

# The dynamics of long-term exploration in the rat

## Part I. A phase-plane analysis of the relationship between location and velocity

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Received: 16 August 1996 / Accepted in revised form: 20 March 1998

**Abstract.** Rat exploratory behavior consists of regular excursions into the environment from a preferred place termed a home base. A phase plane representation of excursions reveals a geometrical pattern that changes during exploration in both shape and size. We first show that with time and repeated exposures to the same large environment there is a gradual increase in the length of excursions; each rat has its own characteristic length of excursions; but all rats share a similar rate of excursion growth. As in our experimental setup the rats perform increasingly longer paths from one location, while locomoting back and forth along the walls of the arena, exposure is more extensive at the proximal part of the route, and less at the distal part. We consequently show that the rat's velocity pattern changes concurrently with the increase in excursion length, and in correlation with the level of exposure (familiarity) to places. The primitive velocity pattern consists of slow progression while moving away from base and fast progression while returning to it. During exposure the asymmetry in velocity is inverted. The inversion spreads across successive excursions from the home base outwards. The rate of spread of this inversion is higher than the rate of increase in excursion length, and is similar across rats. Because it spreads more rapidly than the increase in excursion length, the global shape of the excursion trajectory changes. The dynamics of excursion shape share similar properties with the dynamics of excursion length. Both might reflect the same intrinsic constraints on the amount of novelty that a rat can handle per excursion.

1996; Gallistel 1990; Gallistel and Kramer 1996; Hoffmann 1978, 1983a,b; O'Keefe and Nadel 1978; Poucet 1993). In this study we recover processes of spatial memory from the kinematics of unrestrained (free) exploratory behavior in the rat. In the first part we perform a structural analysis of moment-to-moment locomotor behavior; without being assumed at the outset, certain aspects of exploration and spatial memory emerge as features of locomotor behavior in locale space. In the second part, two of us (O.T. and Y.B.) suggest an analytic model that captures features of the observed kinematic structure.

Free exploratory behavior appears to be stochastic. Yet, as has been shown in the desert ant of the genus *Cataglyphis*, a seemingly unstructured path could obey some rules. Wehner and Srinivasan (1981) and Muller and Wehner (1994) formalized such rules to uncover the searching strategy of the ant. Here we examine structural rules in rat exploration to find learning processes: in the rat, some kinematic variables of exploration show regularity when measured in reference to a natural place of reference termed the rat's home base. During exploration of a novel environment, the rat alternates briskly between progression and stopping. The rat chooses one of the places in which it had stopped and shows a long-term preference for it. This place, the home base, is marked by several behaviors that are either idiosyncratic to it or are performed in it at a significantly higher rate than in all the other places (Eilam and Golani 1989). The home base has been shown to attract the rat during its excursions into the environment in the following sense: as the rat leaves it, its probability of performing the next stop at the home base, thus terminating the excursion, increases with every additional stop it performs. This cumulative process of home base attraction might continue until eventually an intrinsic upper bound on the number of stops is reached, and the return to base becomes 'obligatory' (Golani et al. 1993). This upper bound differs from one rat-session to the next; yet it is intrinsic in the sense that it is not 'increasable' by increasing the size of the testing environment. These kinematics were documented for single exploratory sessions (Eilam and Golani 1989; Golani et al. 1993), but

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### 1 Introduction

Exploratory behavior is the natural manifestation of spatial learning (Biegler and Morris 1996; Etienne et al.

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their possible relations to functional aspects of orientation were not studied. It was shown, however, that during long-term exploration in young rats, the establishment of a home base is a unique event of transition from low and constrained activity in locale space, to a diverse and free movement pattern (Tchernichovski et al. 1996).

It is therefore of interest to examine home base behavior in relation to other aspects of the kinematics of rat behavior in locale space, and to do this in a more natural context of a large environment, in ontogeny, so that the presumed long-term familiarization processes can be related to the moment-to-moment kinematics. This is made possible in the present study by testing young rats daily in the same large (6.5 m diameter) arena and by analyzing phase plane graphs that represent the rat's location vs its momentary velocity (Tchernichovski and Golani 1995).

It is a commonplace observation that the area traversed by a rat increases with time in a large enough environment. In preliminary observations, it was suggested that during a single exposure to a novel environment, the portion of an excursion (round trip from home base and back to it) performed by the rat on the way out takes longer to perform than that performed on the way back (Eilam and Golani 1989). Yet the rate of growth of the rat's path and its velocity profile have never, to our knowledge, been examined. In this study, we first quantify the growth of the rat's paths over a large testing environment during a long-term exposure. Then we characterize its velocity pattern in relation to that path. Finally, we examine the dynamic relationship between the growth of the rat's paths and the change of its pattern of velocity.

## 2 Methods

### 2.1 Animals

Subjects were eight Long Evans hooded rats (Department of Animal Breeding, Weizmann Institute of Science, Rehovot, Israel), belonging to three different clutches. From the age of 14 days, the rats were kept, together with their mother, in two  $35 \times 25 \times 15$  cages connected by a 15 cm diameter black plastic pipe. At 21 days of age, the mother was removed from these cages. All rats used the pipe as a shelter. Each rat was handled

daily for 10 min and was subsequently exposed to a variety of environments for another 10 min. This protocol was followed until the observation period. Observations were performed during 43–50 days post-natally. This age group was chosen to study the phenomenon since at this age rats are already very active, their 'loyalty' to the predefined home base is high, and in this sense their behavior is relatively simple (Tchernichovski et al. 1996).

