogeny of *individual behavior* throughout the life history of an organism as well as the ontogeny, dynamics, complexity, and organization of *group behavior*. In the present modeling framework, we view infant rats as essentially autonomous agents, whose topotaxic behavior can be characterized by relatively simple sensorimotor rules. Only as the infant rat develops, does its behavior become increasingly coupled to its littermates' behavior and it loses its simple topotaxic character. This perspective is a general hypothesis that shaped the modeling framework presented below, and because it is a hypothesis, its ultimate success or failure is a matter of experimental test.

2. Dynamics of Aggregative Behavior: an Experiment

Huddling is complicated by a number of factors. The initiation and maintenance of contact among individuals is modulated by different sensory modalities. Visual, auditory, and olfactory cues complicate the study of huddling because these cues act at various distances between individuals and several cues may be acting and interacting simultaneously (e.g., Schoenfeld & Corwin, 1985). Thermal and tactile cues also complicate the regulatory and adaptive functions of huddling, since huddling itself can alter thermal cues. For infant rats, temperature cues can be affected by heat transfer between mother and pups, among pups, ambient temperature, nest material, fur growth on pups, heterogeneity of body composition and shape, and thermogenesis (e.g., Webb, 1990; Canals, 1989 provide empirical and theoretical analyses of some of these factors). Motor capacities influence the dynamics and geometry of huddling, and the motor capacities of individuals are both species-typical and developmentally dependent. Social factors may also complicate huddling including the sex of individuals and social hierarchies that may form (Salo *et al.*, 1993; Moinard *et al.*, 1992; Andrews *et al.*, 1987; Noske, 1985; Batchelder *et al.*, 1983; Deni, 1981).

In order to achieve greater control and standardization of these factors, we selected subjects and developed a testing arena that controls a number of these factors and facilitates the standardization of measures of contact. In the next sections, we (i)

discuss the selection of subjects, (ii) describe the arena and how it controls for a variety of potentially complicating factors, (iii) define specific measures of the dynamics of aggregative behavior, (iv) describe our experimental design, and (v) present empirical data on the aggregative dynamics of 7-day-old rats, which will serve as the empirical basis for our subsequent theoretical investigation of the dynamics of aggregative behavior.

2.1. SUBJECTS

Infant rats are well-suited for investigating the dynamics of aggregative behavior and the sensorimotor rules modulating contact. Infant rats are severely limited in their sensorimotor capacities (Alberts, 1984); they are blind; olfactory and auditory cues are severely limited; but they do respond to thermal and tactile cues. Their motor capacities are also extremely limited, and they are too young for social dominance hierarchies to have formed (Calhoun, 1962), but they may exhibit sex preferences (Deni, 1981). Nevertheless, despite these sensorimotor limitations individual pups can initiate and maintain contact with littermates, thereby maintaining litter cohesion, regulating body temperature and conserving energy as described earlier. Their behavior can be characterized as topotaxic, which strongly suggests that the sensorimotor rules modulating aggregative behavior in rat pups may be relatively simple, largely limited to contact-thermal and tactile cues, coordinated with individual activity state.

Several considerations went into the selection of the age of subjects used here. First, to ensure limited and local sensory capacities, pups had to be 12 days of age or less, since after this time their eyes begin to open. Second, subjects had to be able to move around on a flat surface, but unable to readily climb on top of each other (see next section). Pilot observations revealed that pups 5 to 8 days of age satisfied these criteria. Third, to control thermal conductance factors, pups 5 to 8 days of age were used, since up to this age they exhibit little fur growth (unpublished observations). Thus, subjects consisted of nine litters of eight rat pups (Sprague–Dawley) each, 7-days-old, bred and born at Indiana University. At 3 days of age, litters were culled to four females and four males in order to avoid possible sex-contact biases (Deni, 1981). The methods used were observational and entirely noninvasive.

2.2. THE ARENA

On a flat and level surface infant rats (i.e., ≤ 8 days of age) rarely, if ever, crawl over or under each other (unpublished observations). This fact was used to

separate experimentally the dynamics of aggregative behavior from other factors contributing to the complexity of huddling. By viewing rats on a flat surface, three types of data on the dynamics of aggregative behavior were collected: activity state of individuals, aggregon patterns (i.e., aggregates of pups in physical contact formed on a flat surface, see Section 2.3.2), and wall topotaxis.

The control of thermal factors also influenced the design of the arena. Infant rats are primarily contact-responsive to thermal and texture cues, though they are responsive to specific olfactory cues (Alberts, 1978a; Alberts & Brunjes, 1978). For 7-day-old rats, texture cues from other pups (e.g., their surface texture) are relatively constant, but thermal cues from objects in their environment are variable and affected by ambient temperature, hysteresis effects (e.g., individuals warming the floor of the arena), and the temperature and the thermogenesis of pups (though small).

To control the various possible thermal factors, an arena was constructed that functioned as an efficient heat sink, controlling both ambient and pup temperature (Fig. 1). Aggregative behavior occurred in a $30 \times 20 \times 5$ cm aluminum arena, which was immersed to the rim in a fluid reservoir and sealed on the top (Fig. 1). The reservoir was maintained at a constant temperature with a temperature-controlled circulator. Thus, the arena surface was a heat sink; a motionless rat cannot warm the surface on which it lies. The smooth, flat, leveled surface prevents geotaxic responses from biasing positions; pups on a smooth surface can crawl across the surface but cannot readily crawl over or under each other. By embedding the arena and its reservoir in a second chamber [see Fig. 1(b)], which was equipped with small radiators and a small fan that gently circulated air throughout the chamber, ambient temperatures could be uniformly maintained and the gentle airflow prevented pockets of slightly heated air from forming around individual pups. Finally, in order to achieve near thermoneutrality, the arena was maintained at a constant $34 \pm 0.5^\circ\text{C}$ (the temperature of 7-day-old rats is normally between $35\text{--}37.5^\circ\text{C}$). By strictly controlling ambient temperature and holding it near thermoneutrality for the pups, tactile cues could be separated (or nearly so) from thermal cues in the modulation of aggregative behavior.

A rack was used to evenly space the pups on the surface of the arena at the start of an aggregative-behavior session [Fig. 1(b)]. The rack consisted of eight partitions ($4.125 \text{ cm} \times 5.625 \text{ cm}$; constructed from $2.1 \text{ cm} \times 0.5 \text{ cm}$ laths of wood painted white) for holding individual pups.

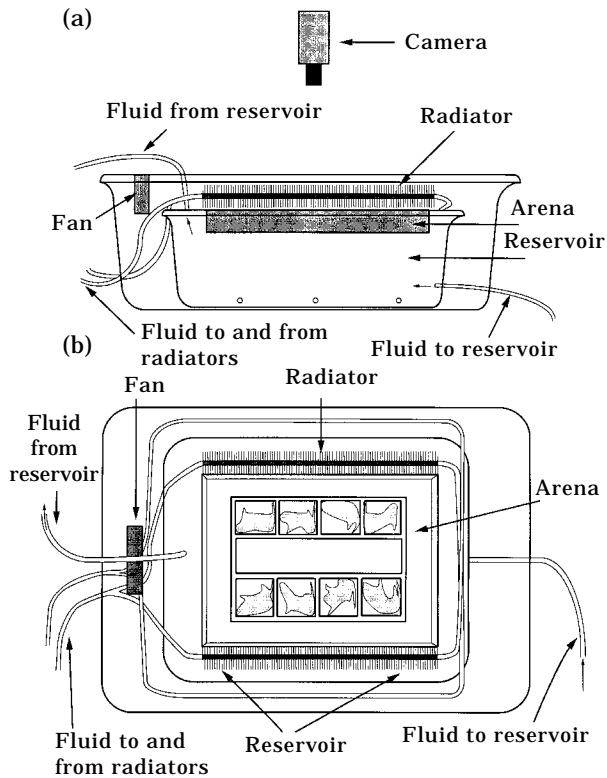


FIG. 1. Two views of the testing arena: (a) side view of the video camera located directly above it and (b) top view with spacing rack and silhouettes of pups (created from images of pups in the arena).

