

The developmental emergence of coupled activity as cooperative aggregation in rat pups

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Rat pups (*Rattus norvegicus*) are born blind and deaf yet manage to wriggle about in a huddle, dynamically adjusting their positions and thereby displaying thermoregulation and energy conservation at the level of the group. As pups develop, their activity and mobility outpace the development of their visual and auditory systems making it increasingly difficult to aggregate and maintain aggregation while still blind and deaf. The developmental emergence of coupled activity may be one mechanism that facilitates aggregation. Our previous research has shown that the activity of a seven-day-old pup is independent of the activity of the litter mates it contacts. However, we hypothesized that, by day 10, more active and mobile pups will exhibit coupled activity, becoming increasingly quiescent when in contact with other behaviourally quiescent pups. In order to test this hypothesis, we used individual-based modelling. Because the structure of the model was complex, we used a Darwinian algorithm for evolving a model that behaved like ten-day-old pups aggregating in an arena. Sensitivity to quiescent individuals was manifested in some litters by the transitory spreading of quiescence across aggregates of both real and virtual pups (a contagion effect). As pups develop, individual behaviour becomes increasingly contingent on the behaviour of others revealing what may be a basic component in the development of cooperative behaviour.

Keywords: coupled activity; cooperative behaviour; aggregation; rat pups; individual-based modelling

1. INTRODUCTION

At birth and for more than one week thereafter, an individual Norway rat pup (*Rattus norvegicus*) is essentially incapable of regulating its body temperature (Alberts 1978a) and shows only meagre thermal responses within a narrow range of ambient temperatures (Conklin & Heggenes 1971). In a huddle, however, pups behave as a 'superorganism', displaying capacities for thermoregulation and energy conservation far beyond those of the individual (Alberts 1978a). When faced with cool ambient temperatures, the surface area of a huddle contracts but expands in warm ambient temperatures (Alberts 1978a). Under these conditions, the movements of pups create convection currents of bodies within a huddle: cool pups circulate into the huddle while hot pups circulate to the surface (Alberts 1978a). As a pup develops, its morphology, physiology and sensorimotor capabilities change dramatically. Huddling is maintained throughout these changes. Indeed, huddling is a lifelong behaviour which, in addition to its thermal and energetic significance, also serves social functions (Calhoun 1962; Barnett 1963).

The aim of the present paper was to go beyond classical experimental and empirical methods for discovering developmental transitions in the sensorimotor abilities of pups. Our aim was to integrate classical experimental techniques with new computational techniques and thereby allow us to discover and quantify subtle ontogenetic transitions in individual sensorimotor behaviour in the context of a huddle or more generally a group.

In order to model these ontogenetic transitions, we must neither assume too much nor too little about a pup's

sensorimotor capabilities at each stage of development. C. Lloyd Morgan's (1852–1936) canon asserts that under no circumstances should 'an animal activity be interpreted as the outcome of the exercise of a higher psychical faculty, if it can be fairly interpreted as the outcome of one which stands lower on the psychological scale' (Costall 1993, p. 116). However, Morgan's canon was not intended as a principle of parsimony, limiting explanations of animal behaviour to simple mechanisms (Costall 1993). Instead, the aim of Morgan's canon was to alert Darwinians to other modes of perceptive and reactive relationships between animals and their environments besides reflective and rational thought (Costall 1993). It is precisely these perceptive and reactive relationships (i.e. the organism's *Umwelt*) (Von Uexküll 1957) and their development that we seek to understand better with the help of computational modelling.

Altricial mammals such as Norway rat pups are born with very limited sensorimotor abilities. As sensorimotor abilities develop, abrupt changes can occur in an organism's *Umwelt* (e.g. when an altricial mammal's eyes open its *Umwelt* expands from tactile and proximate interactions with parents and siblings to more distal interactions afforded by vision). Not only does sensory development alter the developing organism's *Umwelt*, so do changing functional requirements (e.g. the ability to thermoregulate independently or forage for food). How then should we apply Morgan's canon to the development of sensorimotor behaviour and capabilities in the social and/or developmental context of a huddle or aggregate of rat pups?

One approach is to begin with a collection of entities that have no sensory capabilities, no internal motivations and no drives. They move about randomly in their environment. We then ask what capabilities must they have in

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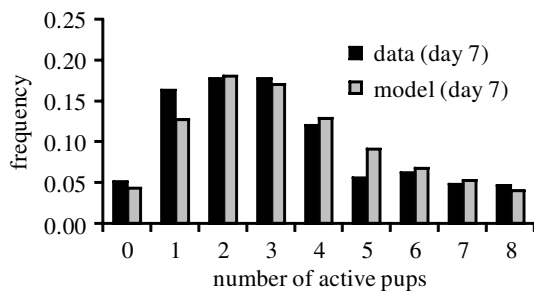


Figure 1. A test of independence of activity among nine litters of eight, seven-day-old pups over a 10 min test (Schank & Alberts 1997). If the activity of a pup is independent of the activity of every other pup in a litter, then the frequency of active pups should be binomially distributed for the probability of activity at each time t given by the best fit of equations (3) and (4) to the data (see Schank & Alberts 1997). The frequency distribution of active pups should not differ significantly from the actual frequency of pups active every minute for the 10 min trial (for all nine litters and a total of 90 min) and it did not differ ($\chi^2 = 2.87$, d.f. = 8 and $p > 0.94$).

order to produce the biological functions and pattern aggregations we observe. This null starting point is analogous to treating newly born altricial mammals as particles of a gas. At the micro level (i.e. an analogue to the individual level), particles of gas randomly collide and at the macro level (i.e. an analogue to the group level), properties of the gas such as temperature and pressure emerge from the 'activity' and 'mobility' of the gas particles. Although unusual organizations of particles are possible at the micro level (e.g. most of the particles aggregated in some region of the container holding the gas), these non-equilibrium states are so improbable by chance that, in practice, they are never observed. Starting with this null model, we seek those sensorimotor rules of individual behaviour that allow pups to form non-equilibrium patterns of aggregation. In computationally modelling these altricial mammals, we must try to follow Morgan's canon and avoid attributing too lavish sensorimotor capabilities on our subjects, but neither should we assume too little; we seek to discover nothing more nor less than the individual and group sensorimotor capabilities at each stage of development.