### 2.2 Testing environment

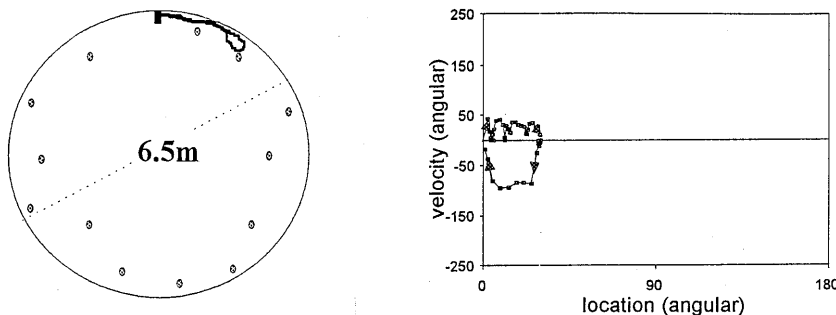
Observations were performed in a 6.5 m diameter circular arena with a concrete floor and 40 cm high metal walls. The large size of the arena and its circular shape reduced trivial interactions between the rat's paths and the environment's boundaries and allowed us to attribute the observed patterns to intrinsic constraints. Several large objects (distal landmarks) were placed outside the arena. In order to standardize the home base location for all rats, a pipe similar to the one used by the rats as a shelter in their cage was inserted through the arena wall, just above floor level, and sealed. Fifteen flat small objects (proximal landmarks) were randomly placed at a 20–150 cm distance from the walls. The circle's center was, therefore, clear of objects. The environment was thus polarized by creating a gradient of distance from the familiar pipe, and another gradient between the walls and the barren central area (Fig. 1A).

### 2.3 Session planning and recording procedure

To cover the process of becoming familiar with the whole arena, each rat was exposed to it daily for eight successive sessions, each 30 min long. Observations were performed at night, under artificial lights. The rat was placed near the pipe, and its behavior was recorded throughout the session by a stationary video camera whose lens covered the whole arena. Immediately afterwards, it was returned to its home cage.

### 2.4 Data acquisition and preparation

**2.4.1 Data acquisition** The rat's path was recorded by an automated tracking system including a Matrox Magic



**Fig. 1.** **A** The testing environment and a path traced by a rat in it during an excursion performed from the pipe. A small rectangle on top represents the home base. Small circles represent object locations. **B** A phase plane representation of the same excursion. The arrow indicates the trajectory's direction. Data points are represented by small squares. The x-axis represents the angular displacement from the pipe; the y-axis represents the momentary speed in cm/s

card, a Telcom T/800/900 time coding system, and software developed in our lab. The recorded  $x$ ,  $y$  coordinates on the video were transformed to the real Cartesian coordinates of the rat's location. These coordinates and timing were recorded every 100 ms, as soon as movement was detected by the system. Average location in polar coordinates and velocity were calculated per 0.5-s interval measured every 0.25 s.

**2.4.2 A phase plane representation of excursions** Figure 1B shows a phase portrait of an excursion performed by a specific rat during its first session in the arena. It describes the rat's momentary angular location (angular component of a polar coordinate system) during a single excursion, and its derivative in time (momentary velocity in units of cm/s to prevent a bias when the rat moves away from the arena's boundary). The  $x$ -axis represents the angular displacement of the rat from the pipe. The  $y$ -axis represents the rat's momentary velocity, clockwise velocity being defined as positive and counterclockwise as negative. The data points in the graph provide the rat's momentary location and velocity, computed per 0.5-s interval.

Figure 1 left shows the path of a typical excursion from the pipe and back. Figure 1 right presents a phase plane representation of the same excursion. The excursion's trajectory starts at the origin of axes, i.e., the rat is located at the pipe with zero speed. As long as the rat does not move, the data points pile up at the origin. As the rat starts to move away, it alternates briskly between acceleration and deceleration. It stops twice, in the middle of the way out (note the data points on the  $x$ -axis). The return trajectory is performed with a higher speed and without stopping. The trajectory crosses the  $x$ -axis only at its extreme right end. This indicates that in this example both progression away from the pipe and progression back to it proceeded monotonically, without intermittent back and forth loops.

The above-described excursion trajectory was selected from the behavior of a rat recorded during eight successive half-hour sessions in the arena, between 43 and 50 days of age. This record was partitioned, by using visits to the pipe as the boundaries, into 200 to 300 excursion trajectories per rat (typically 10–40 excursions per session; excursions of less than 40 cm away from the pipe were not considered). The morphology of these trajectories is the subject of the present study.

## 2.5 Statistical methods

Various quantitative attributes of an excursion, namely its length, average attraction distance, and average repulsion distance, were developed and analyzed. The new measures are presented in detail in the Results section. For their further analysis, the measures were all transformed logarithmically to stabilize variances and were summarized for each rat at the first, the middle, and the third equal parts of a session by their respective medians. These measures were analyzed using ANCOVA and variance components models in which the rat

was used as one (random) factor, the session part as a fixed factor, and session number was used as a covariate. Second order interactions were tested in an ANCOVA model.

Only the angular component of location and velocity vectors were analyzed. Comparison of the results to corresponding results based on calculations of Cartesian location and speed (i.e., scalar velocity) revealed that this reduction from 4 to 2 dimensions caused a relatively small loss of information. This is because most of the excursions were performed along the wall, i.e., most of the data were purely angular anyhow.

