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Stopping behavior: constraints on exploration in rats (*Rattus norvegicus*)

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In the absence of an obvious reference place, rat locomotor behavior in a novel environment appears haphazard. In previous work, one or two places termed home bases, were shown to stand out from all the other places in the environment in terms of the behaviors performed in them and in terms of their behavioral stability. We use home base location as a reference place for rat movement in locale space, by defining an excursion as a trip starting at a home base and ending at the next stop at a home base. We then establish the uniform distribution as an appropriate model for the number of stops per excursion. This way we show that there is an intrinsic upper bound on the number of times a rat stops during an excursion. As a rat leaves the home base, home base attraction increases with every additional stop performed by it, first slowly and then fast. This cumulative process of attraction may be concluded after each stop, as long as the number of stops does not exceed an intrinsic upper bound; once the upper bound is reached, the rat concludes that excursion and returns to base. The session's upper bound does not increase with the size of the explored area.

INTRODUCTION

When placed in a novel environment, a rat alternates between progressing and stopping: it locomotes forward, stops, performs horizontal and/or vertical scanning movements while staying in place, locomotes again, stops in a new place, etc. In the absence of an obvious reference place in relation to which the observer can quantify progressing and stopping, the rat appears to stop haphazardly, showing little regularity in its stopping behavior. Perhaps because of this, researchers who described patterns of rat progression in the open field ignored stopping and recorded only the paths traced by the rat. When such paths are represented on paper or on computer screen[4,6–8,14,15], they provide important general properties of the patterning of rat routes. For instance, they represent the ratio between progression along edges and across the center region of the field, the degree of stereotypy indicated by the amount of repetition of the same paths[5,12], and the relative smoothness of the rat's locomotor path[7,14]. In the absence of natural 'punctuators', however — natural in the sense that they are presumably used by the rats themselves — the rats appear to perform a long unpartitioned sequence of progressions and stops that starts and ends with the session.

The aim of the present study is to offer a quantitative model for rat spontaneous locomotor behavior in a novel environment. To establish such model we first identify a reference place presumably used by rats during their movement in locale space, then isolate measurable quantities of rat movement and measure them in reference to that place. An appropriate model should both predict the observed regularity in the measured quantity and support the initial choice of a reference place.

When a rat explores a novel environment there are one or two places where it stays for a significantly longer cumulative time than in all the other places, and where it typically stops for the highest number of times. In this place, the values of these measures are of *a higher order of magnitude* compared to the respective values scored in all the other places. In it, the rat also shows a high and often the highest incidence of grooming, significantly higher in proportion, compared to that expected by the proportion of time spent there. Finally, this place

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is also marked by the highest incidence of rearing, and by crouching and pivoting around the forelegs, two behaviors which are exclusive for this place. This place which can be readily identified by any observer using the above criteria, has been termed a home base[3].

From the home base the rat performs excursions into the environment. Excursions consist of round trips which start and end at the same home base, and, in the case of rats which establish two home bases, trips which start at one base and end in the other. There have been several allusions in the literature to the fact that in a novel environment animals repeatedly perform excursions which start and end in their home base[1,2,9,11,13,16], but there has been no systematic examination of the constraints imposed on locomotor behavior during such excursions.

The partitioning of the rat's path into intervals of forward progression and intervals of stopping and staying in place offers several measurable quantities, such as the number of stops per excursion, the distance traversed during inter-stop intervals, excursion time, etc. Any of these quantities could be controlled, and in this sense could shape the excursion. In looking for a measurable quantity that would yield regularity, we had the impression that the number of stops performed by a rat during an excursion had an upper bound. Our initial attempts to increase the upper bound, by increasing the size of the area explored, revealed both faces of a phenomenon: while the upper bounds do vary from the session of one rat to that of another, they are not 'increasable' (on average). This suggested some form of active management of stopping behavior.

Based on this observation, we searched for a quantitative model that would represent stopping in reference to the home base, and predict a rat's likelihood of terminating an excursion and returning to base. In particular, the apparent upper bound on the number of stops could reflect, for example, a typical upper limit with data clustering about it on both sides. Alternatively, it could be an artifact of a memoryless behavior in which the rat's decision whether to make additional stops or return to base is taken randomly, at a fixed, relatively high probability, regardless of the number of stops already performed. In such case the probability that the number of stops will exceed a certain large value is negligible, thus creating the false impression of an upper bound. Finally, the upper bound could be an intrinsic one, implying that the decision to return to base after a stop depends on the number of stops already performed after leaving the base, and in this sense entails some form of memory. Note, that all three models predict the form of the distribution in a session, regardless of the question whether the values of the upper bound are session-specific, individual-specific, or species-specific.

