A phase plane representation of rat exploratory behavior

Ofer Tchernichovski *, Ilan Golani

Department of Zoology, George S. Wise Faculty of Life Sciences, Tel-Aviv University, Tel-Aviv, Israel

Abstract

Rat spontaneous spatial behavior is considered to be stochastic and is therefore commonly analyzed in terms of cumulative measures. Here, we suggest a method which generates a moment-to-moment representation of this behavior. It has been proposed earlier that rat spatial behavior can be partitioned into natural units termed excursions (round trips) performed from a reference place termed the rat's home base. We offer a phase plane representation of excursions (plotting the rat's momentary location against its momentary velocity). The results reveal a geometrical pattern, typical of young age and early exposure. It consists of low velocity and intermittent progression while moving away from the home base (upstream segment), and high velocity while moving back to it (downstream segment). The asymmetry between the two segments defines a field of significance in the rat's operational world. This field undergoes regular transformations, revealing thereby the rat's strategy of occupancy of the environment. The presented dynamics could provide a framework for the interpretation of concurrent neural events associated with navigation and spatial memory.

Keywords: Open field behavior; Novelty; Spatial memory; Cognitive map; Navigation; Phase portrait

1. Introduction

To establish a common language between students of animal behavior, brain scientists and neural network scientists, it is necessary to obtain dynamic representations of behavior which correspond to the natural morphology of behavior, and are informative, parsimonious, and of predictive value. Here, we suggest a method which generates such representations of free spatial behavior in the rat.

Open field behavior has been traditionally considered to be complex and stochastic. The common 'open field test' dealt therefore with general cumulative properties of this behavior such as level of activity, time spent in the central vs. peripheral sections of the field, distributions of behavior patterns and the rat's path fractal dimension (Berlyne, 1960; Fray et al., 1980; File, 1985; Geyer et al., 1987; Mueller et al., 1989; Paulus and Geyer, 1991). Such measurements ignore the problematic treatment of the dynamics of moment-to-moment behavior, which is the subject of the present study.

A reduction in the apparent variability of the behavior of a system may sometimes be obtained through a low

dimensional representation (Haken, 1975). One problem is how to determine what are the variables that can provide such a representation. In the study of spontaneous behavior we do not know a priori what these variables are, nor what is the appropriate system of reference for their representation (Golani, 1992; Golani, 1995). We cope with the complexity by first identifying a stable kinematic structure, and then analyzing the behavior in reference to it, within an appropriate coordinate system. In what follows, we demonstrate the construction of such a representation.

1.1. A natural morphology of spatial behavior

When a rat's free behavior is reduced to a point moving in locale space, it can readily be seen that the point alternates between moving and stopping (Golani et al., 1993). An examination of the places in which the rat stopped during an exposure to a novel environment reveals one or two places in which the cumulative time of staying, and the number of visits are of *a higher order of magnitude* compared to the values scored in all the other places. This place was termed the rat's home base. Home base locations differ from rat to rat in the same testing environment. The prolonged preference for a specific location must be based, therefore, on memory (Eilam and Golani, 1989).

* Corresponding author. Tel.: (972) 3-6409391; Fax: (972) 3-6409403; E-mail: ilan99@ccsg.tau.ac.il.

The home base is also marked by a high and often the highest incidence of grooming, significantly higher in proportion compared to that expected by the proportion of time spent there, and by crouching and arrests. It was found that (i) as a rat leaves the home base, home base attraction (the probability of performing the next stop at the home base) increases with every additional stop, first slowly and then fast. The number of stops does not exceed an intrinsic upper bound; once the upper bound is reached, the rat returns to the home base. The rat's path between two successive visits to a home base is termed an excursion (Golani et al., 1993).

(ii) While the upper bounds do vary from the session of one rat to that of another, they are not 'increasable' by increasing the size of the area explored (Golani et al., 1993).

These findings establish the excursion as a natural building block of adult rat locomotor behavior in a novel environment. A subsequent study revealed that after repeated daily exposures to the same environment the home base lost its unique status and several new places were preferred (Tchernichovski et al., 1995). It thus became necessary to obtain a dynamical representation of spatial behavior (Abraham and Shaw, 1992).