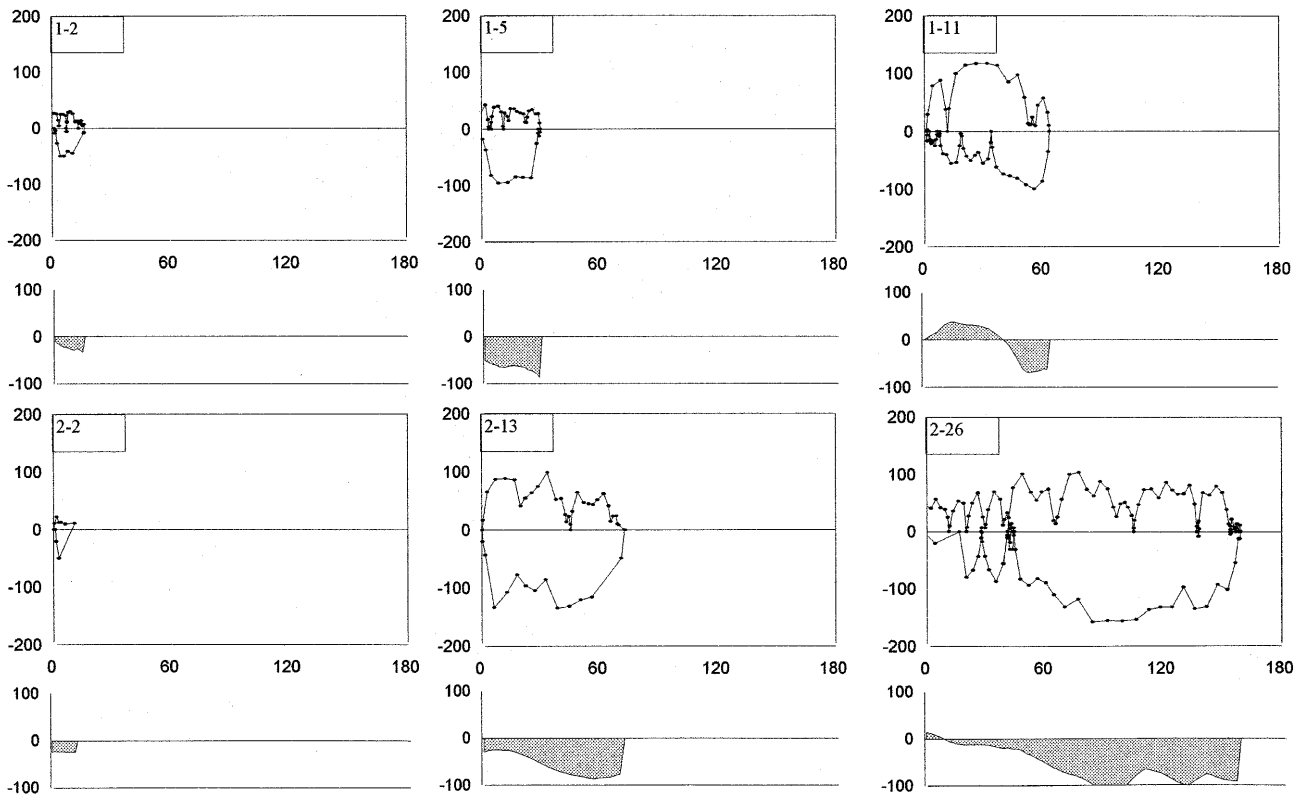
For the purpose of estimating nonparametrically the dependence of excursion parameters on the temporal order of their performance, the Lowess method, as implemented in the statistical software S (Becker et al. 1988), was used. This method employs local linear regression in the neighborhood of each point separately, to yield the predicted value for the dependent variable. The participating points at each location have higher weights the closer they are to the point at which the relationship is estimated. Further automatic down-weighting of outliers assures the robustness of this procedure. For more details about the lowess method, see Cleveland (1979).

## 3 Results

### 3.1 An illustration of the dynamics of home base attraction

We first illustrate the phenomenon we intend to examine by presenting three typical phase planes of the first, and three of the second session of rat B1. Below each phase plane, in a separate graph, the difference between inward and outward speed is represented for each location (Fig. 2; for a formal definition of the bottom graphs see Sect. 3.3). The figure illustrates that (i) the length of excursions (the maximal distance from home base reached by the rat during an excursion) increases during a session and often also across sessions (both from left to right and from top to bottom in Fig. 2); (ii) in the early excursions (i.e., graphs 1–2, 1–5, 2–2, 2–13), for every location that is included in the excursion, the outward speed (the speed on the way out) is lower than the inward speed (the speed on the way back to the home base). In other words, the home base is 'attractive' throughout the excursion; (iii) during late excursions of each of the sessions, the home base is 'attractive' only at the distal segment of the excursion but not in the vicinity of the home base. In Fig. 2, graph 1–11 for example, between 50 and 65° the inward speed is higher than the outward speed, whereas between 0° and 30°, the outward speed is higher.

Our impression was that the movement of the rat was initially restricted to places near the home base, and later to movement further away. During late stages, the rat often behaved as though it was actively avoiding the home base while exploring locations in its vicinity, and as though it was being attracted to the home base while



**Fig. 2.** Typical phase planes of the first and second sessions of rat B1. Numerals in insets indicate session/excursion serial number. Trajectory proceeds from origin of axes (home base, zero velocity) and back to it, in a clockwise direction. For simplicity, only clockwise trajectories are shown. Below each phase plane, we plot a smoothed curve of the difference between inward and outward speeds [denoted as  $V_p$  in Sect. 3.3, (1)]

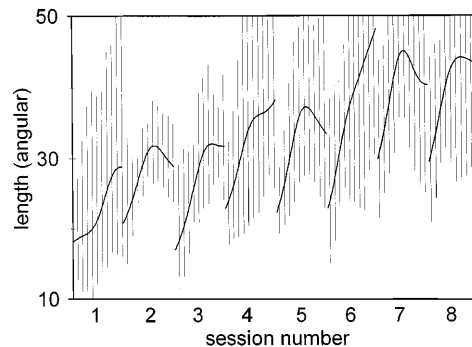
exploring more remote places. These observations lead to the following hypothesis: excursion growth is accompanied by a change in the rat's speed pattern. This change expands proximodistally, lagging behind excursion growth. We are looking therefore for a measure that will estimate the rate of expansion of exploratory movement in space and a measure that will estimate the rat's operational notion of 'near' and 'far' from home base. The two aspects of our hypothesis will now be examined quantitatively.