The establishment of any model other than the memoryless one as appropriate would support stopping as a kinematic quantity indicating some form of measurement performed by the rat in reference to the home base, validate stops at the home base as the natural sutures between excursions, and demarcate excursions as elementary processes of organized locomotor behavior in a novel environment. The establishment of a specific model out of the three, will characterize the attraction exerted on the rat by the home base: is it equally attracted to base throughout its movement in the environment? is it attracted to base only after performing a typical number of stops? or does attraction increase in the course of an excursion?

MATERIALS AND METHODS

In the first part of this study we examine stopping behavior during spontaneous locomotor activity of tamed wild rats on a small glass platform. In the second part we ask whether the maximal number of stops per excursion, established on the glass platform, merely reflects the size of the testing platform or else expresses a more general intrinsic property of rat stopping behavior. To answer this question, we present data on an additional group of laboratory Long–Evans hooded rats tested in small and large outdoor yards.

Wild rats on glass platform

Details on the tamed wild rats, the structure of the testing environment and the procedures of data acquisition and data analysis were described elsewhere, as were the rationale for the structure of the testing environment, and for the use of wild rats[3]. Following are a brief summary of methods and some additional necessary detail.

Animals

Fourteen male and 11 female tamed wild rats (*Rattus norvegicus*), born to rats caught in the wild or to first generation rats raised in captivity were maintained individually in 60 × 50 × 40 cm cages, on a 14-h light/10 h dark cycle (lights on 6 a.m.). Recording sessions took place at the age of 4–12 months (rats weighed 250–400 g). Food and water were provided ad lib.

Observation platform

The testing platform was a glass table (160 × 160 cm and 100 cm high), without walls, placed 60 cm away from 4 walls, each of a different color and texture. A mirror tilted at an angle of a few degrees below the glass top allowed a video camera to capture simultaneously bottom and side views of the rat. To record the places of stopping, the platform was divided into 25 square areas[3]. Videotaping of rats was performed under artificial lights from behind a curtain. Only the camera lens was visible to the rats.

Small vs. large yard

Animals

Sixteen naive hooded rats, 8 males and 8 females, (Dept. of Animal Breeding, Weizmann Institute of Science, Israel) weighing 250–350 g were used. The animals were housed in small groups. All other housing conditions were similar to those described for the wild rats.

Observation yards

Small (2 x 2 m) and large (8 x 8 m) outdoor yards with soil floor were each surrounded by a 70-cm high wall. Walls were constructed of plywood. The yards contained sparse low grass and stones. To record the places of stopping the yards were schematically divided into 25 squares. Each square in the large yard was subdivided into 9 smaller squares. However, this subdivision was not used unless the rat stopped in the same larger square successively more than once (see section on behavioral analysis). Videotaping was performed under natural daylight.

General

Procedure

Each of the rats was placed in the centre of the testing area and its behavior videotaped for an hour on the glass platform, and for half an hour in the outdoor yards. A video camera lens with a 8 x zoom ratio allowed sufficient visual access to behavioral detail in the two small environments, and a tele conversion lens with a 1.5 x magnification was added in the large yard. Videotaping took place during daytime (8 a.m.–5 p.m.). Wild rats were tested only once, on the glass platform. Hooded rats were tested twice: 8 were tested first in the small, and a week later in the large outdoor yard, and 8 were tested first in the large, and a week later in the small yard.

Behavioral analysis

When placed in the testing environment a rat alternates between progressing (i.e. forward walking or running) and stopping: it progresses forward, then stops by performing so-called closing steps (in which the stepping leg lands besides the contralateral leg instead of landing ahead of it), then freezes and/or performs horizontal and/or vertical scanning movements while staying in place. During staying in place it may perform sideways and/or backward steps or steps in place, with each of its legs, and may even step forward for one or two steps. Then it resumes forward progression, stops in a new place, etc. In intact rats, forward progression and scanning movements are always separated in time. In the present study, *forward progression* was recorded as such whenever the rat performed more than two successive forward steps with the same hindleg (more than two successive cycles of all four legs). *Stopping* was recorded whenever the rat ceased to progress forward and froze in place, or ceased to progress forward and performed lateral and/or vertical scanning movements with any or all of the parts of its trunk while staying in place. The rare instances in which the rat ceased to progress forward, stayed in place, then performed two forward steps and stopped again, etc., were recorded as one stop. Instances in which a forward progressing rat turned its whole trunk smoothly in a new direction and commenced to progress forward (without first performing a lateral head (and/or chest) movement in the opposite direction) were not scored as stopping even if the hindlegs did not step during turning.