2.3. BEHAVIORAL MEASURES

Pups placed in the arena and allowed to move about are observed as (i) either active or inactive, (ii) contacting 0 to N other pups, and (iii) either with their snout touching an arena wall or not touching it. Each of these characteristics of their topotaxic behavior (i.e., their orientation and contact behavior) change over time and are precisely defined in the next three sections.

2.3.1. Activity state

At any time t , a pup is either active or inactive. By the term *active* we do not merely mean movement; activity is sensorimotor-coordinated movement required to initiate and maintain contact. Operationally, *activity* in a pup is defined as either (1) moving on the surface by moving its legs or attempting to move on the surface by moving its legs in a “swimming” like motion or (2) moving its head from side-to-side in a scanning motion. There are several other types of behavior (e.g., grooming, suckling movements with the mouth, yawns, and even violent twitches that occur when pups sleep, unpublished observations) that could be classified as

“active”. However, since they do not appear to be elements in the sensorimotor coordination required for initiating and maintaining contact, such behaviors were not classified as active.

2.3.2. Patterns of aggregons

A basic premise of this paper is that contact among rat pups is determined by their topotaxic behavior, which can be characterized (probabilistically) by preferences for objects in the pups’ environment. On a flat surface, pups (≤ 8 days of age) lack the motor capacity to readily climb on top of each other, yet they can move around on a flat surface and make contact forming a variety of contact patterns. These contact patterns are considerably different from the pattern seen in the nest—i.e., dynamic and churning “ball” of pups. To better distinguish these two modes of group aggregation, we introduce the term *aggregon* to refer specifically to the “two-dimensional” contact patterns formed by pups on a flat surface.

Pups form an aggregon if there is a continuous path of physical contact connecting them. For N pups in an arena, several aggregons may form. The smallest possible aggregon is defined as a single pup. If no pup is in contact with any other pup, then N pups are characterized by N aggregons. Thus, the number of aggregons formed by N pups can range from 1 (all pups in physical contact) to N (none of the pups are in physical contact). The aggregons for a given N can be conveniently represented by a sequence or pattern of aggregons (n_1, \dots, n_m) , where n_i is the number of individuals in an aggregon and the m aggregons are ordered by size. If $N = 8$ and none of the individual pups are in physical contact, then the pattern of aggregons would be $(1,1,1,1,1,1,1,1)$ [Fig. 2(a)]; whereas if all of the pups are in contact, then the pattern of aggregons would be (8) [Fig. 2(b)].

For $N = 8$, the number of possible aggregon patterns are easily enumerated and it is computationally convenient to order them according to the following rule (though this is by no means the only way to order aggregon patterns, see Schank, 1997 for related issues in the measurement of synchrony of biological states): an aggregon pattern is ranked higher than another if the largest aggregon in one pattern is larger than the largest aggregon in the other; ties between largest aggregons are resolved by examining the next largest aggregon and so on until the tie is broken. For example, a pattern of $(3,2,2,1)$ is ranked higher than $(3,2,1,1,1)$ because in the third position, $2 > 1$. Since all patterns can be uniquely ranked in this manner, a simple index uniquely orders the aggregon patterns (see Table 1).

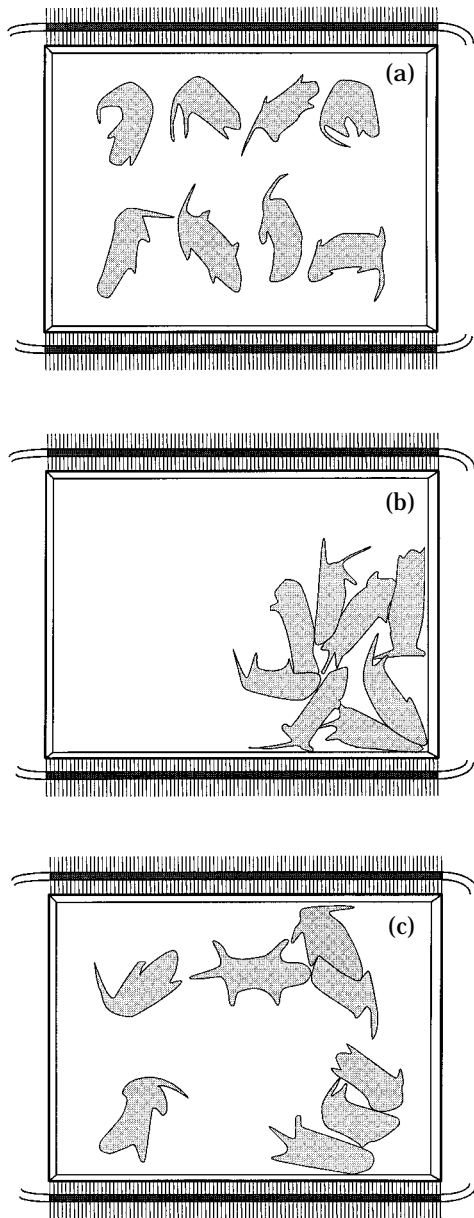


FIG. 2. Three aggregon patterns of eight pup silhouettes in the testing arena: (a) none are in contact, (1,1,1,1,1,1,1,1), (b) all are in contact, (8), and (c) two aggregons of three pups each with the remaining two not in contact, (3,3,1,1).

2.3.3. Wall topotaxis

In the arena, pups encounter three kinds of objects: other pups, walls, and “empty space”. Since pups detect temperature and texture with their snout in a side-to-side scanning motion (Deni, 1981, and unpublished observations), contact between snout and an object should be an indicator of an individual’s preference for a type of object. In the experiments described below, wall topotaxis is operationally defined as contact between an individ-

ual’s snout and a wall. Thigmotaxis implies a general sensorimotor tendency to follow paths next to vertical surfaces (Barnett, 1963), 7-day-old rats do not exhibit this taxis. Thus, we refer to an orientation towards a wall as wall topotaxis, which is not the thigmotactic tendency to follow walls. The aggregon patterns described in the previous section should provide information on preferences, especially preferences for other pups. Wall topotaxis on the other hand should provide additional information about preferences for walls.

2.4. EXPERIMENTAL DESIGN AND ANALYSIS

At the start of an aggregative-behavior session, pups were uniformly spaced on the arena [topologically similar to Fig. 1(b)] allowed to settle down for 1–2 min, and then simultaneously released to move around the arena. The ambient air temperature, surface and walls of the arena were maintained at 34°C (±0.5°C) throughout the 10 min observation period. The arena was cleaned with a small amount of ethyl alcohol between each session and allowed to dry in order to minimize effects of odors left by previous litters of pups.

Experiments were recorded using time-lapse video (record:playback ratio of 12:1) with a camera placed directly above the arena [Fig. 1(a)]. Videotapes were analyzed using NIH Image 1.60 for the Power Macintosh. After observing several video-taped episodes of the contact behavior among litters of pups, we decided that sampling a frame every 5 s

TABLE 1.
Aggregon patterns for N = 8 individuals

Aggregon patterns	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

would adequately capture the dynamics of aggregation in 7-day-old rats. Thus, for each litter, a frame was grabbed every 5 s for a total of 121 frames representing a 10 min session. The first frame was $t = 0$ and marked the beginning of the removal of the pup rack. All videotapes were analysed by the same observer (Schank) and checked a second time for accuracy.