Infant rats, although blind and deaf, are in many respects dissimilar to the particles of a gas. By seven days of age, they can readily move about a small arena and partially aggregate on its surface through tactile interactions. Surprisingly, whether seven-day-old pups are active or not is essentially independent of the activity of the litter mates they physically contact (figure 1) (Schank & Alberts 1997). As a pup develops, while still blind and deaf, it becomes increasingly active and mobile (Alberts 1984). By 15 days of age, odour becomes the predominate cue that attracts and maintains contact between pups (Brunjes & Alberts 1979; Alberts & May 1980) but, prior to that age, temperature and tactile cues are more salient (Alberts 1978*b*; Alberts & Brunjes 1978). Thus, increased activity and mobility of pups prior to 15 days of age may interfere with aggregation because a pup's sensory capabilities are still so limited. In analogy with a thermodynamic gas, increases in the activity and mobility of particles increase pressure leading to the expansion of the

gas and 'disaggregation' of particles. Pups are far from particles of a gas but, with their still-limited sensory capacities, increasing activity and mobility may cause them to lose contact with other pups thereby increasing the likelihood that pups disaggregate or fail to aggregate in an arena.

If the particles of a gas tend to become less active and mobile when they contact other less active particles, then non-equilibrium structures of particles could condense out of the hypothetical gas. Similarly, if pups tend to become less active when in contact with other inactive pups not only might disaggregation be less likely, but also patterns of greater aggregation may be more likely to form even with increased motor activity and severely limited sensory capabilities. This suggests a basic rule for cooperative aggregation in young pups: pups become quiescent as a function of the number of other quiescent pups contacted. We investigated and analysed this hypothesis by evolving a model of ten-day-old pup aggregative behaviour from data on their behaviour in a temperature-controlled arena.

2. METHODS

(a) *Experiment*

We used 19 litters of Norway rats (Sprague-Dawley). Each litter consisted of four males and four females of age ten days. All animals were born and bred at Indiana University Animal Behavior Laboratory from stock originally obtained from Taconic Farms (Germantown, NY, USA). Standard polypropylene maternity cages (48 cm × 20 cm × 26 cm) housed dams and litters. Food and water were provided *ad libitum*. Colony rooms were maintained at $24 \pm 2^\circ\text{C}$ and illuminated from 08.00 to 20.00. Prior to birth, dams were checked twice daily at *ca.* 08.00 and again at 17.00 for the birth of pups. Pups found at these times were marked as born on that day (day 0). At three days of age, litters were culled (arbitrarily) to four females and four males. All animals were treated according to the strict guidelines for animal care at Indiana University.

In order to study aggregative behaviour in litters of pups, a rectangular arena (32.7 cm × 20.5 cm × 5.1 cm) was constructed in which temperature and other variables could be tightly controlled (Schank & Alberts 1997). Both surface temperature and ambient temperature were maintained at 34°C (figure 2). Prior to seven days of age, pups moved about very little on the surface of the arena (J. C. Schank, unpublished observations). Therefore, seven days was deemed the minimum age at which sensorimotor contact could be reliably observed among pups in this apparatus.

Pups were tested between 10.00 and 18.00. They were removed from the nest just prior to testing, sexed, marked on the back with a number from 1 to 8 and a vertical line (female) or horizontal line (male) was made on the top of their head (with a non-toxic marker). Pups were then immediately and arbitrarily placed in the testing apparatus (arena) in a disaggregated state (figure 2). This was accomplished by placing each pup in a compartment of a rack (with eight separate compartments) in the arena (figure 2). When the rack was lifted and the pups released, they were videotaped for 15 min. After videotaping, all pups were returned to their nest.

The videotapes were digitized and a frame was captured every 5 s for behavioural scoring using a version of NIH Image (<http://rsb.info.nih.gov/nih-image/>) which was modified for

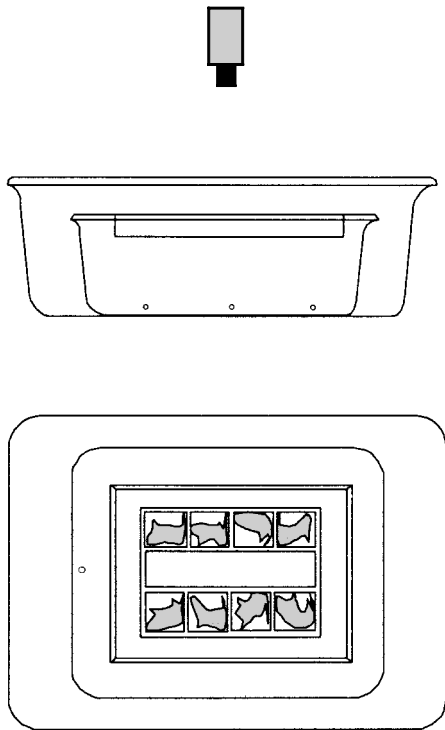


Figure 2. An illustration of the placement of pups in the arena at the start of each test session (Schank & Alberts 1997).

these purposes. The data used were the activity state of each pup, the contact relationships between pups and the number of pups in subgroups. The activity state of a pup was operationally defined as a pup displaying coordinated movement of the head (back and forth) and/or legs in a 5 s interval. This in turn was determined by using NIH Image's image mathematical functions in order to add images at t and $t + 5$ s into a composite image that could be inspected for movement (see Schank & Alberts (1997) for more details).