Time-coded videotapes of rat behavior were displayed on screen at a desired low speed, and the places where the rat stopped were coded using custom programs that allowed the computer keyboard to serve as an event recorder. Whenever stopping behavior fulfilling any of the above criteria was observed, the observer pressed a key representing the stopping area. The same key was pressed again when the rat left the place. In the large yard, the subdivision into smaller squares was used only if the rat stopped successively more than once in the same larger square (based on the division into 25 squares). The sequence of stops, their duration, frequencies of stops in particular places, and cumulative durations of staying in each place were calculated. Videotapes were then replayed in slow motion and the occurrence of grooming and rearing were recorded for each of the places. The entire session was coded for each rat. Data were added cumulatively for each rat, for each place, to obtain the total amount of time spent in it during the session, and the incidence (total number per session) of grooming, of rearing, and of stops per place. Based on these cumulative records, and following the procedure described in ref. 3 (see also present introduction), each rat's home base locations were established. Some of the rats were found to have only one home base, others were found to have two. A normal rat was hardly ever observed by us to locomote through a home base without stopping there. Therefore, in the present study, visits to base imply stopping at base. Since presence in other places was not recorded unless the rat stopped there, visits to places and stops are used interchangeably and mean the same.

Once home base locations were established, visits to a home base were used to divide the sequence of all stops performed in the session into smaller sequences called *excursions*. Each excursion starts immediately after leaving the home base, and ends just before stopping again at base. The initial and final stops at the base are not included in counting the number of stops per excursion. The sequence of all stops performed in the session is thus represented in terms of excursions, separated from each other by stops at a home base. Excursions are classified as '*round trips*' — excursions that start and end at the same base — and '*excursions between 2 different bases*'. The expression '*excursion size*' refers to the number of stops per excursion, as opposed to '*excursion length*' which refers to the distance traversed.

Statistical methods

The probability distribution of the number of stops per excursion was investigated using histograms, density estimators, and quantile plots.

The histogram. This is the simplest means to describe the relative concentration of observations along different sections of the stops per excursion scale — the probability density. In the histogram the scale is divided to equal-size non-overlapping bins, and the density for each point in the bin is estimated by a constant: the number of observations which fell in the bin divided by the total number of observations and further divided by the bin length. The result is displayed using bars, but if we examine the estimated densities alone, it shows discontinuities where one bin ends and its neighbour starts. Furthermore, the estimate of the densities has other statistical disadvantages closer to the boundaries between bins.

Density estimators. To overcome these problems it is common to estimate the density at a specific point by constructing a bin centered around the point. As we move from one point to the other over a fine grid, the centered bin moves as well. Furthermore, different weights are assigned to the points in the bin, those closer to the point where the density is estimated getting higher weights. The resulting smooth presentation of the histogram has good statistical properties as an estimator of the probability density function (see for example, ref. 17).

The quantile plot. This describes each observed value against its rank. For example, suppose that the number of stops recorded in successive excursions of the same session are 2,10,3,7,9,7,9,1,5. We first sort them and rank them accordingly, the first lowest gets 1 and, in this example, the last largest gets 9. The quantile plot displays for each excursion its number of stops on the vertical axis and its rank on the horizontal axis. (The quantile plot for this sample data is the M29 panel in Fig. 2). Note that each rank when divided by the number of excursions recorded in a session, represents the fraction of the excursions having values smaller or equal to its observed excursion value (in M29, for example, 1/9 of the excursions included 1 or fewer stops, 2/9 included 2 or fewer stops, and 4/9 included 5 or fewer stops). Thus, if the observations are from a *uniform distribution*, the intervals between consecutive observations, after ordering them, are expected to be constant regardless of their location. Under such circumstances, the quantile plot should exhibit a linear relationship. The linearity is an evidence of the appropriateness of the uniform probability model.

Assessment of linearity. To judge the quality of fit to a uniform model the usual methods of judging the fit to a line cannot be used, and inference should rely on a confidence band which can be superimposed on the plot, helping to judge the deviation from linearity. This is accomplished by using Kolmogorov's distribution of the maximal deviation, which results in a tolerance band about the diagonal of the quantile plot (+ 0.08 to + 0.12 in our examples of pooled data). We shall omit the details of the construction and remark that when trying to show that some model is appropriate, merely showing that the model cannot be rejected at some usual level, say 0.05, is not a strong enough evidence, and the visual check for linearity is usually more stringent.

The estimation of the upper limits on the number of stops. Having a sample of size n from a uniform distribution over the unknown range $[0,R]$ (meaning that the population ranges between zero and an unknown maximal value R), we may use the k-th largest of the n observations to estimate R. However, the expected value of the largest of a sample of n observations from a uniform distribution is smaller than R, namely, $(n/n+1)R$. (Again, the 9 observations of the sample in M29, when uniformly spread over the range 0 to R, are expected to divide this range to 10 intervals of equal length; the estimated maximum R should therefore lie to the right of the ninth largest observation at a distance of one such interval length.) An unbiased estimator of the range R is, therefore, the k-th largest observation times the inflating factor $(n+1)/n$. (In our example this would give an estimate of 11.1.) This estimator, however, is extremely sensitive to small deviations from the uniform distribution. An example of such a deviation, which is prone to arise realistically, can be produced by a single failure to identify a stop at a home base. This might create a seemingly long excursion, consisting in fact of two successive excursions. Not only will R be overestimated in this case, but the distribution will not appear uniform. As a remedy, we use a more resistant estimator of the maximum, based on the estimated 90% percentile of the observations, rescaled by the factor 10/9. (Alternatively, the estimates based on the 70% and 80% percentile were also used, and gave similar results.)