2. Methods

2.1. Experimental animals

Subjects were 24 juvenile Long Evans hooded rats (Department of Animal Breeding, Weizmann Institute of Science, Rehovot, Israel). Rats belonged to 3 age groups (4 males and 4 females in each group; 30–39, 43–52, and 53–62 days postnataly). From the age of 14 days, each group of rats was kept in two $35 \times 25 \times 15$ cm cages connected by a 15 cm diameter black plastic pipe which was used as a shelter. Each group included 3–5 rats of one clutch. 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.

2.2. Testing environment

Our testing environment was much larger than the area traversed by a rat in several sessions, but small enough to allow it to ultimately cover it. In this way, observed constraints could be attributed to intrinsic constrains rather than to trivial interactions between the rat's paths and the environment's boundaries. Observations were performed in a 6.5 m diameter arena with a concrete floor and 40 cm high walls. Several large objects (distal landmarks) were placed outside. A pipe, similar to the one used by the rats in their cage and the only object in the arena that could be used as a hiding place, was inserted through the arena
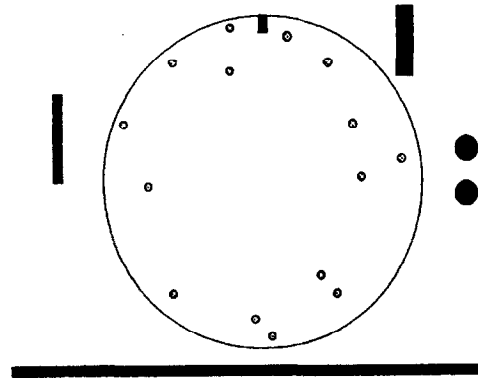

Fig. 1. The testing environment.

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, empty. The environment was thus polarized by creating one gradient, of distance from the familiar pipe, and another gradient, between the walls and the empty central area (Fig. 1).

2.3. Session planning and recording procedure

Observations were made on the 3 age groups. Each rat was exposed to the arena daily for 10 successive sessions, each of 30 min. 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 the rat was returned to its cage.

2.4. Data acquisition

The rat's path was recorded by an automated tracking system including a Matrox Magic/color card, a Telcom T/800/900 time-coding system, and software developed in our lab. The recorded X,Y coordinates were transformed to the real coordinates of the rat's location. These coordinates and timing were recorded every 50 ms, as soon as movement was detected by the system. Average location and velocity, in polar coordinates, were calculated for 0.5 s intervals measured every 0.25 s.

2.5. Data representation

A phase plane representation of free spatial behavior

The behavior of a non-linear dynamic system is often complex and irregular in time. Many times, however, a much clearer representation of a system's behavior is obtained from a map of its present state relative to its former state. Such a map is termed a phase space representation. It is of value only if we measure variables which are close enough to the real state variables of the system.
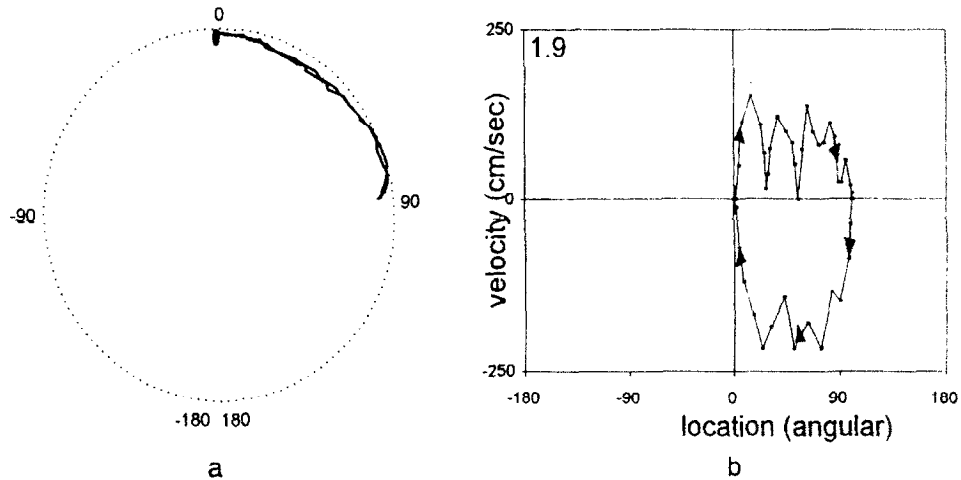
Fig. 2. a: path traced by a rat during an excursion performed from the pipe. The pipe's location is marked by a black spot. b: phase portrait of the same excursion. The arrows indicate the trajectory's direction. Data points are represented by small dots. X-axis represents angular displacement from pipe; Y-axis represents momentary velocity in centimeters/second. Numerals at upper-left hand corner of graph designate, from left to right, the session's number, and the number of excursion within that session.