(b) Theory

We used individual-based modelling (IBM), which is widely used in ecology (DeAngelis & Gross 1992; Judson 1994) as a paradigmatic strategy for tackling problems of emergent organization (Holland 1995; Bar-Yam 1997), for modelling aggregation on the surface of the arena (Schank & Alberts 1997). The model arena consisted of a two-dimensional array of cells (6×5 , reflecting the relative size of the pups). Each cell was either empty or contained a pup or wall (figure 3). Orientation to and movement towards a cell was probabilistically determined by the contents of cells adjacent to a model pup and its preferences for the contents of a cell (Schank & Alberts 1997). These preferences were constant over time and the same for each pup. Based on observation, we assumed that a pup detected the contents of a cell by tactile contact with its head and nose (figure 3). Thus, only the three cells at the head end of a model pup formed its preference sensory field (Schank & Alberts 1997).

A very general way of representing the types of behaviour (B_i) that a rat pup performs is with conditional probabilities for their occurrence and we represented these probabilities in two steps. First, to behave implies an organism is active. We can model activity (inactivity) as conditional on prior activity (inactivity) and a variety of other variables including internal

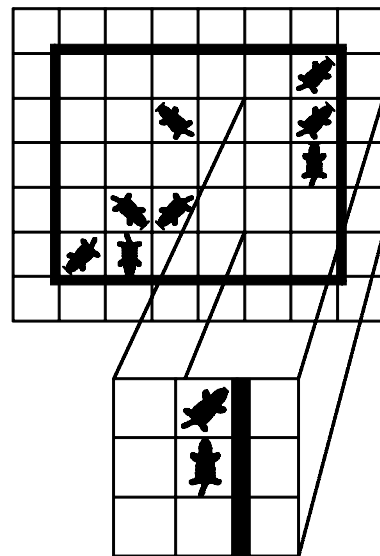


Figure 3. An illustration of the cells and model pups comprising a simulated test session. Pups are assumed to detect objects tactilely by sweeping their heads back and forth and, thus, a pup's tactile field (the grey cells in the blown-up illustration) are the three cells in front of it (see Schank & Alberts (1997) for more details).

physiological state and sensory inputs (such as the number of active and inactive pups a pup physically contacts) that influence transitions from activity to inactivity and inactivity to activity. We represented these conditional probabilities as

$$P(I_t | A_{t-\Delta t}, x_1, \dots, x_n), \quad (1)$$

and

$$P(A_t | I_{t-\Delta t}, x_1, \dots, x_n), \quad (2)$$

where A is activity, I is inactivity or behavioural quiescence and x_1, \dots, x_n are variables (the time-indices of these variables are implicitly understood as $t - \Delta t$) influencing behaviour. Second, given that an animal is active at t , the probability that it produces a specific behaviour B_i is $P(B_i | A_{t-\Delta t}, x_1, \dots, x_n) \geq 0$ where $P(B_i | I_{t-\Delta t}, x_1, \dots, x_n) = 0$ when behaviourally quiescent. In this case, B_i is orientated movement of the pups which depends on the local spatial arrangement of pups, the walls surrounding each pup and a pup's preferences for objects in its environment at $t - \Delta t$.

The probability of activity over time when all other variables affecting activity are ignored, including dependencies on the activity state of other pups, yields a basic equation for uncoupled activity (by coupled activity we mean that the probability a pup is active is conditional on the activity state of other pups with which it is in physical contact):

$$P(A_t) = P' A_t + [P(A_0) - P' A_t] e^{-t[P(I_t | A_{t-\Delta t}) + P(A_t | I_{t-\Delta t})]}, \quad (3)$$

where

$$P'_{A_t} = \frac{P(A_t | I_{t-\Delta t})}{P(A_t | I_{t-\Delta t}) + P(I_t | A_{t-\Delta t})}. \quad (4)$$

(c) Coupled activity

By day 10, animals are more mobile and active (Alberts 1984). If the activity of a pup depends on the number of active and inactive pups it contacts, then the conditional probabilities

for activity are more complicated, requiring a more complex model of activity. Conditional probabilities of activity for day 10 pups were defined in order to vary with time and the number of active (N_A) and inactive (N_I) pups contacted, yielding a system of equations with a total of 12 parameters:

$$P(A_t|I_{t-\Delta t}, N_A, N_I) = P(A_{t=0}|I_{t-\Delta t}, 0, 0) e^{\ell[\alpha_{AI}N_A + \beta_{AI}N_I + c_{AI}] + \gamma_{AI}N_A + \lambda_{AI}N_I} \quad (5)$$

and

$$P(I_t|A_{t-\Delta t}, N_A, N_I) = 1 - P(A_{t=0}|A_{t-\Delta t}, 0, 0) \times e^{\ell[\alpha_{AI}N_A + \beta_{AI}N_I + c_{AI}] + \gamma_{AI}N_A + \lambda_{AI}N_I}, \quad (6)$$

where $P(A_{t=0}|I_{t-\Delta t}, 0, 0)$ and $P(A_{t=0}|A_{t-\Delta t}, 0, 0)$ are constant initial probabilities of a pup alone when the rack is lifted, and the exponential components are explained in Appendix A. Equations (5) and (6) can be substituted into equations (3) and (4) for day 10 coupled activity under the mathematical constraint that equations (5) and (6) behave as probabilities.