Side-by-side boxplots displays[10]. They were used to display the estimates of the maximal number of stops for the three types of excursions: round trips in single base rats, round trips in double base rats, and excursions between bases in double base rats. The maximal values were displayed for the glass platform (Fig. 7), and for the two outdoor yards (Fig. 8). The boxplot displays graphically, numerical summaries of groups of observations. The box is plotted by drawing its bottom and top at the 25% and 75% percentiles respectively of the data, and thus contains the central half of the data; the box is cut by a line whose height is that of the median of the data; two whiskers extend from the top and the bottom of the box to the farthest observations that are still no more than two box lengths away from the sides of the box; observations outside this range are plotted individually. The boxplot displays are used to study and compare the location, spread, and shape of the distribution of the estimated upper limits. The notches in the boxes give approximate 95% confidence intervals for the comparisons of medians. If two sets of notches are non-overlapping, their corresponding medians are significantly different.

The significance of the difference between the estimated upper limits for round trips, and for excursions between bases for the two-base rats, is further determined by the Wilcoxon signed rank and rank sum tests, depending on whether the excursion of the same or different rats were compared.

RESULTS

Number of stops per excursion on the glass platform

One-base rats

One-base rats establish a home base within the first few minutes of the session by staying there for extended periods of time, grooming, etc. (see Introduction and ref. 3). They then keep visiting (stopping in) this place, finally settling in it for the rest of the session. According to our definition, a round trip starts upon leaving base and ends upon re-entering it, initial and final stops at base excluded.

Fig. 1 presents the frequency distribution of the number of stops per round trip in individual rats that established only one such home base in the course of the 1 hour session. We shall first study this frequency distribution in rat F13 (Fig. 1): its mean number of stops is 4.6, its median is 5, and the maximum number of stops per round trip is 8. It is clear from the histogram that there is no clustering of the observations about this maximum, but the number of stops observed spans the entire range from 1 to 8. Nor is there a trailing tail of

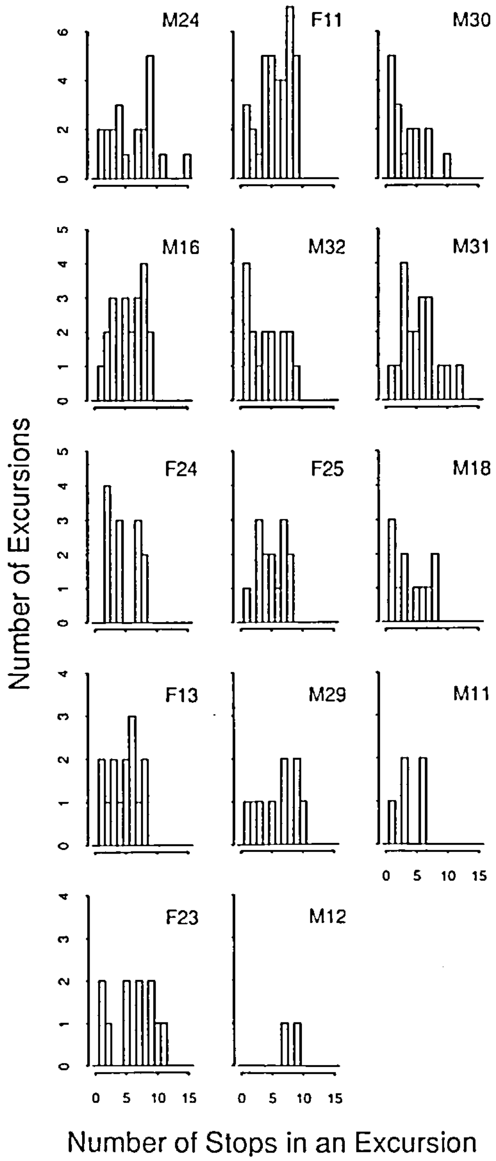

Fig. 1. Frequency distribution of the number of stops per round trip in individual one-base rats.

ever decreasing frequencies which would suggest a geometric model for the distribution. In fact, this histogram of F13 suggests that an appropriate model for the distribution of the number of stops per round trip in this rat's session should assign equal probability to any excursion size over the range of sizes observed in this rat. We are thus led to a closer inspection of the uniform distribution as a model.