On the other hand, even a limited knowledge about some of the state variables might be sufficient to reveal some of the global structure of the system (Shaw, 1984). In taking into account the natural morphology of exploratory behavior we chose to consider the rat's trajectory (location vs. velocity) per excursion (Eilam and Golani, 1989; Golani et al., 1993). Because the vast majority of excursions were performed along the wall, it was convenient to represent location by the angular component of a polar coordinate system centered in the middle of the arena.

3. Results

Figs. 2-5, which were selected sequentially out of 400 excursions performed by a single rat in the course of our experiment, illustrate regularities found in all the 24 rats examined so far. Fig. 2a presents the path traced by the

periadolescent rat during its 9th excursion in an unfamiliar arena. The circle represents a 6.5 m diameter arena; the dark spot at the top represents the pipe, whose location is designated by 0 and used as the origin for the measurement of the angular displacement of the rat from it – 180° clockwise, and 180° counterclockwise. All rats established a home base near the pipe, and performed excursions from it, first and foremost along the wall (Fig. 2a), then also into the open.

Fig. 2b provides a phase portrait of the same excursion presented in Fig. 2a. The straight X-axis in Fig. 2b was obtained by cutting down the bottom of the circular axis of Fig. 2a, at the ± 180° coordinate, and flattening it. The X-axis represents the angular displacement of the rat from the pipe, whose location is designated by 0°. The Y-axis represents the rat's momentary velocity, clockwise velocity being defined as positive and counterclockwise as negative. For convenience, the angular component of the veloc-
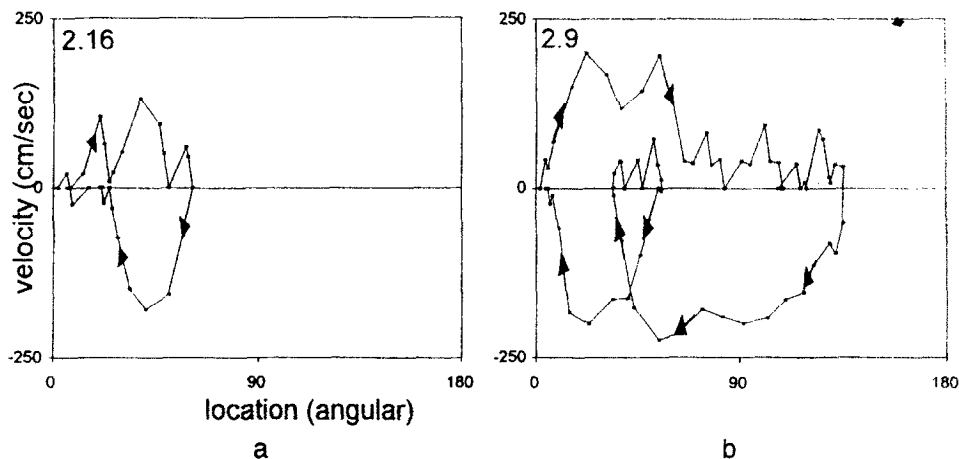

Fig. 3. a: for explanation see legend to Fig. 2b and text. Note that only the right-hand half of the coordinate system which was presented in Fig. 2 is presented here. b: for explanation see legend to Fig. 2 and text.

ity is presented in metric rather than angular units. In Fig. 2b, the excursion's trajectory starts at the origin of axes (rat at the pipe, zero velocity). As long as the rat does not move, the data points pile up at the origin. As it starts to move away, it alternates briskly between accelerations and decelerations. It stops twice, in the middle and at the end of the way out (again, the graph does not tell us how many data points piled up on the coordinates located on the X-axis). The return trajectory is performed with high velocity and without stopping. The trajectory crosses the X-axis only at its extreme right end. This indicates that both progression away from the pipe and progression back to it proceeded monotonically, without intermittent back and forth loops.