A fundamental difficulty with using IBM is finding good models for analysing complex behavioural systems. While complex optimization problems involving many degrees of freedom are often analytically intractable or intractable to brute-force search, there have been many recent successes using a variety of Darwinian algorithms (e.g. Mitchell 1998). We applied Darwin's principles (Lewontin 1970) of heritable variation in phenotypic fitness to the relationship between the model parameters and data. Specifically, we developed a modified version of simulated annealing (Kirkpatrick *et al.* 1983; Press *et al.* 1992) for a Monte Carlo simulation framework (Metropolis *et al.* 1953).

In outline, our simulated annealing algorithm worked as follows. The 14 real-value parameters (12 for the activity model and two for preferences) of the model were mapped into a 'chromosome'. The current model reproduced a single 'offspring' model at each generation with a mutation rate r at each locus. Thus, mutations were Poisson distributed over offspring loci. We found that a per locus mutation rate of $r = 0.05$ worked well for the results reported here.

A mutation at the i th locus was the current value of that locus $\pm \Delta_i$ and Δ_i was calculated as $\Delta_i = c_i\beta$, where c_i is the maximum change allowed at the i th locus given that a mutation occurred and β is a random real number in the range $[1, -1]$ (pseudo-random real numbers in the range $[0, 1]$ were generated using RAN2 (Press *et al.* 1992) and transformed to the range $[1, -1]$).

The new model was selected at each generation based on the probability of it surviving into the next generation as a function of 'fitness':

$$P(\text{new model}) = \begin{cases} 0 & \text{if inconsistent} \\ 1 & \text{if } f_n > f_o, \\ 1 - \exp(-[f_n - f_o]/kT) & \text{otherwise} \end{cases}, \quad (7)$$

where the new model is rejected if inconsistent and accepted if its fitness (f_n) is greater than the old model's fitness (f_o); otherwise it is accepted with probability $1 - \exp(-[f_n - f_o]/kT)$. In the latter case, k is a constant and the analogue of Boltzmann's constant and T is the analogue of temperature. A new model was deemed inconsistent if its new parameters violated the mathematical assumptions of the model. For example, all probabilities must be in the range $[0, 1]$; if a set of parameters

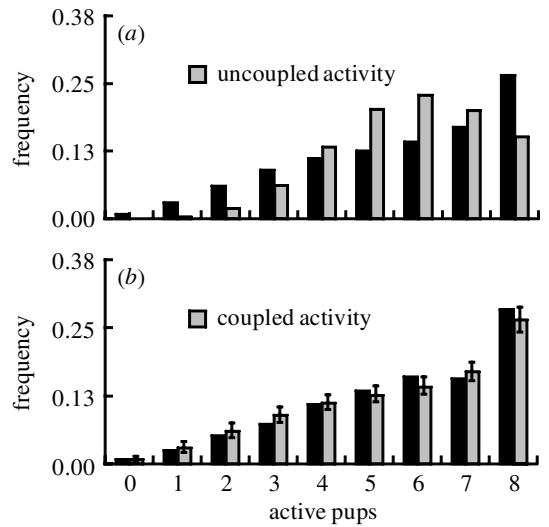


Figure 4. A test of independence of activity among 19 litters of eight, ten-day-old pups over a 15 min test. If the activity of a pup is independent of the activity of every other pup in a litter, then the frequency of active pups should be binomially distributed for the probability of activity at each time t given by the best fit of equations (3) and (4) to the ten-day-old pup activity data. (a) The frequency distribution of active pups should not differ significantly from the actual frequency of pups active every minute for the 15 min trial (for all 19 litters and a total of 285 min) but it did differ ($\chi^2 = 117.6$, d.f. = 8 and $p \ll 0.001$). (b) However, when activity is coupled (see figure 5), the model does not significantly differ from the data (95% confidence intervals, $\chi^2 = 2.96$, d.f. = 7 and $p > 0.93$).

produced probabilities outside this range, the entire model was rejected. Checking for consistency saved a considerable amount of computation time.

The fitness of the model was assessed by running n Monte Carlo simulations with the offspring model and then computing fitness functions of the form $|X - Y|^a$, where X is an empirical data measure, Y is a model data measure and a is an exponent regulating the strength of selection. For example, for one of the fitness functions used, X was the average number of subgroups formed in the 19 litters over the 15 min test session and Y was the average number of subgroups (see §2(d)) formed in n Monte Carlo-simulated experiments with model pups. The total fitness of a model was the sum of 30 fitness functions between the model and data.

The fitness landscapes had two sources of ruggedness (see Kauffman (1993) for a theoretical discussion of rugged fitness landscapes), i.e. nonlinearity and stochastic error introduced by the Monte Carlo simulations of aggregation. Increasing the number (n) of simulation experiments at each generation can reduce stochastic error. However, increasing n comes with computational time costs. Thus, we found that a good strategy for finding good-fit models was to start out with $n = 100$ and $a = 1$ and then slowly lower T over many generations (e.g. 50 000) until progress ceased. Next, we raised n to 1000 and adjusted the range of mutational change (c_i) at each locus to ca. 10% of the parameter value at that point. The annealing process was continued again until progress ceased. In the final set of annealing runs, n was raised to 10 000 and $a = 2$. This greatly reduced the stochastic error component and, by increasing a , a model could be fine-tuned around a local optimum. We repeated this procedure several times in order to determine whether we would find similar sets of parameter