The appropriateness of the uniform distribution model to the data is judged by using a quantile plot. In such plot, the excursions are ordered according to the number of stops included in them (*y* axis), vs. their rank (*x* axis; see Materials and Methods section). It can be seen that in Fig. 2, which is the quantile plot for the data in Fig. 1, the points corresponding to the number of stops of rat F13 tend to cluster along a straight line — as expected when the model is appropriate.

The rest of the subfigures in Figs. 1 and 2 present similar histograms and quantile plots individually, for each of the other one-base rats. The first observation is that the uniform distribution model appears to be quite appropriate for most rats. The second observation is that the recorded maxima vary considerably across rats (range: 6–12 stops).

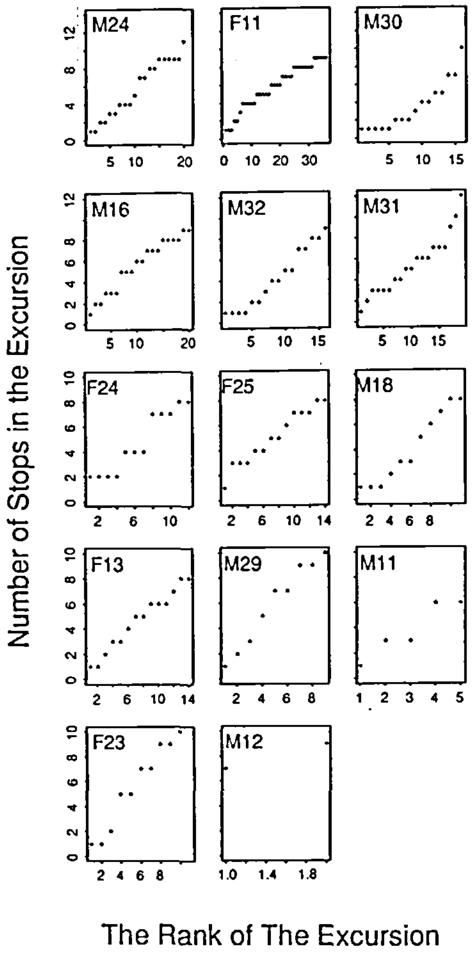

Fig. 2. Quantile plot of the number of stops per round trip in individual one-base rats.

As to the first observation, the fit might not look as good as the extraordinary fit of F13, but the quantile plots are pretty linear and the histograms constant, when taking into consideration such small samples (even for M30, which might look the furthest from uniform, the data are consistent with a uniform model). But this is not enough evidence to infer about the distribution of the number of stops. As an extreme example, M12 has only two points so that a straight line would be the best fit here, but also for any other probability model. The linearity of the quantile plots of individual rats could not be assessed by using tolerance bands (see Materials and Methods), because they were extremely wide for such small samples, and therefore not informative. It can be assessed stringently, however, with large samples of data. Thus, the only way to support or refute the emerging uniform distribution, as a model for the number of stops per excursion performed in a session, is by pooling together the data from all rats together.

Here enters a difficulty in pooling the individual distributions. The wide range in the maxima implies that the number of stops per round trip is uniform over different ranges for different rats. Rat M24, for example, shows a good fit over the range of 1–15 stops per round trip; according to a uniform model over this range, the probability of, e.g., all 14 round trips of rat F25 ending with no more than 8 stops per trip is extremely small — 0.00015. Such an hypothesis should be clearly rejected.

To overcome these difficulties we normalize the data for each of the rats over the same range and then pool all the rats (sessions) together. The normalized range extends between 0 and 1 and expresses the number of stops in an excursion belonging to a specific session as a proportion of that session's upper limit. Because this upper limit is unknown, we estimate it (see Materials and Methods).

We thus model the number of stops per round trip of the *i*-th rat by a uniform distribution over the range $[0,R_i]$, R_i expressing the individually maximal size of a round trip in the specific session.

If R_i is known, each observation t_{ij} about the number of stops which rat *i* makes at the *j*-th excursion can be normalized by $n_{ij} = t_{ij}/R_i$. The normalized number of stops per excursion n_{ij} now presents the number of stops at excursion *j* of rat *i* as a proportion (between 0 and 1) of the (unknown) upper limit on the excursion size of this rat at this session. If the original t_{ij} are uniformly distributed over $[0,R_i]$, the normalized ones are uniformly distributed over $[0,1]$ for the entire group

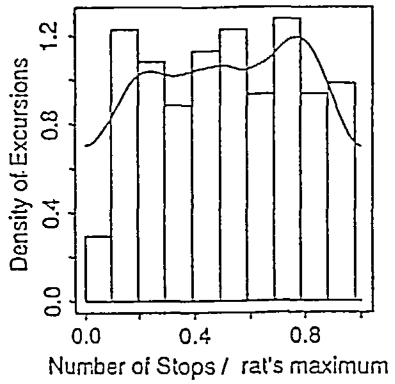

Fig. 3. Histogram and estimated density function of the pooled data on number of stops per round trip in one-base rats divided by the rat session's estimated maximum (ratio ≤ 1).

of rats. Therefore, all the observations across the different sessions of the different rats may be pooled together, and it is possible to check the appropriateness of the model using the entire data set. Because the R_i's are not known, we use their estimates in order to normalize the excursion sizes. Fig. 3 displays the histogram and the estimated density function from the pooled data. It can be observed that the estimated density is quite constant, as predicted by the uniform distribution model. Fig. 4 displays the corresponding quantile plot, which is fairly straight (see 'assessment of linearity' in the statistical methods section). The only noticeable deviation from the model is towards the low end. The reason is that the smallest number of stops in a round trip is one, zero having never been observed in normal one-base rats. This gives the rise at the bottom left, at values less than 0.1.