While the paths of all the excursions which are performed along the wall look similar, their phase portraits reveal a variety of forms. The trajectory presented in Fig. 3 belongs to a prototype accounting for about half of the trajectories performed by all rats examined so far. It has the following features: (i) a lower velocity on the way out than on the way back, (ii) stops performed only on the way out, and (iii) monotonicity in progression away and in progression back to the pipe: there is a single segment of progression away, and a single segment of progression back. It is as though the home base attracts the rat throughout the excursion; this results in low velocity and intermittent progression while moving away (upstream segment), and a single segment of high velocity while moving back to the pipe (downstream segment). Therefore, we termed this prototype an *attraction cycle*. The attraction cycle is primitive because (i) it is characteristic of early ontogeny, and is performed for a long time before being transformed to other geometrical patterns, (ii) it is prevalent in the early sessions of each of the age groups, and (iii) it is also characteristic of the early stages of each session.

Our experimental setup ensures that during an early stage, the rat's pattern of movement is examined in relation to a pre-established polarity. It turns out that this environmental polarity is expressed in the pattern of movement by the 'upstream' and 'downstream' segments of the prototypical trajectory. Once this polarity is imprinted on the behavior in the form of a geometrical asymmetry, the behavior can be used to evaluate the presence and directions of environmental polarities as they are self-assembled by the system itself in the course of repeated exposures.

In what follows we examine the trajectories of our rat, having this model in mind. Fig. 3a illustrates a trajectory which is similar to an attraction cycle, except that in the return portion its higher velocity segment (right bottom quarter) ends before reaching the pipe. This change, which becomes common with repeated exposures, eliminates the asymmetry in velocity in the vicinity of the pipe.

Fig. 3b presents a phase portrait that appears to be very different from the one presented in Fig. 3a, but nevertheless illustrates a similar phenomenon. As in Fig. 3a so here, the asymmetry is preserved in the right-hand portion of the trajectory. In the vicinity of the pipe, however, the asymmetry and the monotonicity are eliminated. The velocity away is initially high, and only later low, consisting of intermittent progression typical of the upstream segment of the attraction cycle. On the way back, the velocity is initially high and continuous, but upon approaching the pipe, there is a stop. Then, instead of proceeding slowly in the pipe's direction, the rat reverses direction, tracing a nested loop, first away, and then back to the pipe.

These two examples illustrate a process observed in all the rats. At first, the asymmetric portion of the trajectory extends along the whole path; then, with experience, it is reduced proximodistally: the sharp distinction between the upstream and downstream segments is diminished and then eliminated in an expanding region around the pipe.

Following a long period during which asymmetry is in reference to the pipe, there is an emergence of trajectories whose asymmetry is reversed (Fig. 4a), prevailing now in reference to a new place which was not set experimentally to attract the rat. This reversal is location specific: trajecto-
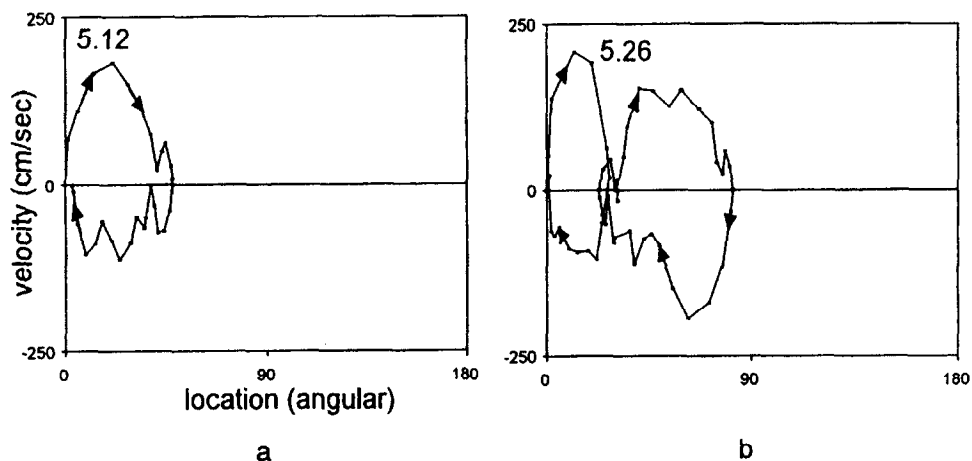

Fig. 4. For explanation see legend to Fig. 2 and text.

ries which do not include the new reference place (e.g., those performed to the left while the new reference is to the right of the pipe) maintain the original asymmetry.

The significance of the new place is further disclosed in the phase portrait presented in Fig. 4b. Here, while asymmetry is absent in reference to the pipe, it prevails on both sides of a new stopping location. It is as though the rat has abandoned the old reference place and replaced it with a new one, moving away from the new place at low, and toward it at high velocity. It appears that nested back-and-forth loops such as the one illustrated in Fig. 3b are either performed at the vicinity of an established reference place or from a location where a new reference place will be established later on.