### 3.2 A quantitative analysis of excursion length

We will first examine the change in the length of excursions within and across sessions. Excursion length was defined as the maximal distance reached by the rat within an excursion. Figure 3 plots a summary of excursion length values for all rats as a function of their temporal order of performance, for each session separately, session by session. All sessions are scaled to have equal length. Ten  $\pm 1$  standard deviation bars indicate the variability at different parts of each session. As shown, excursion length increases both within and across sessions. The most prominent increase occurs during the first half of the session, whereas later the length stabilizes or even decreases. Excursion length drops at the beginning of each session, but then increases

again, reaching in most cases a higher value than the maximum of the preceding session.

As shown in Fig. 3, the standard deviation values are high, indicating that even after considering the possible differences due to different stages and different sessions, the remaining variability is still high. In order to examine the source of this variability, we performed an analysis of covariance (ANCOVA) of excursion length



**Fig. 3.** The average values of the excursion lengths within the first eight sessions. Data are smoothed (Lowess nonparametric scatter plot smoothing method in S-plus) and are presented together with  $\pm 1$  standard deviation bars, computed at ten parts of each session. The  $x$ -axis represents the temporal order of excursions, while the  $y$ -axis represents angular distance from the home base. The numbers below the  $x$ -axis represent the temporal sequence of sessions

**Table 1.** Analysis of covariance (ANCOVA) results for examination of the variance of excursion length. The examined factors are: rat, the influence of the specific rat; observation stage, the influence of session stage; observation no., the influence of the session's number. The four bottom rows examine the independence of the former factors by estimating the level of significance of possible interactions between them

Factor	Degrees of freedom	Sum of squares	Mean of squares	<i>F</i> value	Significance Pr ( <i>F</i> )
Rat	7	7.18	1.03	4.86	< 0.001
Obs. stage	2	4.78	2.39	11.32	< 0.001
Obs. no	1	7.03	7.03	33.31	< 0.001
Rat × Obs. stage	14	2.41	0.17	0.82	0.65
Rat × Obs. no	7	0.90	0.13	0.61	0.74
Obs. stage × Obs. no	2	0.07	0.04	0.18	0.84
Residuals	122	25.75	0.21		

(transformed to the logarithmic scale; see Methods for detail). We examined the influence of three factors and their interactions: that of the specific rat, that of the repeated exposures (i.e., the session's number), and that of the progression of a session (estimated by the three session stages).

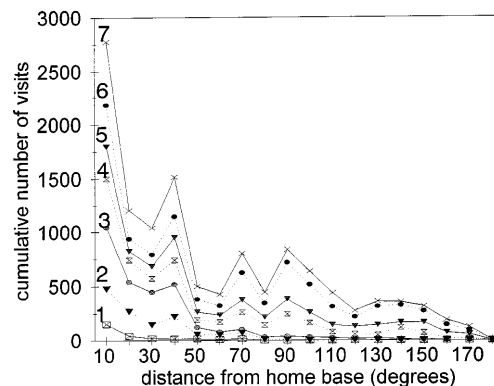
As shown in Table 1, ANCOVA revealed a significant difference between the excursion lengths of different rats, different session stages, and different sessions, but there was no significant interaction between these factors. In other words, each rat had an excursion length that characterized all its sessions and session-stages, while the session stage and the session number contributed additional effects which were similar for all rats. A suitable model for the examination of excursion length should therefore include the random effect of the specific rat, the effect of the session number, and the effect of the stage in the session.

We therefore examined the contribution of each factor to this process by a variance components model, where the rat and session stage (one, two, or three) were used as fixed effects, and session number was used as covariate. The results of this analysis, transformed back to the scale of degrees, give an estimate ( $\pm$  standard error interval) of the typical excursion length during the first stage of the first session as  $18.6^0(16.5^0-20.9^0)$ . The increase in excursion length from one session to the next was 8.8%(7.3%–10.4%) on average; this value did not depend on the session number, fitting a linear model. This suggests that the exploratory process is additive from one session to the next, and that the rate of increase is constant and independent of the previous experience of the rat.

An additional effect is that of progression within a session: The increase in excursion length from the first to the second stage of a session was estimated as 39%(28%–52%). Excursion length increased also from the second to the third stage of the session, but this increase of 7%(–1%–17%) did not reach a statistically significant level. These estimates can be judged against the background variation among the rats, which has a standard deviation of  $1.2^0$ . Each random rat is thus characterized by a typical excursion length, while excursion length increases largely and significantly at a similar rate in all the examined rats, both within and across sessions.

In our experimental setup, most excursions consisted of a simple path performed from the home base and back to it, either to the left or to the right of the home base, along the arena's wall. As we have just shown, there is a gradual increase in the length of excursions across the sequence of excursions. At any given time, therefore, the cumulative number of times a rat walked through a place depended on the distance of that place from the home base: places that were closer to the home base were traversed both during short and long excursions, whereas distant places were traversed only during long (and late) excursions. If a rat's familiarity with a place is influenced by its exposure to that place, then the cumulative duration of staying in that place reflects, at least partly, its familiarity with it. A simple way to measure the exposure of the rat to a place is by examining the distribution of the coordinates traversed by the rat, as recorded by the video tracking system. Figure 4 shows the amount of one rat's exposure to places as a function of their distance from the home base.