Two-base rats

We may now study the behavior of rats that established two bases in the course of the hour. In such rats the bases are distant from each other. Some of the rats visited repeatedly one base without approaching the other for an extended period of time, then transfered their activity to the second base which was then visited repeatedly without visiting the first base, etc. In such rats, bouts of round trips in relation to one base were separated in time from similar bouts performed in relation to the other base. These bouts were interconnected by occasional excursions between bases. In other rats, round trips and excursions between bases intermingled sporadically throughout the session.

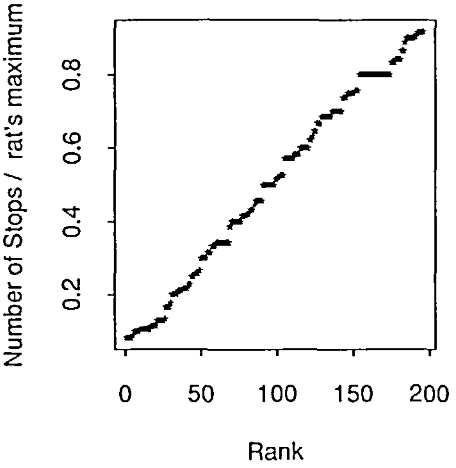

Fig. 4. Quantile plot of the pooled data on number of stops per round trip in one-base rats.

Fig. 5 is the histogram of the number of stops per (any type of) excursion in one such rat — M27. The mean number of stops per excursion for this rat is 3.6, the median is 3, and the maximum is 11. The overall height of the bars in the histogram suggests that the uniform distribution is not the right model for the behavior of this rat. In particular, note the hump at the smaller numbers, evident in the histogram.

In order to try and reveal the source of the deviation from the uniform model, we have divided the excursions into round trips and excursions between bases. Going back to rat M27, we observe that the means, medians, and maxima for the 2 types of excursions differ, the summaries for excursions between different bases showing a smaller number of stops: 4.4 vs. 3 for the means, 3 vs. 2 for the medians, and 11 vs. 6 for the maxima. Thus, it was decided to examine the distribution of each subset of excursion types separately. To do so, we define

R^s as the estimated maximum of round trips in a specific session (*s* for 'single'), and

R^d as the estimated maximum of excursions between bases in that same session (*d* for 'double').

Note, that if in fact the distribution of the number of stops per round trip is uniform over the interval from

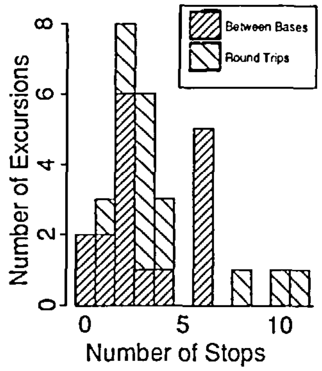

Fig. 5. Frequency distribution of the number of stops per excursion in a specific two-base rat — M27.

0 to the round trip session's maximum R^s, and if the distribution for excursions between bases is uniform over a shorter interval, from *0* to the excursions between bases session's maximum R^d, then mixing the 2 types together will yield a distribution whose density is higher from *0* to R^d then the remainder from R^d to R^s. this could explain the source of apparent deviation from the uniform distribution model, in the rats which established 2 bases in the course of the hour.

Therefore, for each of these rats, 2 session maxima were estimated: R^d and R^s. The data across rats were then pooled separately for round trips and for excursions between bases. Fig. 6a shows the estimated density curve for round trips superimposed on the histogram, as well as the quantile plot for two-base rats. Fig. 6b is its equivalent for the subset of excursions between bases. The fit is better for the excursions between bases than for the round trips. In both cases, one source of lack of fit is in the highest 20% of the observations, where the rightmost part of the density function of excursion sizes trails off rather than descending abruptly to *0* as predicted by the uniform model. This can be seen in the density estimate of the combined set of observations and also, to some extent, in the distribution of individual rats. In the distribution of round trip size only, a further peak is noticeable, caused by many short excursions and none of size 0. It may be concluded, that the uniform distribution model can be used as a reasonable first approximation of the number of stops per excursion also in rats with 2 bases, after it is enriched with an additional parameter — that of the individual session's maximal range of excursions between bases — for each such rat.