Our procedure for classifying pups as active warrants a brief discussion. Active pups were determined by adding images at t and $t + \Delta t$ ($\Delta t = 5$ s) together using NIH Image math algorithms. This produced a composite image in which an image of each pup at time t could be compared with its image at $t + \Delta t$. Activity as defined above was determined for each individual if the composite image indicated (1) coordinated change in position or coordinated movement of legs, and/or (2) head movement from side-to-side.

2.5. RESULTS

2.5.1. Activity state

The frequency of activity (A) in infant rats decreased for the first 5 min of an aggregative-behavior session and then approached an apparent plateau [Fig. 3(a)]. Near the plateau, the mean frequency of activity for all nine litters combined was $\bar{f}(A) = 0.27$. If the activity state of a pup is independent of the activity state of its littermates, then the frequency of activity in 7-day-old pups should fit a binomial distribution at the activity plateau. If this hypothesis is correct, then the actual frequency distribution of pups active at any given time during the final 5 min should not differ significantly from an appropriate binomial distribution. During the last 5 min of activity there were 60 observations per litter of the number of active pups for a total of $n = 540$ observations for all nine litters. A binomial distribution was calculated for the expected frequency of pups active by setting $p = \bar{f}(A) = 0.27$ (i.e., the mean level of activity over the final 5 min), where r = the number of pups active, and $N = 8$ is the total number of pups [Fig. 3(b)].

The data and binomial distributions are very similar and the Kolmogorov–Smirnov test revealed no significant difference between them. This suggests that the probability of a 7-day-old rat being active is largely independent of the activity state of its littermates, and thus justifies modeling activity with probabilities conditional only on the prior activity state of a pup. Later this data will be used to find the best fit conditional probabilities for activity states in these pups.

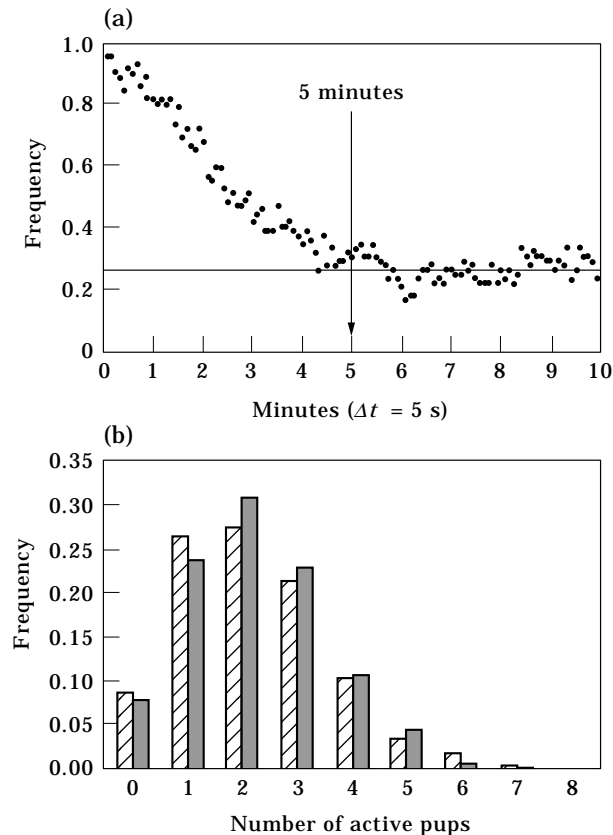


FIG. 3. Two views of activity. (a) The frequency of activity in 7-day-old pups over a 10 min observation period. The arrow indicates the time when an apparent plateau in activity was approached, and the horizontal line marks the mean frequency of activity (0.27) during the final 5 min. (b) A comparison between the expected frequency of active pups (binomial distribution, $p = 0.27$, r = the number of active pups, $N = 8$) and the observed frequency distribution of active pups during the final 5 min in (a). Key: ▨ active pups; ▤ binomial distribution. There was no significant difference between the two distributions using the Kolmogorov–Smirnov test.

2.5.3. Patterns of aggregons

The nine litters of pups did not exhibit any consistent pattern of change over time in their aggregon patterns [see Fig. 4(a)]. This suggests that if there is any underlying order in aggregon patterns, it lies in a different view of the data. For all nine litters, the mean frequency of change in patterns was 0.359 and the frequency distribution of observed patterns (1080 data points) is illustrated in Fig. 4(b). The distribution depicted in Fig. 4(b) is very multimodal as indicated by the lines connecting the points representing the frequencies of different aggregon patterns. The frequency of pattern change together with this multimodal distribution is used below to find a best fit individual-based model of the data.

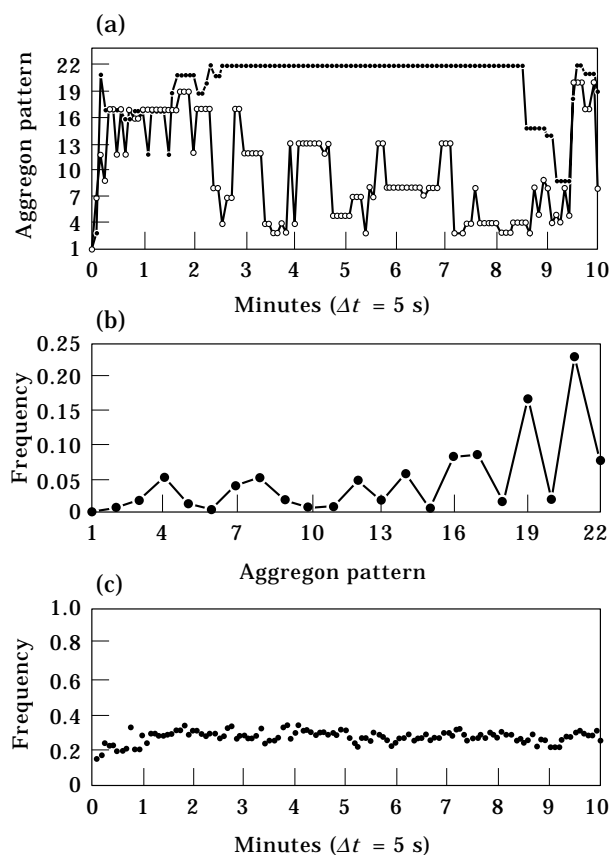


FIG. 4. Three views of contact. (a) Change in aggregon patterns for two litters over a 10 min session. No discernible pattern of change over time emerged for any of the nine litters. (b) The multimodal frequency distribution of aggregon patterns for all nine litters. (c) The frequency of wall contact over 5 s intervals for all nine litters.

2.5.2. Wall topotaxis

The frequency of pups exhibiting wall topotaxis over time climbed rapidly immediately after the pups were released reaching an apparent plateau after the first minute and then remaining at a relatively stable frequency for the rest of the 10 min session [Fig. 4(c)]. The wall-topotaxis data is used below as an indicator of a pup's preference for walls and to test the consistency of the best fit individual-based model of the data.