As shown, although the exposure changes continuously, there is a stable gradient of decreasing exposure to places as a function of their distance from the home base. Because early excursions are typically short, and



**Fig. 4.** The exposure of the rat to places according to their distance from the home base. The data are the summation of the angular locations of the rat, tracked automatically. The numerals on the right of the y-axis designate the specific graph's session number, the x-axis represents the angular distance from the home base, and the y-axis represents the number of data collected at each location (10°–20° from home base, 21°–30°, and so on)

include relatively unexposed places, whereas typical late excursions are long, later excursions consist of a proximal part including extensively exposed places and a distal part including less exposed places. It is important to note, however, that the term amount of exposure to a place does not necessarily imply visual exposure, and is used as synonymous with cumulative amount of time spent in that place.

We may now examine the speed pattern of the rat in relation to this measure of exposure.

### 3.3 A quantitative analysis of the rat's speed profile during an excursion

For any location  $p$  within an excursion, the 'attraction' of the home base can be described using

$$V_p = |\text{outward speed at } p| - |\text{inward speed at } p| \quad (1)$$

Negative values indicate a higher speed in the home base direction (attraction) and positive values a higher speed on the way out ('repulsion' of the home base at that location). Note that this sequence has no temporal order since the subtraction of outward from inward speed involves two different chronological times. In our experimental setup, the majority of excursions consisted of two monotone segments: a pure outward and a pure inward segment without nested back-and-forth loops. If present, such loops were omitted from the data, and not included in the analysis. Each excursion was therefore described by topographically successive locations with their corresponding values of  $V_p$  (see Fig. 2). Before categorizing each location as either attractive or repulsive, we eliminated noise by using a running median filter. Then, we categorized each  $V_{p_i}$  as attractive for  $|V_p| < -10$  cm/s, and repulsive for  $V_p > 10$  cm/s. The attraction/repulsion level was not defined for  $V_p < 10$  cm/s since such a difference was within the noise level of the tracking system.

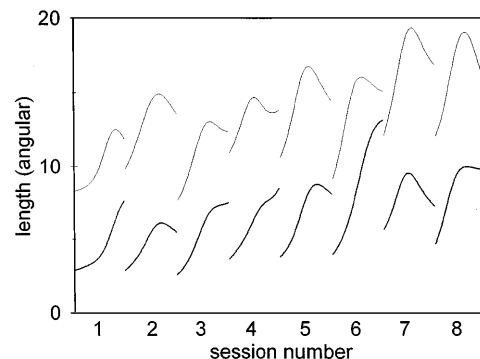
We were thus left with a group of places in which the home base is attractive and a group of places in which it is repulsive. The average values of each of the groups were termed average attraction distance (AD) and average repulsion distance (RD), respectively. For the set of all places  $p_i$ 's visited during an excursion  $i$  (each place is represented by its angular deviation from the home base)

$$\begin{aligned} \text{AD} &= \text{Average}\{p_i\} \\ V_{p_i} &< -10 \\ \text{RD} &= \text{Average}\{p_i\} \\ V_{p_i} &< 10 \end{aligned} \quad (2)$$

Each excursion was characterized by these two measures and by the maximum distance reached in that excursion (in excursion 1–11 of Fig. 2, for example, the excursion length is  $65^\circ$ ,  $\text{RD} = 20^\circ$  and  $\text{AD} = 60^\circ$ ). In excursions which were purely attractive or purely repulsive, the value of the empty group was designated by zero.

Figure 5 plots the AD and RD values in relation to the same axes as in the analysis of excursion length (Fig. 3). The Ancova test was performed on the AD and RD values, and the following results were found to be significant at the  $P < 0.01$  level, both during and across sessions: (i) AD increases, (ii) RD increases, (iii) AD is larger than RD. In the spatial domain, each place is thus first home base attractive and later home base repulsive. This process proceeds proximodistally. This change is related to the amount of exposure of the rat to places, which is in turn related to the distance of these places from the home base (Fig. 4). As shown in Fig. 4, a rat's pattern of performing increasingly longer excursions from the home base and back to it creates a gradient of exposure that also progresses from the home base and out. Since the change from home base attraction to home base repulsion corresponds to the change in exposure, we interpret RD to reflect the average distance of 'familiar', and AD to reflect the average distance of 'unfamiliar' places.

We will now examine the rate of growth of these two measures by a variance component model. Since for both AD and RD values there was no interaction between the effect of session stage, session number, and rat, the pattern of change can be described in a relatively simple way. It was found that the typical AD value for the first stage of the first session (and the 95% confidence intervals in parentheses) was  $11.6^\circ$  ( $10.0^\circ$ – $13.4^\circ$ ), while the RD value was  $1.5^\circ$  ( $1.0^\circ$ – $2.1^\circ$ ) which is negligible relative to the noise level. AD increased from the first to the second stage of an observation by 43% (27%–60%), while RD values increased more steeply, and almost doubled, by 195% (131%–279%). Similarly, AD increased from the second to the third stage of an observation nonsignificantly by 4% (–7%–17%), and again RD values increased more steeply, by 23% (–3%–58%), but still not statistically significant. AD increased from one session to the next by 7.8% (5.8%–9.8%), and again, RD values increased more steeply, by 10.8% (6.5%–15.4%).