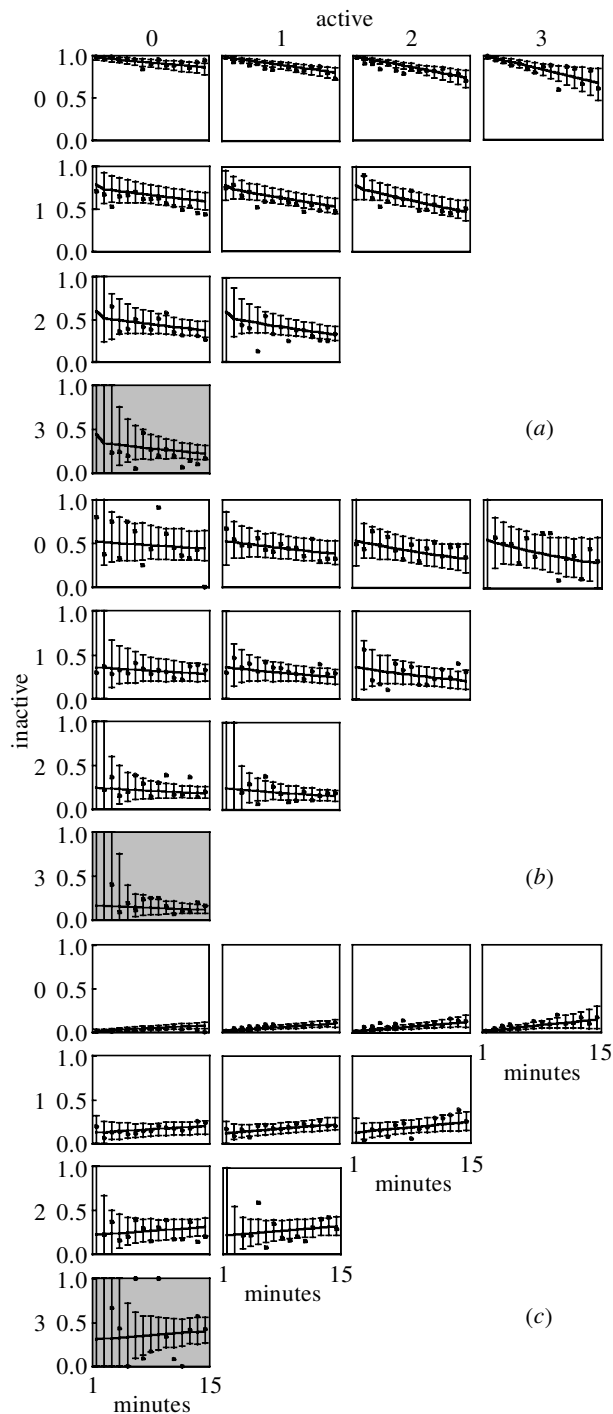


Figure 5. Match of the model (equations (3)–(6)) and the data for day 10 pup activity (95% confidence limits). The figures represent the frequency of activity over time (15 min) given the number of active and inactive pups contacted. Data points are plotted with black dots and the model predictions are with lines (confidence limits are estimated from the model). The number of active pups contacted runs from left to right and inactive pups runs from top to bottom. (a) Frequency of activity (equations (3) and (4) with equations (5) and (6) substituted in as conditional probabilities), (b) activity given prior inactivity (equation (5)) and (c) inactivity given prior activity (equation (6)). Contact with more than four pups was negligible as was contact with three inactive pups early in a session (grey). These conditions were not used in evolving the model.

Table 1. Numerical values evolved by simulated annealing (see Appendix A)

parameters	values
activity	
$P(A_{t=0} I_{t-\Delta t}, 0, 0)$	0.521314
α_{AI}	-0.000987
β_{AI}	-0.000408
c_{AI}	-0.000958
γ_{AI}	-0.382934
λ_{AI}	0.019047
$P(A_{t=0} A_{t-\Delta t}, 0, 0)$	0.988809
α_{AA}	-0.000152
β_{AA}	-0.000161
c_{AA}	-0.000368
γ_{AA}	-0.115153
λ_{AA}	0.001541
preferences	
pups	1.0
walls	0.05
empty cells	0.18

values each time which we did. Here we report on the best-fit model that we found.

(d) Subgroups and aggregons

We have previously distinguished patterns of group formation on the surface of an arena as patterns of aggregons (Schank & Alberts 1997). For example, one aggregon pattern is (3, 3, 2) while another is (4, 2, 2). In both examples, this means that three groups of pups formed isolated physical contact groups on the surface of the arena. In the first case, two groups of three pups were in physical contact and a third group of two were in contact. In the second case, four pups were in contact and there were two other groups of two in contact. Aggregons take into consideration the number of individuals in each subgroup that forms on a surface and there are 22 different aggregon patterns for eight individuals. Aggregon patterns are complex and how to go about imposing order on them is not always intuitive (Schank & Alberts 1997). Thus, we devised a new way of looking at pattern formation in terms of the number of subgroups that form on the surface of an arena. A subgroup is an aggregate of pups in physical contact. If one subgroup forms, then all ($n=8$) pups are in physical contact. If none of the pups are in contact with each other, then by definition there are eight subgroups. There is only one way in which all eight pups can be in contact, but for two subgroups there are several ways (i.e. aggregon patterns), i.e. (7, 1), (6, 2), (5, 3) and (4, 4). The number of subgroups provides a method for measuring the degree of aggregation in a litter, where fewer subgroups indicate a higher degree of aggregation.