3. Dynamics of Aggregative Behavior: an Individual-Based Model

In the next sections a simple individual-based model is developed for exploring the dynamics of aggregative behavior in infant rats. Based on the empirical results described in the previous sections, we hypothesized that the topotactic behavior of

individual pups can be characterized by two types of parameters: conditional probabilities of activity and preferences for objects in their environment. Our goal was to determine whether there is a set of parameter values for the topotactic behavior of pups that fit the data presented in the previous sections, and thus whether the dynamics of aggregative behavior in 7-day-old rats could be explained by relatively simple sensorimotor rules (characterized by preferences for objects in a pup's local environment and the probability of a pup moving or reorienting itself in the arena).

3.1. ASSUMPTIONS

Model pups occupy discrete spaces or cells in a rectangular array \mathbf{H} . A pup is located at any time t in an $(m-2) \times (n-2)$ region of cells in \mathbf{H} , which represents the arena [compare Figs 1(b) and 5(a)]. The edge cells are occupied by walls as illustrated in Fig. 5(a) (i.e., indicated by heavy lines). Pups can be in any of eight orientations (i.e., starting from—e.g., focal pup in Fig. 5(b)–(c)—and moving clockwise every 45°). At each time t a pup, if active, can move to any unoccupied cell adjacent to it as illustrated in Fig. 5(c) (arrows indicate the neighboring cells to which a model pup can move). The motion of pups at each time t , is determined entirely by (i) their activity state (active or inactive) at t , (ii) their preferences for objects in adjacent cells, and (iii) whether adjacent cells are empty or occupied.

The number of cells in the model arena was determined using two assumptions. First, the number of cells in the model arena should be such that the initial spacing of pups is topologically similar to the spacing of pups in the experimental arena [Fig. 1(b)]. Second, the number of cells should be comparable to the area occupied by real pups. Cell number was derived using these assumptions, resulting in an array of 40 cells (5×8) that topologically approximated the 30×20 cm experimental arena.

3.1.1. Preferences

The movement of a model pup is determined by its activity state (active or inactive) and its preferences for moving to any of its eight neighboring cells [see Fig. 5(b) and 5(d)]. For the convenience of discussing the rules for assigning preferences, we will only consider the north orientation of a pup since any orientation can be locally transformed into any of the other seven orientations. A pup's view—based on the side-to-side scanning of the head and snout of actual pups—consists of the three cells in front of it (in

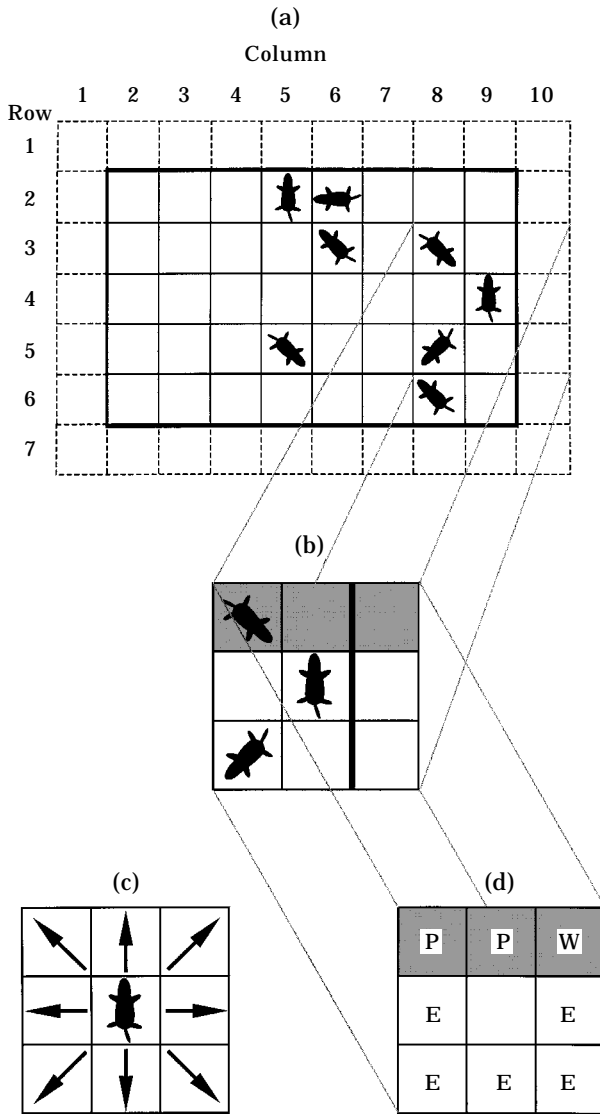


FIG. 5. A graphical representation of the model pups and arena. (a) The array of cells in which model pups move about. Edge cells of the array are occupied by walls and the inner cells are either empty or occupied by other model pups. (b) A blow up of the indicated region in (a). The center pup is the focal pup (oriented "north") and the shaded three cells in front of it represent a model pup's view (i.e., the local space in which a pup can detect other objects by scanning its head back and forth). (c) A focal pup with arrows pointing in the directions it can move. (d) A preference matrix for the focal pup in (b), where P is the preference for pups, W the preference for walls, and E the preference for empty cells that are not in a pup's view.

Fig. 5(b), (d) the shaded area). The rules for assigning preferences are

- (i) cells not in a pup's view are empty and assigned the empty preference, E;
- (ii) cells in a pup's view and occupied by a wall are assigned the wall preference, W;

- (iii) cells in a pup's view occupied by another pup are assigned the pup preference, P;
- (iv) empty cells in a pup's view that are next to another cell in the pup's view which contains another pup are assigned the pup's preference (i.e., pups like to move around other pups), P;
- (v) otherwise the empty cells in a pup's view are assigned the empty preference, E.

For example, Fig. 5(b) depicts a focal pup with a wall to its right, one pup to its front left and another pup to its left rear. Like a real pup's scanning from side-to-side, the model pup scans only the three cells in front of it [gray area in Fig. 5(b)]. The rest of the model pup's world is empty. Fig. 5(d) depicts the preferences for Fig. 5(b). The pup preference, P, is assigned to the cell occupied by the pup to the left-front of the focal pup (rule iii); P is also assigned to the empty cell to the middle-front of the focal pup (rule iv); a wall preference, W, is assigned to the cell in front of and to the right-front of the focal pup (rule ii); and the rest of the cells are assigned the empty preference, E (rule i). Finally, the conditional probabilities (given a pup is active) of moving into any of the these eight adjacent cells are calculated from the pup's preference matrix [see Fig. 5(d)] using eqn (1).

$$P(c_{ij}|A_i) = \frac{\text{cell } i,j \text{ Preference}}{\text{Total Preferences for adjacent cells}} = \frac{\text{Pref}(c_{ij})}{\sum_{h=1}^n \sum_{k=1}^m \text{Pref}(c_{hk})} \quad (1)$$

where $i,j (i,j \neq 2)$ and $h,k (h,k \neq 2)$ are indices of a pup's preference matrix [e.g., Fig. 5(d)]. If a pup is active, it will always attempt to move to another cell.

3.1.2. Conditional probabilities of activity states

The activity states (activity, A , or inactivity, I) of a pup are modeled with conditional probabilities. This is a convenient way to model activity in infant rats if the probability of activity or inactivity depends only on prior activity or inactivity. The experimental results presented above (Section 2.5.1) provide empirical justification for this assumption, since the activity of pups conformed to a binomial probability model, which assumed that the activity of a pup is independent of the activity of other pups. In addition, conditional probabilities allow us to do discrete time simulations without the potential errors introduced by treating a continuous process as discrete. Our conditional probability model assumes only that the probability of activity at time t is based on activity at a prior time $t - \Delta t$, where Δt can approach 0.