The establishment of a new reference place is merely a beginning of a process only partly explored by us, including the successive establishment of new reference places, invasion of the central area, and more generally, the performance of increasingly complex trajectories.

At some stage the rat starts to perform trajectories whose return path differs from their path out. One type of these is a full circle around the arena. Whereas previously the decision point of returning to base involved the act of

turning around and proceeding in the opposite direction along the same geographical path, in the full circle trajectory the path does not disclose an indication for such a decision; the rat could have made no decision at all and still reach the point of origin, or else could have made such a decision anywhere along the path.

Fig. 5a–c presents the phase portraits of 3 full circle excursions, in the order of their appearance in the behavior of our rat. In the first, the whole trajectory consists of a single upstream segment. In the second, the upstream segment turns into a downstream segment at 210°, and in the third, at 150°. By shifting the transition point between the upstream and downstream segments back toward the point of origin, the rat defines a changing field of potential over an otherwise homogeneous geographical circle.

4. Discussion

By sticking to observables and avoiding assumptions about the proximate functions of spontaneous locomotor behavior, we follow the emergence of meaning in behavior. Even 'self evident' functions such as exploration,
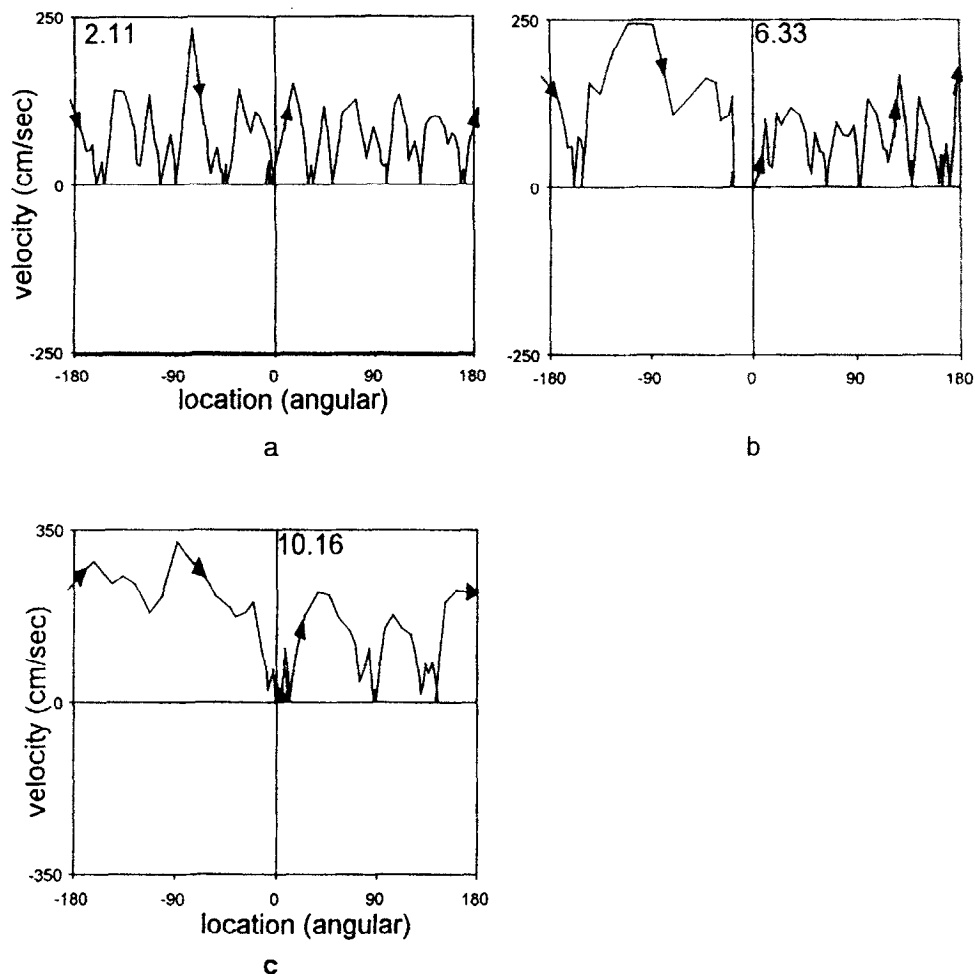