(e) Confidence limits

Evolving good models requires many data points, with the assumption that the larger the data set, the closer the data will be to the true parameter values. However, increasing the precision of the data by increasing the number of data points for the evolutionary process makes it less likely that the model found will fit the data for some pre-established significance level. Thus, evolving models based on large data sets and searching for models that do not differ from the data at some level of significance can be conflicting goals. Approximately true models will often be rejected given large enough data sets,

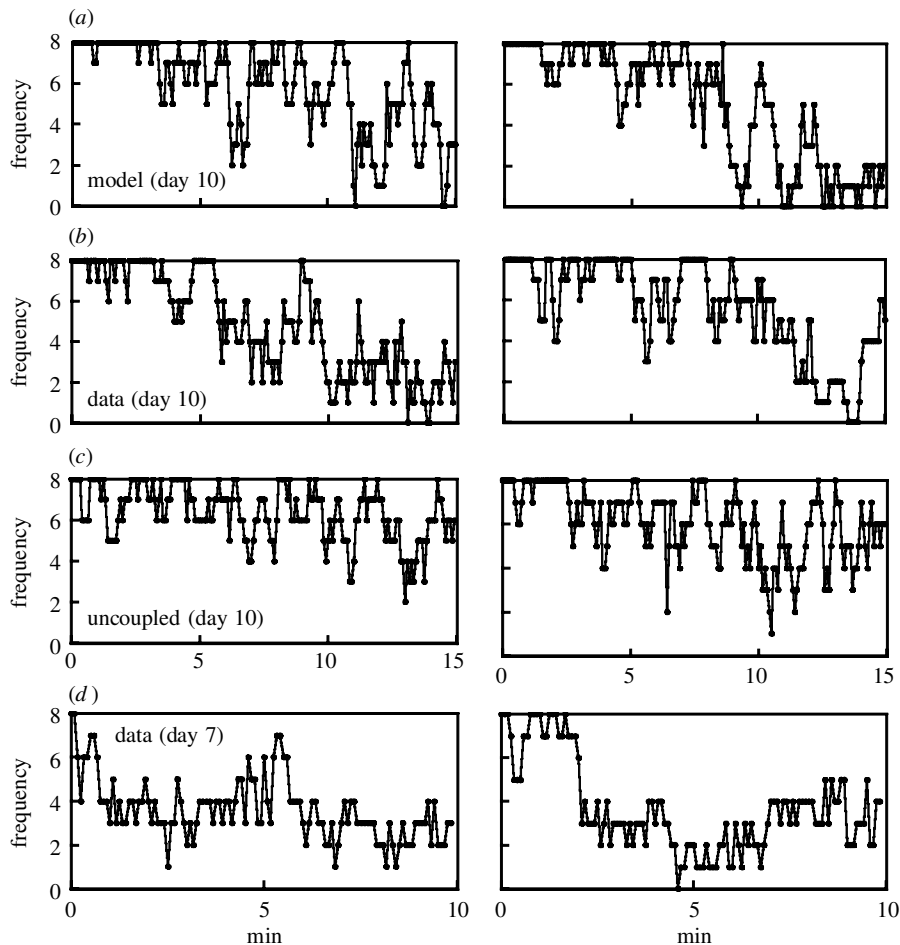


Figure 6. Examples of patterns of activity in a litter of pups. (a) Two examples of patterns of change in activity in litters over time observed in simulated experiments and (b) two examples from ten-day-old litters. There are transitory periods in both cases in which all eight animals are behaviourally quiescent. (c) Two model litters assuming uncoupled activity and (d) patterns of activity in two litters of seven-day-old rats (Schank & Alberts 1997).

although approximately true models are the starting point for finding truer models (Wimsatt 1987). Nevertheless, we want to know whether the model evolved is empirically plausible. Using Monte Carlo simulation (Metropolis *et al.* 1953; Press *et al.* 1992), we assumed that, for an evolved model M , if a large number of simulated experiments $E_i/(M)$ are run, then the statistical behaviour of the model converges on limiting values with a distribution of experimental outcomes about these mean values $E_i/(M) - \bar{E}/(M)$ from which confidence limits can be estimated. These limits allow us to evaluate how probable or improbable the data are given the model. The 95% confidence limits estimated below are from 1000 simulated experiments of 19 litters each.

3. RESULTS

(a) Coupled activity

We obtained good agreement between the model and data for individual activity (see figures 4 and 5) (table 1 lists the parameter values evolved). The model also predicted aspects of activity under the sparse data condition of a pup in contact with three inactive pups (figure 5a) (this condition was not used to evolve the model). The Monte Carlo generation of confidence limits (95%) indicated that the data were generally consistent

with the model. Small intervals indicated that many data points were available in the model and large intervals indicated relatively few data points. These patterns were also characteristic of the empirical data, further indicating that the model had captured essential aspects of the underlying biological or behavioural processes producing these patterns of individual activity.

Individual activity decreased with time, but the rate of decline and the frequency of activity at any given time were a function of the number of active and inactive pups contacted (figure 5a). If a pup contacted zero or more active pups its activity was relatively high but declined gradually with time during an experimental session (top row in figure 5a). However, the number of inactive or behaviourally quiescent pups contacted had a dramatic effect on the probability of activity; the entire distribution shifted down as the number of inactive pups increased, while contact with one or more active pups had little influence on overall activity. The same situation occurred with the transitional probabilities $P(I_t|A_{t-\Delta b}, N_A, N_I)$ and $P(A_t|I_{t-\Delta b}, N_A, N_I)$. Contact with one or more inactive pups decreased the likelihood of a transition from inactivity to activity (figure 5b), while it increased the likelihood of making a transition from activity to inactivity (figure 5c).