**Fig. 5.** Smoothed average attraction distance (AD) and average repulsion distance (RD) within the first eight sessions (Lowess nonparametric scatter plot smoothing method in S-plus). Data are computed at ten parts of each session. The  $x$ -axis represents the temporal order of excursions, and the  $y$ -axis represents angular distance from the home base. The numbers below the  $x$ -axis represent the temporal sequence of sessions

Comparing these results to those of the increase in excursion length reveals that AD increased in a similar rate to that of excursion length: the ratio between AD and excursion length varied within a narrow range of 0.6–0.63, without an effect of the session stage or number. In contrast, the proportion between RD and excursion length was less than 0.08 in the first stage of the first session and 0.21 in the third stage of the fifth session. Early excursions were therefore of short length, and the home base was attractive during them in almost all the excursion area, which was indeed less familiar. Although late excursions were typically long, the RD values were not only higher – as expected – but a larger portion of the excursion area had been explored. Only a distal part of the excursion was less familiar.

### 3.4 The ratio of AD to RD changes during exploration

The progression of the exploratory process might be examined only in terms of the geometrical shape of the excursion trajectory, regardless of its size. For that purpose, we now examine the RD/AD ratio which captures the relative location in the excursion of its more familiar to its less familiar portions. Again, we use the ANCOVA model for the ratio

$$\log(\text{RD/AD}) = \log(\text{RD}) - \log(\text{AD}) \quad (3)$$

The results of this ANCOVA model (Table 2) are qualitatively similar to those of the ANCOVA model of excursion length (Table 1): The specific rat, the session number, and the session stage have a significant effect on RD/AD, and similarly, the interaction between these factors is not significant. We therefore conclude that each rat is characterized by a typical RD/AD ratio, while RD/AD changes at a similar rate in all the rats examined, both within and among sessions. We will now again fit a variance component model in which the rat's effect is a random variable, session stages are fixed effects, and session number is the other explanatory variable. According to the results of the model, the estimated RD/AD ratio for the first stage of the first session is 0.13(0.1–0.17). From the first to the second session stage, this ratio increases by 57%(47%–65%), and from the second to the third session stage, this ratio continues to increase, this time significantly, by 23%(6%–37%). From one observation to the next, the RD/AD ratio increases by 7.2%(4%–10%).

## 4 Discussion

### 4.1 Summary of main findings

The results for rats making excursions from the home base and back to it can be summarized by three main findings.

1. During exposure, the excursion length increases according to the following pattern:
  - (i) Each rat is characterized by a typical excursion length.
  - (ii) Excursion length increases during a session at a similar rate across rats.
  - (iii) Excursion length increases from one session to the next at a similar rate across rats.

The respective contributions of the individual rat, of the stage of the session and of the number of the session are not affected by each other.

2. The speed profile of the rat changes from a home base attraction profile to a home base repulsion profile. This change progresses from the home base and out.
3. Both measures of the exploratory process share similar properties: By measuring the RD/AD ratio, we normalized the excursion length and examined only the shape of the excursion. Examination of excursion shape and of excursion length lead to similar conclusions: Each rat is characterized by a typical excursion length and a typical RD/AD ratio; each of them increases during and across sessions by a similar rate among rats, and by a similar rate during early and late sessions.

### 4.2 A first approximation model of the dynamics of exploration

The process of excursion growth appears to reflect the progression of familiarization with the environment. It does not tell us, however, what the nature of this familiarization is. In contrast, the corresponding speed profile does tell us that familiarization progresses from the home base outwards. Having an intrinsic operational measure of familiarity, we could examine whether and how the rat controls the amount of novelty to which it is exposed. Early excursions are short and include only places of low familiarity, while late excursions are

**Table 2.** ANCOVA results of the ratio RD/AD

Factor	Degrees of freedom	Sum of squares	Mean of squares	F value	Significance Pr (F)
Rat	7	34.7	5.0	4.7	<0.001
Obs. stage	2	34.3	17.1	16.2	<0.001
Obs. no	1	5.8	5.8	5.5	0.02
Rat × Obs. stage	14	15.3	1.1	1.0	0.43
Rat × Obs. no	7	7.9	1.1	1.1	0.39
Obs. stage × Obs. no	2	0.4	0.2	0.2	0.82
Residuals	122	129.1	1.1		

typically long and include unfamiliar places at their distal end. The size of the unfamiliar portion of an excursion (estimated by the RD/AD ratio) grows less than the excursion length. It could be that all excursions contain a similar number of unfamiliar places. In other words, the size of the familiar portion increases with time, and the size of the unfamiliar portion of the trip stays constant. As a result, the ratio between the distances of the familiar and less familiar portions as a function of excursion length should increase, as observed in this study. The similarity between the measures of excursion length and the measures of the ratio between the familiar and less familiar distances are an additional support for this hypothesis.

A first approximation hypothesis would therefore be that the rat begins every excursion equipped with the same potential of exploration of a novel area, so that the rate of increase in excursion length is determined by the rate of familiarization. This hypothesis is in agreement with a previous analysis of stopping behavior (Golani et al. 1993), which showed a cumulative process of increasing attraction to the home base during excursions (in terms of the probability of returning to the home base). A model proposed in the second part of this study shows how several properties of natural free spatial behavior could emerge out of the few simple assumptions proposed here.

#### 4.3 Amount of exposure and familiarity

A kinematic analysis of exploration in reference to the home base brings forth a behavioral polarity which defines a potential field generating attraction and repulsion, and revealing something about the rat's operational world. Had the polarity in behavior been constant, so that the prototypical attraction cycle is maintained throughout, not much could be learned. However, sooner or later the asymmetry between way out and way back is transformed, suggesting a change in the rat's potential field, and defining a concept of becoming familiar with places in the environment. This happens when a particular place along the rat's path is traversed repeatedly and the home base, which was attractive, becomes repulsive from that place. It should be noted that the speed ratio of the rat in a place is correlated with its familiarity with that place when it is measured in reference to the home base.