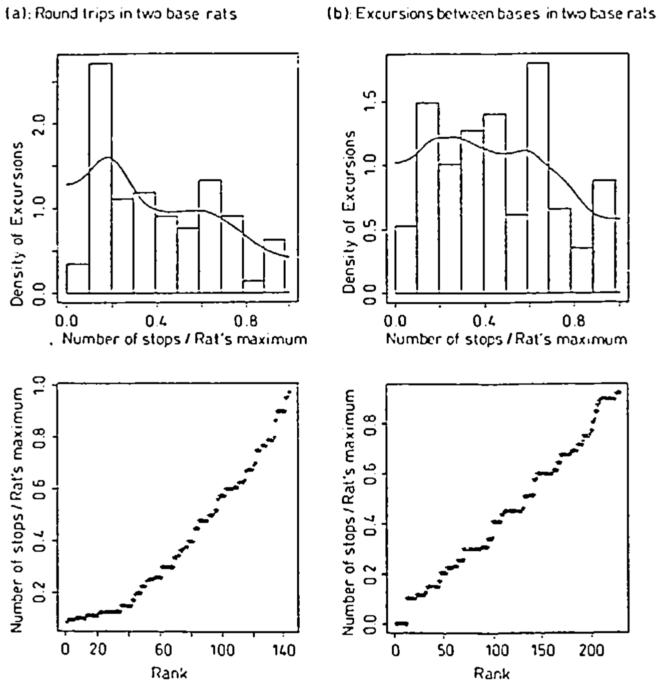

Fig. 6. a: histogram density function and quantile plot of the pooled data on number of stops per round trip divided by the rat session's estimated maximum (ratio ≤ 1) in two-base rats. b: histogram density function and quantile plot of the pooled data on number of stops per excursion between bases divided by the rat session's estimated maximum (ratio ≤ 1) in two-base rats.

Maximal number of stops per excursion

Since the maximal number of stops per excursion is an individual parameter characterizing the behavior of the individual rat in a specific session, it is of interest to examine the distribution of this parameter among the rats (2 parameters in the case of the 2 base rats). Practically, all we can study is the estimates of the R-s.

Fig. 7 presents side-by-side boxplots of the R_i-s for the single base group and the R^s-s and R^d-s for the double base group. These distributions are quite symmetric. The median maximal size estimate is 9.6 among the round trips of the one-base rats, 8.2 among the round trips of the two-base rats, and 6.9 among the excursions between bases of the two-base rats. Furthermore, it can be seen in Fig. 7 that the difference in the upper limits between the round trips in one-base rats and the excursions between bases in two-base rats is significant (P-value < 0.001). The difference between round trips and excursions between-bases in the two-base rats, although not significant (P-value = 0.062) is of the same magnitude as the difference between the two types of round trips.

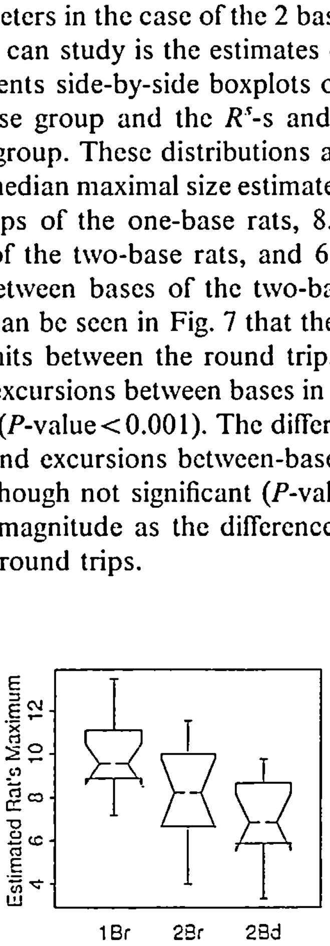

Fig. 7. Side-by-side notched boxplots of the estimated maximal number of stops on the glass platform, in: Round trips in one-base rats (left), round trips in two-base rats (middle), and excursions between bases in two-base rats (right). The range between the bottom and top of the box contains the central half of the data; the box is cut by a line whose height is that of the median of the data; two whiskers extend from the top and the bottom of the box to the farthest observations that are still no more than two box lengths away from the sides of the box. The notches in the boxes give approximate 95% confidence intervals for the comparisons of medians. If two sets of notches are non-overlapping, their corresponding medians are significantly different. Thus the difference between the medians for 1Br and 2Bd is significant while the difference between 2Br and the other two are not. For further explanation see methods section.

The effect of excursion length on the upper limits on stops

The low values of the upper limits on the number of stops per excursion could merely reflect the (high) probability of bumping into a home base on the small glass platform. To examine whether increasing the size of the environment would increase the upper limits, an additional population, this time of laboratory rats, was tested, each rat being tested both in a small and a large yard (see methods).