Fig. 5. For explanation see legend to Fig. 2 and text.

information processing, or map building are not taken for granted, and yet, a proper choice of a coordinate system reveals a behavioral polarity which defines a potential field in the rat's operational world. If the polarity in behavior is congruent with the environment's metrics or with the experimental setup, as in the case of the prototypical attraction cycle, not much can be learned. But sooner or later the two disagree, revealing the rat's strategy of occupancy of the environment. This happens when a rat is moving along a circular wall, approaching the home base geographically while still moving away on the potential field. It also happens when an unmarked, seemingly arbitrary location becomes a junction – a saddle point – for outgoing upstream trajectories and incoming downstream trajectories, while the pipe which has been the original saddle point is ignored.

Von Uexkull's view that organisms perceive a meaningful environment and respond to it in ways which reflect this meaning, and his belief that this 'subjective' meaning can be uncovered, might after all be sensible (Von Uexkull, 1934) Paradoxically, it might imply complete refrain from initial assumptions about function and meaning, so as to allow these properties to emerge by themselves. The rat's operational definition of 'proximity to a reference location' is illustrated in the *signature* presented in Fig. 3a. Its definition of the establishment of a reference location is illustrated in the signature presented in Fig. 4b, etc.

Once a structural account of the morphology of behavior is available, it can also be used to evaluate current hypotheses about the nature of animal spatial representations. The hypothesis that a cognitive map consists of a metric global representation of the environment (Gallistel, 1990), implies direct access to any location in that environment. Others (e.g., Poucet, 1993) hypothesize that at least during early stages, the animal's map consists of several location-dependent representations, where each location functions as a distinct frame of reference. This hypothesis postulates the existence of 'privileged places' which are used as local reference locations. It implies intrinsic constraints on the animal's paths: with multiple charts, the freedom to perform a path between any two places would depend on the two being represented within the same chart. Once the local charts are connected into a 'Multiple-Point Reference System' (Poucet, 1993), the constraints on the paths should disappear. In spite of the extensive work on exploration, there is little support for Poucet's hypothesis in available descriptions of open field behavior. The method presented here can be used to test the local charts hypothesis.

Roboticists now build robots which explore unforeseen environments, construct representations of these environments using neural networks, and then use these representations in subsequent exploratory activity (Mataric, 1991; Nehmzov and Smithers, 1991). The observations of the present study suggest that the relevance of such 'animats' to real animal behavior might be increased by taking into

account the constraints isolated in the present study. This will also ensure that basic adaptive abilities will not be missing when higher levels of coping with uncertain environments are reached (Meyer and Wilson, 1991).

Finally, the rat's trajectory in phase plane could serve as a specification of the global demands made on the brain, and, therefore, as a framework for the interpretation of concurrent neural events associated with navigation and spatial memory.

Appendix A

Video tracking

Most video tracking systems can track a rat in an arena as large as the one used by us. The system should supply a data file consisting of successive screen coordinates with their corresponding time codes in a frequency of at least 10 Hertz. Only records in which movement of the target was detected by the system should be preferably included in the file; otherwise, the file will be extremely long. Because the rat's image on the screen is very small (about 10–20 pixels or so), and the background might contain shadows and objects, the rat should be contrasted from the background. Therefore, lighting should be diffuse and homogeneous, the rat should be dark colored (by natural, non-oxidizing hair color), and the background surface and top of objects in the arena should be light colored. A video image of the arena without the rat can be used as a reference which is then subtracted from every grabbed frame. This will eliminate all structures in the arena except for the rat. Subtraction of background should be used in addition to, and not instead of the other procedures.

Correction of angular deformation

In a large environment the screen coordinates are not proportional to the arena coordinates even when the camera is exactly above the arena's center. A straightforward trigonometric calculation should be performed to correct this deformation. The height and horizontal distance of the camera from the center of the arena, and the screen coordinates of the arena's longitudinal and horizontal boundaries should be specified for the calculation. Detailed

instructions and a program to correct the angular deformation are available from the authors free of charge.

Data smoothing

We have found the noise of our tracking system negligible for the phase plane representations. Differentiation of velocity is, however, sensitive even to low noise levels and any of several smoothing methods could be used (see Mottet et al., 1994). A program calculating from the raw data file the average location and velocity in terms of their polar components for any requested time interval is available from the authors free of charge. Such data may be plotted in phase space by any graphical software.

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