Uexküll's (1934) view that organisms perceive a meaningful environment and act in it in ways which bring forth its meaning, and the belief that this 'subjective' meaning can be uncovered, might after all be sensible. Paradoxically, it might imply completely refraining from initial assumptions about function and meaning, so as to allow these properties to emerge by themselves.

#### 4.4 Relevance to other setups

In early exploratory stages, the home base is an unique reference place. During repeated exposures to the same

arena, a single home base is only a transient stage, followed by an establishment of several preferred places. The spatiotemporal diversity of the rat's trajectory increases as the rat 'connects' these preferred places, and the rat's path becomes increasingly unpredictable (Tchernichovski et al. 1996). The setup of the current study was designed to examine kinematics in reference to one stable home base.

The simplicity of the descriptive model presented in this part and of the corresponding analytical model presented in part II is, however, not a mere reflection of the simplicity of the setup. Rather, the setup has been constructed so as to highlight what we have previously observed in a seminatural outdoor habitat (Golani et al. 1993) and in a room environment (Tchernichovski et al. 1996). The analysis used here would obviously fail in advanced stages of exploration of adult rats in a complex environment. Documenting the familiarization process in the current setup might, however, be considered as a 'probe', illuminating the more challenging kinematics in reference to several, less focused reference places: If the kinematics in reference to each preferred place changes in a similar way to that described here, several questions could be examined: what happens when the rat shifts from one reference place to another? What happens when the home base is at the center of the arena? Would familiarity of a place in reference to one preferred place survive also in reference to a second preferred place? In terms of geometry, this would imply a fast continuous trajectory from A to B and from B to A.

#### 4.5 A similar pattern of exploration in invertebrates

The growth pattern described in the present study shows several similarities to the searching behavior of the desert ant (*Cataglyphis* sp.). Wehner and Srinivasan (1981) have shown that when this ant misses its nest, it performs excursions of ever increasing size, starting and ending at the place of origin where the nest should have been according to the path integrator. As in the rat, the maximal distance from the origin per excursion is increased nonmonotonically. Similarly (Tchernichovski and Golani 1995), the ant does not necessarily move monotonically towards the origin but may often, before having reached the origin, move outwards again. Likewise, desert ants belonging to the same type of workers within the same species do not show significant interindividual differences in the rate of expansion of the maximal distance from the nest per fixed time intervals. Somewhat similarly to the ant, the desert isopod *Hemilepistus reaumuri* searches for its burrow when moved away from it to another point of origin (Hoffmann 1978, 1983a,b). The search is performed in increasing loops around the current point of origin.

The ants, unlike the rats, were reported to keep a fixed speed during the search and, in particular, were not reported to make stops. The conclusion about the ants speed was derived, however, from information about the average speed per 10-s intervals. This resolution might



not be sufficient to capture stops or changes of momentary speed.

During early excursions, the attractive properties of the home base, expressed in the velocity profile of rats, reflect in part the monotone dependency of inbound speed on the distance from home. Such a dependency, of linear form, can also be inferred from Mittelstaedt's navigational model for the funnel-web spider (family Agelenidae), as described in Mittelstaedt (1985 p. 314, Fig. 11).

In the three invertebrates, the experiments were set up to induce search behavior. In the studies of Wehner and his collaborators (Muller and Wehner 1994; Wehner and Srinivasan 1981), most of the observations were made after the ants, which were trained to home, were picked up, just as they were about to enter the nest, and placed in a novel location. Optimal search behavior was suggested as the analytic model to explain the behavior in the novel environment, with movement organized around the point of origin, where the ant was placed and where the lost nest 'should have been'.

What we see in our experiment is that the rat's movement about a home base is organized in a similar way, even though there is no reason to assume search activity. The location of the home base is well known to the rat, and its behavior around it suggests that no search is going on. Instead, as we have argued, a familiarization process goes on, that cannot be explained away by the suggested optimal search models.

In part II, an analytic model is suggested that treats the home base as the point of minimum unfamiliarity, and other locations as having a level unfamiliarity which increases with distance from the home base. The animal builds its motivation while staying in the home base and then starts an excursion. As it traverses other locations, it loses its motivation in proportion to the unfamiliarity gradient it traverses, while at the same time lowering the unfamiliarity of the traversed places. Once it consumes all its motivation, it has to return to the home base where unfamiliarity is minimal, before starting a new excursion. We show how this simple model can explain the empirical findings of part I.

Turning again to the ant and isopode studies, we can now identify the unfamiliar location in which these animals are placed as the location where they first discover that they are in a novel environment and from which they implement exploratory behavior. Therefore, the pattern of exploratory behavior organized around a chosen home base, and the analytical model of part II, can explain the ever increasing size of excursions starting and ending at the place of origin in all three species, with no need for the optimal search explanation. Which of the two hypotheses is more appropriate could be tested, for example, by placing a *Cataglyphis* nest in a novel environment. If, upon coming out of the nest, the ants perform the pattern they perform after having been picked up near the nest (path integrator equals zero) and placed in a novel location, then our exploration hypothesis is the correct one, since nest location is well known to the ants in this situation, and it would not be reasonable to assume that they search for it.

Whatever the correct interpretation, the descriptive model presented in this part allows for different future explanatory principles. One such principle may be, for example, that movement develops on an idiothetic basis by repeating the same scheme over and over, each time extending its reach further away from the starting point. It might thus be that even getting familiar with the environment is not required for the emergence of this pattern, which could, at least to some extent, 'free run' in the absence of sensory feedback from the telereceptors. This possibility is supported by studies made by McNaughton, Barnes, and collaborators (1996).