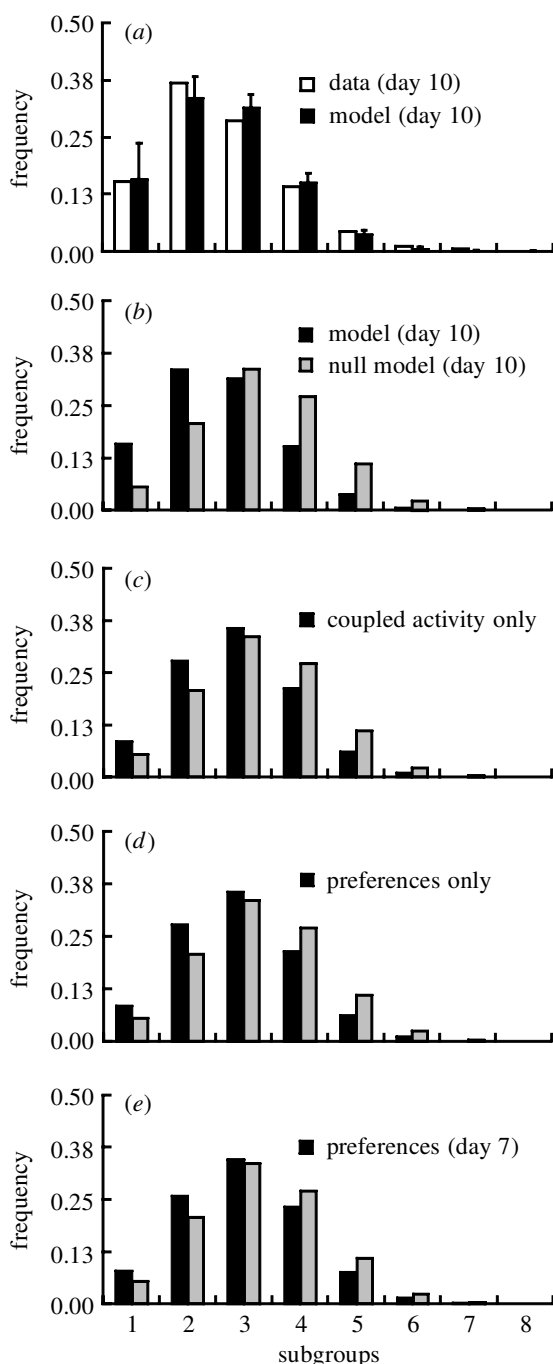


Figure 7. (a) Subgroup distributions for both the model and data (95% confidence limits). Comparisons of the null model (grey) with four surrogate models: (b) the complete model (day 10), (c) coupled activity only (no preferences), (d) preferences only (day 10) and (e) ten-day old model pups with day 7 preferences and uncoupled day 10 activity.

We also observed transitory patterns of synchronized behavioural quiescence during the latter part of some of the experimental and simulation sessions, in which deactivation of pups quickly spread across a litter when all or most of the pups were in contact (a contagion effect) and ended as pups became active along the periphery of an aggregate in both litters (figure 6a) and virtual litters (figure 6b). Figure 6c,d illustrates typical patterns of activity for the model assuming no coupled activity (see § 3(b) for a description of this null model)

and for data from two typical seven-day-old litters (Schank & Alberts 1997). We did not observe transitory periods of synchronized quiescence in these last two cases.

(b) Subgroup formation

The model also fit the pattern of subgroup formation in the data (figure 7a). A fundamental precept of our work is that evolved models can function as surrogate systems for experimental analysis by computer simulation. Using the model evolved as an experimental surrogate, figure 7b–e illustrates how coupled activity and preferences affect aggregation by comparing them to a null model. The null model assumed (i) no difference in preferences for pups, walls and empty cells, and (ii) that conditional probabilities of activity are uncoupled and constant as with seven-day-old pups (figure 1) (Schank & Alberts 1997). Activity in the null model approximated activity levels in real pups by fitting equations (3) and (4) to the ten-day activity data.

In order to analyse the contributions of preferences, coupled activity and development to aggregation, the frequency of simulation outcomes with only one or two subgroups (i.e. high-aggregation outcomes) was compared with the null model under different theoretical conditions. Figure 7b illustrates the full model compared to the null model illustrating 23% more high-aggregation outcomes for the full model. Figure 7c illustrates the model with coupled activity only (no differences in preferences) compared to the null model resulting in only 8.5% more high-aggregation outcomes. Figure 7d illustrates the model with preferences only compared to the null model resulting in only 10% more high-aggregation outcomes. Thus, both coupled activity and differences in preferences contributed to aggregation, but their effect was not additive.

Figure 7e illustrates the model without coupling and with day 7 preferences (pups = 1.00, walls = 0.38 and empty cells = 0.27) (Schank & Alberts 1997) compared to the null model resulting in only 7.4% more high-aggregation outcomes, which is only a little less than the magnitude of change produced by day 10 preferences (compare figure 7d,e). The theoretical developmental change in preferences from day 7 to day 10 does facilitate aggregation but is complicated. Ten-day-old model pups (table 1) preferred walls ($0.18/0.38 = 0.47$) and empty cells ($0.05/0.27 = 0.19$) less than seven-day-old pups, which should facilitate their aggregation. However, ten-day-old pups also preferred walls to empty spaces ($0.18/0.05 = 3.6$) more than seven-day-old pups ($0.38/0.27 = 1.41$), which may have interfered with their aggregation.

4. CONCLUSIONS

We view aggregation and how it emerges from individual behaviour as a practical starting point for a science of social behaviour and organization. Evolving IBMs, by simulating Darwin's principles of natural selection, in order to understand and predict group behaviour and organization better is a promising approach for the rigorous study of aggregation in animal behaviour, both theoretical and applied (also see Watts 1998). By evolving models, we may find them generally useful as surrogate

models for experimental analysis by computer simulation. Indeed, we believe that this approach opens up a new empirically based approach to studying aggregative and social behaviour, which cannot be accomplished by experimental analysis alone.