If a pup is active or inactive at time $t - \Delta t$, there are two conditional probabilities that determine whether or not the pup is active at time t , $p(A_t|A_{t-\Delta t})$ and $p(A_t|I_{t-\Delta t})$. Similarly, there are two conditional probabilities that determine whether or not the pup is inactive at time t , $p(I_t|I_{t-\Delta t})$ and $p(I_t|A_{t-\Delta t})$. Since, $p(A_t|A_{t-\Delta t}) + p(I_t|A_{t-\Delta t}) = 1$, $p(I_t|I_{t-\Delta t}) + p(A_t|I_{t-\Delta t}) = 1$, $p(I_t|A_{t-\Delta t}) = 1 - p(A_t|A_{t-\Delta t})$, and $p(A_t|I_{t-\Delta t}) = 1 - p(I_t|I_{t-\Delta t})$, the conditional probabilities are completely determined by:

$p(A_t|A_{t-\Delta t})$ = the probability of activity at time t given activity at time $t - \Delta t$, and

$p(I_t|I_{t-\Delta t})$ = the probability of inactivity at time t given inactivity at time $t - \Delta t$.

3.2. MODELING ACTIVITY WITH CONDITIONAL PROBABILITIES

Modeling activity with conditional probabilities permits the derivation of analytical results that are useful for finding the best-fit model of the data. Conditional probabilities make no assumption about the size of the time step Δt from prior to current activity. Thus, by considering the limiting case where $\Delta t \rightarrow 0$, the rate of change in the frequency, $f(A_t)$, of active pups can be defined by conditional probabilities using the differential eqn (2):

$$\frac{df(A)}{dt} = p(A|I)(1 - f(A)) - p(I|A)f(A) \quad (2)$$

Eqn (2) specifies the ‘‘flow’’ of pups into and out of the active state over time, and by setting $df(A)/dt = 0$, the equilibrium frequency of activity, \hat{f}_A , can be calculated as well as the expected frequency of activity for any time t by integrating equation (2):

$$f(A_t) = \hat{f}_A + (f(A_0) - \hat{f}_A)e^{-t(p(A|I) + p(I|A))},$$

where

$$\hat{f}_A = \frac{p(A|I)}{p(A|I) + p(I|A)} \quad (3)$$

By explicitly reintroducing Δt into (3), we have an equation for the frequency of activity with discrete time changes:

$$f(A_t) = \hat{f}_A + (f(A_0) - \hat{f}_A)e^{-t(p(A_t|I_{t-\Delta t}) + p(I_t|A_{t-\Delta t}))},$$

where

$$\hat{f}_A = \frac{p(A_t|I_{t-\Delta t})}{p(A_t|I_{t-\Delta t}) + p(I_t|A_{t-\Delta t})} \quad (4)$$

Using a nonlinear curve fitting algorithm (Press *et al.*, 1992), eqn (4) was fit to the activity data in order to find the best fit values for $p(I_t|A_{t-\Delta t}) = 1 - p(A_t|A_{t-\Delta t})$ and $p(A_t|I_{t-\Delta t}) = 1 - p(I_t|I_{t-\Delta t})$. The

best fit conditional probabilities were $p(I_t|A_{t-\Delta t}) = 1 - p(A_t|A_{t-\Delta t}) = 0.022$, $p(A_t|A_{t-\Delta t}) = 0.978$ and $p(A_t|I_{t-\Delta t}) = 0.005$, $p(I_t|I_{t-\Delta t}) = 0.995$ assuming a constant $\Delta t = 5$ s. Figure 6 illustrates eqn (4) plotted against the data in Fig. 3(a) assuming that at $t = 0$, the probability of activity for pups is $f(A_0) = 1.0$ (i.e., when the rack is lifted, all pups are active). In the simulations described in the next section, the conditional probabilities used were the best fit values.

3.3. SIMULATION DESIGN AND ANALYSIS

The simulation program was written in Code-Warrior[®] C for the Power Macintosh. The simulations described below were all Monte Carlo simulations using the pseudo-random number generator RAN2 (Press *et al.*, 1992).

Each simulation consisted of 120 time units, and at the start of each simulated experiment ($t = 0$), model pups were placed in cells in the model arena similar to that depicted in Fig. 1(b). Since all simulated experiments started with $N = 8$ pups, pups were placed in rows 2 and 4 and columns 3–6 [see Fig. 5(a)]. The orientations of pups were either east or west and these orientations were assigned randomly with probability of 0.5 for either orientation. Each pup was set to the active state at the start of a simulation experiment.

At each time t a probability matrix was calculated for each active model pup from its preferences [see eqn 1 and Fig. 5(d)]. A cumulative series of eight terms [$u_1 = p_{11}, u_i = (u_{i-1} + p_{ij}), \dots, u_8 = (u_7 + p_{21})$ where $i, j \neq 2$] was generated by moving in a clockwise direction starting in the top left corner of the matrix [see Fig. 5(d)]. A pseudo-random number in the range [0,1] determined the direction a pup would attempt to move [see Fig. 5(c)]. If the pseudo-random number was less than or equal to u_i , then the pup attempted

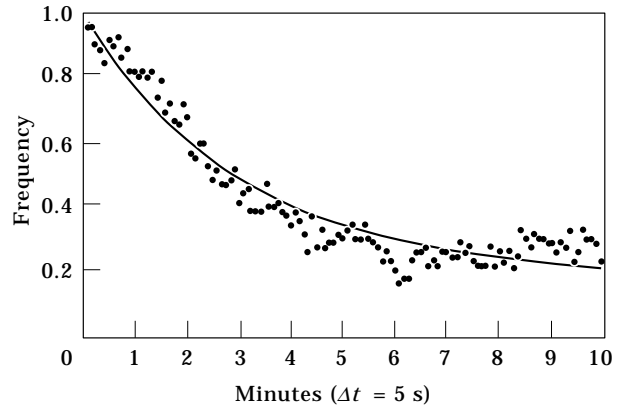


FIG. 6. The best nonlinear fit of equation (4) with the activity frequency data [Fig. 3(a)] $p(I_t|A_{t-\Delta t}) = 0.022$ and $p(A_t|I_{t-\Delta t}) = 0.005$.

to move to cell c_{11} in its local neighborhood, or else the next term u_2 was tested and so on in a clockwise direction until a neighboring cell was found. Since the pseudo-random numbers were in the range $[0,1]$ and the term u_8 must equal 1.0, a direction of movement was always found. It was often the case, however, that a pup could not move to a given cell because it was already occupied by a wall or another pup. In such cases the pup remained in its current cell, but oriented its head and body in the direction of the cell into which it was attempting to move. In addition, at each time t , three types of data were recorded: aggregon patterns, the number of pups oriented towards and in contact with a wall (i.e., wall topotaxis), and the number of active pups.

A technical problem arose in the simulation system because pups were assumed to move simultaneously at each time t , but two or more pups may attempt to move into the same empty cell. How should this be handled in a serial program? In this simulation system, the program first checked to see which cell each pup was attempting to move into; if more than one pup attempted to move into a cell, then a pseudo-random number was used to determine which pup would occupy the cell (each competing pup had an equiprobable chance of moving into the cell). Another problem arose when a pup, on its turn, attempted to move into a cell that was filled by a pup but which emptied after its occupant moved. Again, the program looped back through (as many times as necessary) to check whether this had happened, in which case the pup was then moved to the vacated cell.