#### 4.6 Is path integration involved?

The above authors maintain that the rat's hippocampus acts as a path integration system. They report several results, both their own and others, that support the view that place-specific firing of hippocampal cells has an idiothetic basis, and that the binding of place fields to visual landmarks takes place secondarily. In the absence of familiar landmarks, or in darkness without prior spatial reference, the system appears to adopt an initial reference for path integration, independently of external cues. Returning to the structure described in this study, it might be that the rat uses the home base as an initial reference for path integration. This could serve as a framework background to which the rat would fall back in the process of becoming familiar with a novel environment.

The progressive nonmonotonic expansion of the behavior from excursion to excursion in the behavior of the rats, the ants, and the isopodes is characteristic of so-called innate behavior patterns (Lorenz 1937) and is similar to the 'warm up' reported in the transition from immobility to extensive mobility in rats and other vertebrates (Eilam and Golani 1988; Golani 1992).

It should be noted, however, that from the first excursion onwards, the rats alternate briskly between progression and stopping, performing scanning movements with their forequarters during each stop, from the first stop onwards (Eilam and Golani 1988; Golani et al. 1993). Since the scanning movements are psychomotor in nature, i.e., they involve directed attention, reduction of unfamiliarity with the environment most probably takes place from the start as well. It would be of interest to examine if and how the kinematics of this pattern change as a function of sensory feedback (including the absence of such feedback from the telereceptors).

*Acknowledgements* This work was supported by a grant from the Israel Science Foundation administered by the Israel Academy of Sciences and Humanities. We are thankful to Daniel Yekutieli from the Statistical Laboratory of Tel Aviv University for handling the statistical computations, and to an anonymous referee for his useful comments. Elisha Kaspari of Ron Soferman Image Processing and Computer Vision programmed our tracking system.

## References

- Becker RA, Chambers JM, Wilks RA (1988) The new S language. Wordsworth and Brooks, Pacific Grove Cal.
- Biegler R, Morris RGM (1996) Landmark stability: studies exploring whether the perceived stability of the environment influences spatial representation. *J Exp Biol* 199:187–193
- Cleveland WS (1979) Robust locally weighted regression and smoothing scatterplots. *J Am Stat Assoc* 74:829–836
- Eilam D, Golani I (1988) Ontogeny of exploratory behavior in the house rat (*Rattus rattus*): the mobility gradient. *Dev Psychobiol* 21:679–710
- Eilam D, Golani I (1989) Home base behavior of rats (*Rattus norvegicus*) exploring a novel environment. *Behav Brain Res* 34:199–211
- Etienne AS, Maurer R, Seguinot V (1996) Path integration in mammals and its interaction with visual landmarks. *J Exp Biol* 199:201–209
- Gallistel CR (1990) The organisation of learning. MIT Press, Cambridge, Mass.
- Gallistel CR, Kramer AE (1996) Computations on metric maps in mammals: getting oriented and choosing a multideestination route. *J Exp Biol* 199:211–217
- Golani I (1992) A mobility gradient in vertebrate behavior: the perception of movement through symbolic language. *Behav Brain Sci* 15:249–308
- Golani I, Benjamini Y, Eilam D (1993) Stopping behavior: constraints on exploration in rats (*Rattus norvegicus*). *Behav Brain Res* 53:21–33
- Hoffmann G (1978) Experimentelle und theoretische analyse eines adaptiven Orientierungsverhaltens: die 'optimale' Suche der Wustennassel *Hemilepistus reaumuri*, Audouin und Savigny (Crustacea, Isopoda, Oniscoidea) nach ihrer Hohle. PhD thesis, Regensburg
- Hoffmann G (1983a) The random elements in the systematic search behavior of the desert isopod *Hemilepistus reaumuri*. *Behav Ecol Sociobiol* 13:81–92
- Hoffmann G (1983b) Optimization of Brownian search strategies. *Biol Cybern* 49:21–31
- Lorenz K (1937) Über die Bildung des Instinctbezuges. *Naturwissenschaften* 25:289–331
- McNaughton BL, Barnes CA, Gerrard JL, Gothard K, Jung MW, Knierim JJ, Kudrimoti H, Qin Y, Skaggs WE, Suster M, Weaver KL (1996) Deciphering the hippocampal polyglot: the hippocampus as a path integration system. *J Exp Biol* 199:173–185
- Mittelstaedt H (1985) Analytical cybernetics of spider navigation. In: Barth FG (ed) *Neurobiology of arachnids*. Springer, Berlin New York, pp 298–316
- Muller M, Wehner R (1994) The hidden spiral: systematic search and path integration in desert ants, *Cataglyphis fortis*. *J Comp Physiol [A]* 175:525–530
- O'Keefe J, Nadel L (1978) The hippocampus as a cognitive map. Oxford University Press, New York
- Poucet B (1993) Spatial cognitive maps in animals: new hypotheses on their structure and neural mechanisms. *Psychol Rev* 100:163–182
- Tchernichovski O, Golani I (1995) A phase plane representation of rat exploratory behavior. *J Neurosci Methods* 62:21–27
- Tchernichovski O, Benjamini Y, Golani I (1966) Constraints and the emergence of freedom in the ontogeny of rat exploratory behavior. *Behavior* 133:519–539
- Uexküll J von (1934) *Streifzuge durch die Umwelten von Tieren und Menschen*. Springer, Berlin Heidelberg New York. Translated into English in: Schiller CH (ed) (1957) 'Instinctive behavior'. Methuen, London
- Wehner R, Srinivasan MV (1981) Searching behaviour of desert ants, genus *Cataglyphis* (Formicidae, Hymenoptera). *J Comp Physiol [A]* 142:315–338