We hypothesized that mechanisms for facilitating aggregation should develop. We found that, over a span of three days or less (from days 7 to 10), the activity of a rat pup appears to become coupled to the activity of the other pups it contacts (i.e. the probability of a pup being active or inactive is conditional on the activity states of the other pups it contacts with physically). This corresponds to increased activity and mobility of ten-day-old pups while still blind and deaf. We also found that behavioural quiescence in one or more pups increased the likelihood that behavioural quiescence would spread across an aggregate of pups (a contagion effect). Using computer simulation, we showed that pups aggregated better in the arena with coupled activity than without it and that preferences and coupled activity interacted non-additively in enhancing aggregation in ten-day-old pups. Preferences are attributes of the individual, whereas coupled activity is an interaction between individuals. Thus, the developmental emergence of coupled activity may signal the emergence of a basic component of sociality in rats which changes and becomes more complex with further sensorimotor development and social interactions at later stages of development.

The empirical data were collected at Indiana University and the final model and simulation analysis were developed and performed at the University of California, Davis. This work was supported by the US National Institutes of Health. We thank two anonymous referees for their insightful and critical comments on an earlier draft of this paper.

APPENDIX A

This appendix briefly explains how equations (5) and (6) were derived and their meaning. We sought the simplest equations that could account for (i) coupling, and (ii) change in activity as a function of time. We need only consider two cases, $P(A_t|I_{t-\Delta t}, N_A, N_I)$ and $P(A_t|A_{t-\Delta t}, N_A, N_I)$, where N_A is the number of active animals and N_I is the number of inactive animals. Both probabilities are expected to decrease (and not increase) over short periods of time after animals are 'activated' by placing them in the arena. We assumed the rate of change involved no interaction terms among the numbers of animals in either state. If we let Δt approach zero, then we can define the change in $P(A_t|I_{t-\Delta t}, N_A, N_I)$ as an ordinary differential equation. i.e.

$$\frac{dP(A|I, N_A, N_I)}{dt} = [\alpha_{AI}N_A + \beta_{AI}N_I + c_{AI}]P(A|I, N_A, N_I), \quad (A1)$$

where α_{AI} and β_{AI} determine the effects of active and inactive individuals contacted on the rate of change of $P(A|I, N_A, N_I)$, respectively, and c_{AI} is that portion of the rate of change that remains constant.

Upon integrating equation (A1) we obtain

$$P(A_t|I_{t-\Delta t}, N_A, N_I) = Ce^{t[\alpha_{AI}N_A + \beta_{AI}N_I + c_{AI}]}, \quad (A2)$$

where C is a constant of integration and $0 \leq P(A_t|I, N_A, N_I) = Ce^{t[\alpha_{AI}N_A + \beta_{AI}N_I + c_{AI}]} \leq 1$.

The initial conditions for equation (A2) are still undefined and so we must find a term for C . Assume an individual is only surrounded by active or inactive individuals but not both. For these cases, we have two differential equations at $t=0$:

$$\frac{dP(A_{t=0}|I_{t-\Delta t})}{dN_A} = \alpha_{AI}P(A_{t=0}|I_{t-\Delta t}) \quad (A3)$$

and

$$\frac{dP(A_{t=0}|I_{t-\Delta t})}{dN_I} = \beta_{AI}P(A_{t=0}|I_{t-\Delta t}). \quad (A4)$$

Upon integrating, we respectively obtain

$$P(A_{t=0}|I_{t-\Delta t}, N_A) = e^{\gamma_{AI}N_A} e^{C_1} \quad (A5)$$

and

$$P(A_t|I_{t-\Delta t}, N_I) = e^{\lambda_{AI}N_I} e^{C_2}. \quad (A6)$$

We defined the initial probability for an experimental session as a simple multiplicative relation for N_A and N_I pups and a constant probability for a pup alone when the rack is lifted as

$$P(A_{t=0}|I_{t-\Delta t}, N_A, N_I) = r_{N_A}r_{N_I}P(A_{t=0}|I_{t-\Delta t}, 0, 0), \quad (A7)$$

where r_{N_A} and r_{N_I} are constants that scale the initial constant probability for a pup alone by the number of active and inactive pups it is next to at $t=0$ (we ignored $N_A \times N_I$ interactions in scaling in this simple model). If we multiply equations (A5) and (A6) we obtain

$$P(A_{t=0}|I_{t-\Delta t}, N_A, N_I) = e^{\gamma_{AI}N_A} e^{\lambda_{AI}N_I} e^{C_1} e^{C_2}, \quad (A8)$$

where $r_{N_A} = e^{\gamma_{AI}N_A}$ and $r_{N_I} = e^{\lambda_{AI}N_I}$. By defining $e^{C_1+C_2} = P(A_{t=0}|I_{t-\Delta t}, 0, 0)$, substituting into equation (A8) and simplifying, we obtain

$$P(A_{t=0}|I_{t-\Delta t}, N_A, N_I) = e^{\gamma_{AI}N_A + \lambda_{AI}N_I} P(A_{t=0}|I_{t-\Delta t}, 0, 0) \quad (A9)$$

which defines an initial conditional probability for equation (A2).

Now we are ready to substitute the initial conditions in equation (A9) into equation (A2), resulting in equation (5):

$$\begin{aligned} P(A_t|I_{t-\Delta t}, N_A, N_I) &= e^{\gamma_{AI}N_A + \lambda_{AI}N_I} P(A_{t=0}|I_{t-\Delta t}, 0, 0) e^{t[\alpha_{AI}N_A + \beta_{AI}N_I + c_{AI}]} \\ &= P(A_{t=0}|I_{t-\Delta t}, 0, 0) e^{t[\alpha_{AI}N_A + \beta_{AI}N_I + c_{AI}] + \gamma_{AI}N_A + \lambda_{AI}N_I}. \end{aligned} \quad (A10)$$

We derived equation (6) in a similar manner.

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