In all simulation experiments, the conditional probabilities of activity and inactivity were set to $p(A_t|A_{t-\Delta t}) = 0.978$ and $p(I_t|I_{t-\Delta t}) = 0.995$ as determined by fitting eqn (4) to the activity data (Section 3.2). This left three free parameters: preferences for pups, walls, and empty cells. We can effectively reduce this number to two parameters by setting one of the preferences to 1.0 and systematically varying the other two to determine which preference values best fit the empirical data on aggregon pattern change. A biologically reasonable assumption is to start with preferences for pups of 1.0 and systematically vary preferences for walls and empty cells starting with values less than 1.0.

The aggregon pattern change data [Fig. 4(b)] was used to select best-fit parameter values for object preferences. This was accomplished by constructing a “fitness function” for two aspects of the aggregon pattern data. The first aspect was the fit between the simulation and data frequency *distributions* and the other was the fit between *frequencies* of pattern

change over time. The distribution matching function was:

$$M_d(\mathbf{S}, \mathbf{D}) = 1 - \frac{1}{2} \sum_{i=1}^n |s_i - d_i| \quad (5)$$

where \mathbf{S} is a vector containing the simulation frequency distribution of aggregon patterns and \mathbf{D} is the data frequency distribution of patterns. Thus, $M_d(\mathbf{S}, \mathbf{D})$ is the match between the two frequency distributions and since they are both frequency distributions, the match must range from 0 (no match) to 0.57 (uniform random distribution match for these data) to 1 (perfect match).

The frequency of pattern change over time is defined by (6):

$$M_f(\mathbf{A}, \mathbf{B}) = |1/N_A \sum_{i=1}^g \sum_{j=1}^{r-1} \Delta(a_{ij}, a_{ij+1}) - 1/N_B \sum_{i=1}^h \sum_{j=1}^{r-1} \Delta(b_{ij}, b_{ij+1})| \quad (6)$$

and

$$\Delta(x_{ij}, x_{ij+1}) = \begin{cases} 1 & \text{if } |x_{ij} - x_{ij+1}| > 0 \\ 0 & \text{otherwise} \end{cases} \quad (6)$$

where \mathbf{A} (simulation) and \mathbf{B} (data) are matrices of aggregon pattern indices with r columns representing the number of time units t ($r = 120$ for both simulation and experiments). \mathbf{A} has g rows (the number of simulation experiments) and \mathbf{B} has h rows (the number of experiments), where $N_A = g(r-1) =$ the number of simulated pattern changes and $N_B = h(r-1) =$ the number of observed pattern changes for all nine litters. Thus, $M_f(\mathbf{A}, \mathbf{B})$ is the absolute difference in the frequency of pattern change between simulation and experiment.

The match between data and simulation is defined by the difference between (6) and (5):

$$M_{df} = M_d(\mathbf{S}, \mathbf{D}) - M_f(\mathbf{A}, \mathbf{B}) \quad (7)$$

which is in the range: $1 \geq M_{df} \geq -1$. Thus the pattern match M_{df} combines both static and dynamic information about aggregon patterns.

The match between the data and simulated wall topotaxis distributions is defined by (8).

$$M_w(\mathbf{S}, \mathbf{D}) = 1 - \frac{1}{2} \sum_{i=1}^n |s_i - d_i| \quad (8)$$

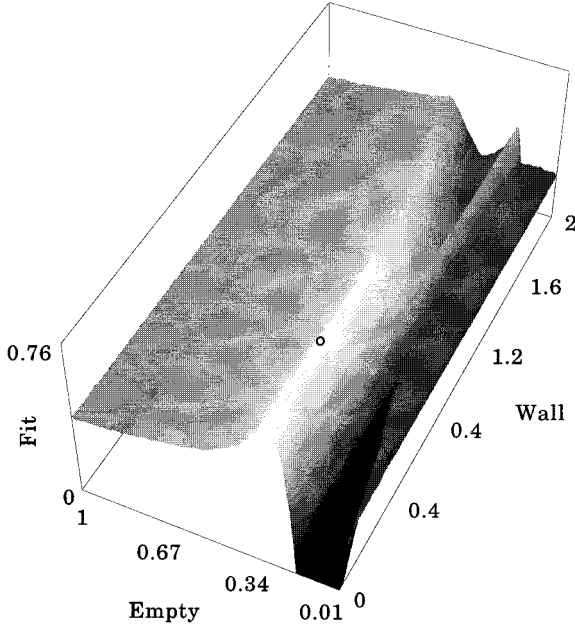


FIG. 7. Fitness landscape defined by eqn (7). Empty preferences ranged from 0.01–1.0 and wall preferences ranged from 0–2.0 with increments of 0.01. Each point on the landscape represents 10000 simulated aggregative-behavior sessions, and the gray scale indicates the goodness of fit (the lighter the better). The small circle indicates the location of the optimal fit point.

where \mathbf{S} is a vector containing the mean frequency of wall topotaxis for simulated experiments for each time t , \mathbf{D} is a vector containing the mean frequency of wall topotaxis for all nine litters, and $1 \geq M_w(\mathbf{S}, \mathbf{D}) \geq 0$, since it is the mean match of the frequency of wall topotaxis at each time t .

Finally, since the activity state of pups was modeled using conditional probabilities, this implied that there must be sequences of activity and inactivity over time for model pups, the mean and variance of which are determined by these conditional probabilities. Assuming a constant Δt , the mean and variance in the length of activity ($1/p(I_t|A_{t-\Delta t})$ and $p(A_t|A_{t-\Delta t})/p(I_t|A_{t-\Delta t})^2$ respectively) or inactivity ($1/p(A_t|I_{t-\Delta t})$ and $p(I_t|I_{t-\Delta t})/p(A_t|I_{t-\Delta t})^2$ respectively) are defined by infinite sums, which converge on simple solutions in the limit. Monte Carlo simulations with 10 sets of 10000 simulations yielded values that varied within a range of less than 1% for the predicted means and variances of activity and inactivity. Thus, 10000 simulated experiments per set of parameter values were deemed adequate for all simulations described in the next section.

3.4. RESULTS

3.4.1. Patterns of aggregons: best fit preferences

The best fit between simulation and data occurred when the preference for walls (0.38) was greater than

the preference for empty cells (0.27), which are both considerably less than the preference for other pups (1.0). Figure 7 illustrates a fitness landscape defined by eqn (7) for wall preferences ranging from 0–2 and empty cell preferences ranging from 0.01–1.0 [the minimum value for cells must be greater than 0, otherwise there are circumstances in which eqn (1) is undefined] with increments of 0.01 for each. The best fit point is indicated on this landscape by a small circle.

The fit between the model and data distributions is 0.75 [Fig. 8(a); uniform random distribution is 0.57 and no match is 0], but the most striking feature of Fig. 8(a) is how the two distributions follow each other as indicated by the lines connecting the points representing the frequency of each aggregon pattern. This suggests that the combinatorial character of aggregon patterns is a major component of their observed frequencies.

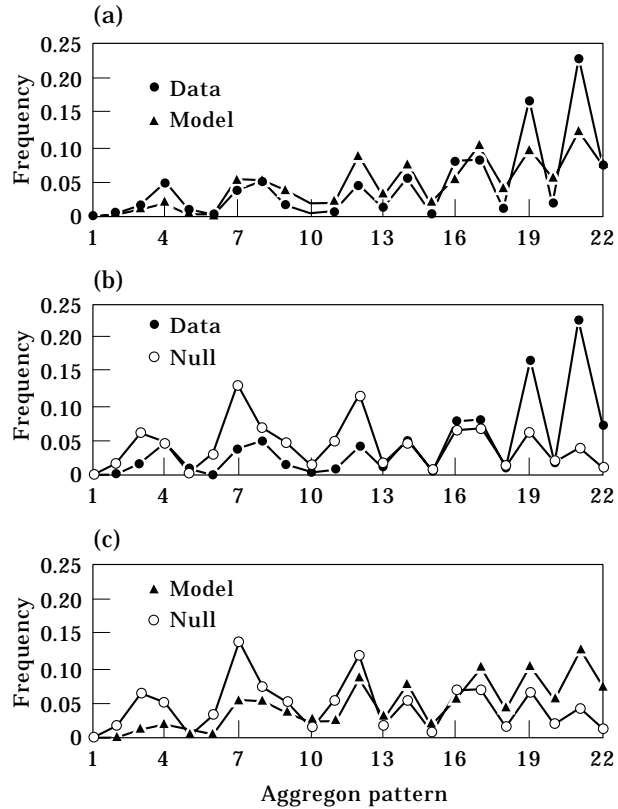


FIG. 8. Three comparisons of aggregon frequency distributions. (a) A comparison of the data and best fit simulation distributions (fit = 0.75). The lines connecting points illustrate how the distributions follow each other revealing their multimodal and combinatorial character. (b) A comparison of the data and null distributions (fit = 0.62, uniform random fit = 0.57). Though the fit as expected is relatively poor [compare (a) and (b)], the lines connecting points indicate that the change in frequencies for both distributions tend to follow each other indicating the importance of the combinatorial character of aggregon patterns in determining their frequency distributions. (c) A comparison of null model and the best fit simulation in [(a); fit = 0.69].

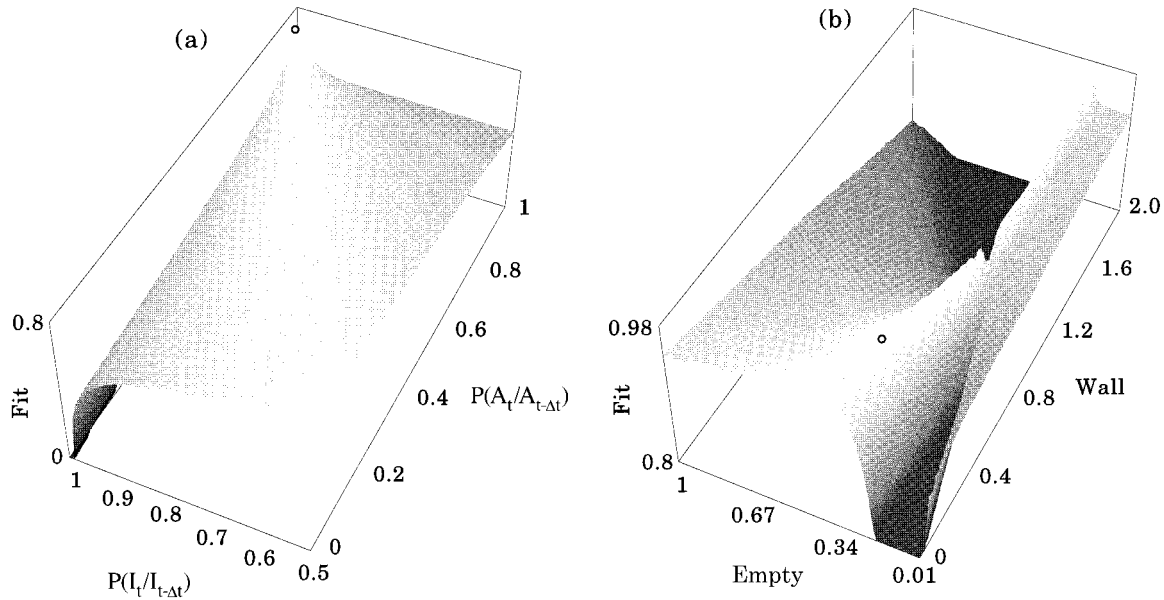


FIG. 9. Two fitness landscapes. (a) Wall (0.38) and empty cell (0.27) preferences are held constant and the conditional probabilities of activity and inactivity are varied in the range $P(A_t|A_{t-\Delta t}) = 0.0-1.0$ and $P(I_t|I_{t-\Delta t}) = 0.5-1.0$ with increments of 0.01 (see Fig. 7). The circle indicates the location of the best fit conditional probabilities, which are located close to the best fit region of conditional probability values on the landscape, and thus support the overall consistency of the data with the model. (b) Fitness landscape defined by eqn (8) for wall topotaxis. Empty cell preferences ranged from 0.01–1.0 and wall preferences ranged from 0–2.0 (see Fig. 7). The circle indicates the location of the best fit point (wall = 0.38 and empty cell = 0.27) depicted in Fig. 7. This point (fit = 0.9774) lies in a region near the best-fit wall-contact (best fit = 0.978), which further supports the overall consistency of the model.

To separate the contribution of combinatorial character of aggregon patterns from the contribution of object preferences, we compared data and best-fit simulation distributions with a “null” distribution in which preferences for pups, walls, and empty cells were set to 1. The match between the data and the null model is 0.62 which is close to a random match (0.57), but the change in the frequency of aggregon patterns for both distributions is typically in the same direction, indicating that the multimodal character of these distributions is largely due to the combinatorial character of aggregon patterns [compare Fig. 8(a) and (b)]. The effect of optimal preference values is to shift the distribution to the right [i.e. to greater contact, Fig. 8(a)]. The match between the model and null preferences models is 0.69, which is intermediate between the fit of the data to the model and the null model [Fig. 8(c)].

Finally, the simulated frequency in change of aggregon patterns was 0.363 compared with 0.359 for the data, a difference of only 0.004. Thus, the match between the best-fit simulation and data of frequency in aggregon pattern change is exceptionally close, and the qualitative match between aggregon pattern distributions is striking [Fig. 8(a)], revealing combinatorial and preference components in the determination of aggregon pattern frequency distributions (Fig. 8).

3.4.2. Conditional probabilities and preferences

The consistency of the fitted values of the conditional probabilities (see section 3.2) with the aggregon pattern data was validated by generating a fitness landscape in which wall (0.38) and empty cell (0.27) preferences were held constant. This time the conditional probabilities were varied (0.01 increments) over the range: $P(A_t|A_{t-\Delta t}) = 0.0-1.0$ and $P(I_t|I_{t-\Delta t}) = 0.5-1.0$. The fitted values of the conditional probabilities produced a best fit of 0.75, which is very close to the best fit (0.766) that could be found by varying the conditional [Fig. 9(a)]. This supports the overall consistency of the model with the data.

3.4.3. Wall topotaxis

The match between the frequency of wall contacts in the data and simulations can be measured using eqn (8). Figure 9(b) illustrates the fit of the simulations with the wall topotaxis data for wall preferences ranging from 0.0–2.0 and empty cell preferences ranging from 0.01–1.0 again with increments of 0.01. The small circle indicates the approximate location of the optimal aggregon pattern fit (wall = 0.38 and empty cell = 0.27). The fit of the points on this landscape ranged from a low of 0.529 to a high of 0.978 (wall = 0.66 and empty cell = 0.21). The best-fit aggregon data preferences (wall = 0.38

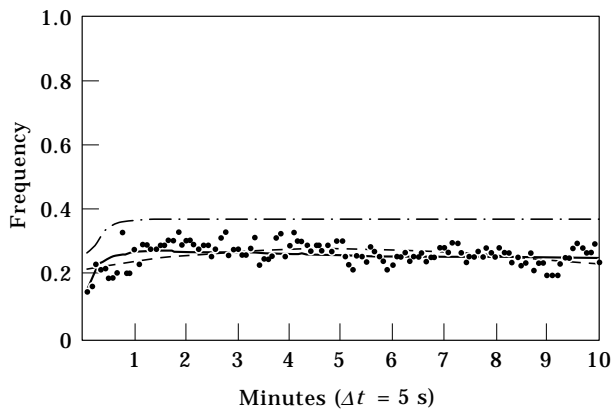


FIG. 10. A comparison of the best fit preferences [Fig. 9(b)], the wall-contact data [Fig. 4(c)], and the null model. The effect of assuming all preferences are the same (the null model) is to shift the distribution up 9% but it does not alter the form of the distribution over time. The model fits the data better than the best polynomial fit ($y = 0.221 + 0.002x - 0.000015x^2$). Key: ● Wall data; — simulation; - - - null; ··· polynomial.

and empty cell = 0.27) yielded a match of 0.9774, which is almost identical to the best fit found and is well within the range of error for these simulations.

The fit of the stimulated wall contacts is striking and considerably better than the best polynomial fit we found (Fig. 10). The null frequency distribution over time of wall contacts is similar in form to the best fit preferences except that the frequency of wall contacts is shifted up about 9%. Finally, other simulations of wall topotaxis for conditional probabilities that were lower than those reported here but in the range of best fit frequencies shown in the landscape of Fig. 9(a), did not fit as well as conditional probabilities that are close to the best fit probabilities. Taken together, these results indicate a very good match between simulation and data, especially considering that the best fit parameters for the aggregon data yielded a near best fit for the wall topotaxis data.

4. Discussion

Technological and conceptual advancements in the study of complex systems have made it possible to study biological systems at various levels of organization (Holland, 1995; Kauffman, 1971). Researchers can now build individual-based models in which space is made explicit (e.g., see Holland, 1995) and thus are ideal for integration into the study of animal behavior. To date these techniques have found their broadest application in ecology (Judson, 1994), but we believe that they can also be applied widely to social and group regulatory behaviors in development. In this paper we have

described a simple individual-based model and its experimental application to the dynamics of aggregative behavior in infant rats. We believe that the present model and the approach that shaped it can provide a framework for further studies into the dynamics of aggregative-behavior in mammals and other taxa. Below we will discuss two implications of these results. First, this model and its theoretical framework can serve as a baseline approach for further empirical/theoretical investigation of group regulatory behaviors and development in rats and related systems. Second, our approach has broad implications for investigating self-organization in development and evolution.

4.1. BASELINE MODEL

This is the the first model of sensorimotor control of individual behavior in the context of group interactions in a vertebrate species. As such, it provides a baseline model for further research on sensorimotor coordination, development, and group-regulatory behavior in at least three ways: first, using the highly controlled environment of the arena we have shown that the dynamics of aggregative behavior in infant rats fit a model that postulates topotaxic behavior, characterized by sensorimotor rules that specify an individual's preferences for objects and conditional probabilities of activity and inactivity. Comparisons of the model's behavior and the behavior of infant rats robustly support the view that the behavior of 1-week-old pups is essentially topotaxic, and that the dynamics of their aggregative behavior can be explained by *individuals* behaving according to simple sensorimotor rules. Thus, the model illustrates that searching for simple sensorimotor rules may be a promising strategy and starting point for explaining other complex and group regulatory behaviors.

Second, while our results strongly suggest that the group regulatory behaviors serving the functions of thermoregulation and energy conservation can be explained by topotaxic behavior, the model described above does not fully explain the group regulatory behavior required for thermoregulation and energy conservation in 7-day-old rats. In order to extend this model to these group regulatory functions, more detailed models will be required. In particular, we will need to specify how preferences and conditional probabilities of activity depend on (i) internal states of pups and (ii) external thermal factors (e.g., thermal gradients). Our view is that the model presented here provides a baseline model for developing more complex models of the group regulatory behaviors of thermoregulation and energy conservation.

Third, an interesting implication of this work is that the activity of 1-week-old rats is approximately independent of the activity of other pups. This independence of activity ceases as rats develop and thus individual rats become increasingly coupled to the activity of others as evidenced by the emergence of social behaviors (Calhoun, 1962). However, patterns of activity and inactivity begin to become synchronized by 12 days of age (unpublished pilot data). This suggests to us that the model can also serve as a baseline model for studying the development of coupled and synchronized activity in rats—which is essential for the development of social behavior in contact species—by, for example, incorporating into it time-dependent and contact-dependent models of conditional probabilities of activity.

4.2. SELF-ORGANIZATION: DEVELOPMENT AND EVOLUTION

The frequency of formation of large aggregons of pups (i.e. aggregons with six, seven and eight pups in contact) is much greater than what is expected by chance [Fig. 8(b)], and the best-fit model exhibits a similar pattern [Fig. 8(a), (c)]. Since large aggregons of pups can be viewed as characterizing more ordered states in this system—and their increased frequency is due to local interactions among pups modulated by simple sensorimotor rules—the aggregative behavior exhibited by pups in the arena is self-organizing.

We view self-organization as playing an important role in the development and evolution of aggregative and group regulatory behaviors in rats and other species. The role of genes in development is often described by metaphors of *program* or *blueprint*, but these metaphors are ultimately useful only to the extent that they lead to a deeper understanding of the structures and mechanisms of development. The program and blueprint metaphors, while superficially structuring the relationship between genes and phenotypic characters, are nevertheless systematically misleading. The program metaphor breaks down when rigorously applied to development: there is no overall temporal sequencing of developmental events encoded in genomes (Nijhout, 1990). Nor does the blueprint metaphor fare any better, since genomes do not encode a spatial representation of the morphology, physiology, and behavior of organisms at each stage of development. Instead, the morphologies, physiologies, and behaviors that emerge during development are more adequately viewed as the interactions of gene products within a range of environmental contexts (Nijhout, 1990). Or, perhaps more generally, the role of genes in development is via

epigenetic interactions of gene products, cells, morphological structures, physiologies and behavior which emerge from the complex morphologies, physiologies and behaviors we observe during development. These epigenetic interactions are paradigms of self-organization, and if our analysis is correct, the relatively complex group regulatory behavior of huddling in infant rats emerges as a self-organizing process from the topotaxic behavior of infant rats. Thus, neither group selection nor group level mechanisms are needed to explain aggregative or group regulatory interactions. They can emerge at any level as a consequence of components (e.g., rat pups) locally interacting according to relatively simple rules at a lower level.

Self-organization is therefore an important concept for understanding how evolution and development can produce complex systems and behavior. The discussion of self-organization and selection in evolutionary processes has recently focused on the opposing influences of selection and generic constraints on the evolution of complex systems (e.g., Kauffman, 1993). However, self-organization can complement selection. If this initial research is correct, then aggregative dynamics and group regulatory processes can emerge from the local interactions of individuals, even individuals with severely limited sensorimotor capacities and that behave topotaxically according to a limited number of simple rules. Selection may act at the level of the group by selecting those huddles that are able to maintain cohesion, conserve energy, and thermoregulate well, but the behaviors that are heritably selected for are not necessarily at the level of the group. Instead, they are likely the simple sensorimotor rules of individual behavior from which aggregative and group regulatory behaviors emerge. If this view is correct, then it is the simple sensorimotor rules and the genes or gene complexes that play a causal role in their epigenesis that must be heritable. Thus, if the complex group behavior of huddling emerges from individuals behaving topotaxically and these topo-taxic behaviors are heritable, then selection and self-organization can act symbiotically to produce group aggregation, cohesion and other regulatory behaviors out of the simplicity of topotaxic behavior.

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