Three types of excursions in each of the two yards form six groups. Summarizing the estimated maxima of each type of excursion in both yards, by medians, provides the following results: the median estimated maximal round trip for one-base rats is 7.5 stops on the large yard and 14 on the small yard (groups L1 and S1 in Fig. 8). Similarly, for two-base rat round trips, the medians are 9 on the large, and 10 on the small yard (L2r and S2r in Fig. 8). For excursions between bases the medians are 9.5 on the large, and 7.5 on the small yard (L2d and S2d in Fig. 8). We see that contrary to our concern, in two of the three comparisons the medians for round trips in the large yard were in fact lower than the respective medians in the small yard, and for the S1–L1 comparison this was even almost significant (the only significant difference being between two types of excursions in the small yard) (Fig. 8). It is thus evident that an increase in the size of the testing environment does not induce an increase in the upper limits on the number of stops per excursion.

Could the medians of the upper limits on stops be similar in the two environments merely because rats actually explored only a small portion of the large yard, similar in area to that explored in the small yard? Fig. 9 presents the farthest round trips per session, in terms of the portion of the perimeter of the yard traversed, in one-base rats in both yards. While the average portion of the perimeter covered during maximal excursions in the small yard is 9.1 m, the corresponding value in the large yard is 22.9 m (P-value<0.0001). The difference between the two yards is also reflected in the average interstop distance, which is about 2.5 times larger in the large yard (3.1 m vs. 1.3 m).

In both yards, the farthest round trips are spread out, covering a large proportion of the perimeter of the respective yards. The ratio between the average distances covered during farthest round trips in the two yards is, however, much smaller than the ratio between the respective full perimeters of the yards (2.5 vs. 4). In other words, the increase in the maximal distance traversed by the rat, which was induced by the large yard, was not as large as the difference in the respective perimeters. The large yard was thus covered differently than the small yard. Still, the upper limits on the number of stops did not increase. It appears, therefore, that the

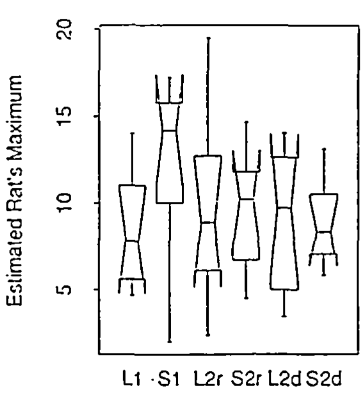

Fig. 8. Side-by-side notched boxplots of the estimated rats maxima for the large and small yards. Single base rats on large yard L1; Round trips of two-base rats on large yard L2r, on small yard S2r; Excursions between different bases on large yard L2d, on small yard S2d. For explanation of plots see legend for Fig. 7. Based on the degree of overlap between the notches, the only significant difference in this plot is between S1 and S2d. Note that the medians of L1 and L2r are smaller than the respective medians in the smaller yard.

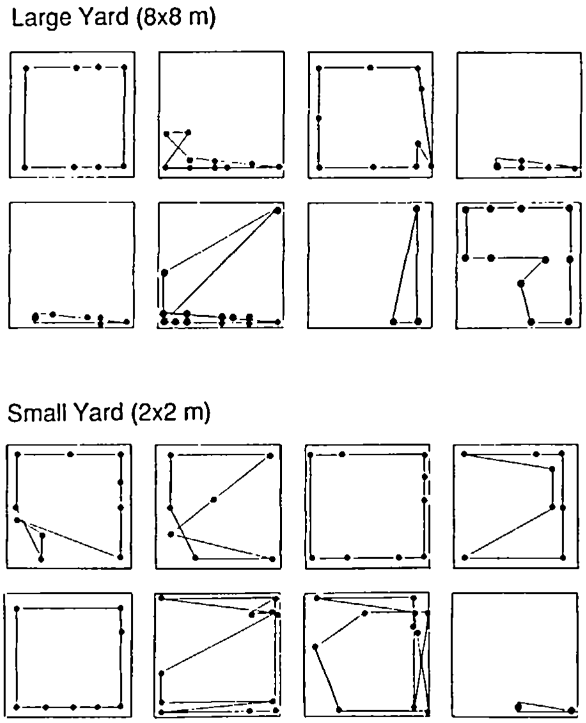

Fig. 9. Farthest round trips (in terms of the area explored), performed by one-base rats in the small and large outdoor yards. Each square represents the yard with a trace of the round trip in which the rat traveled along the longest portion of the perimeter of the yard in a session. Circles represent stops. As shown, during such trips rats cover large portions of both the small and large yards. Thus, the similarity in the upper limits on the number of stops in the two yards does not reflect a similarity in the area explored by the rat.

upper limits established in the small and large yards reflect an intrinsic property of rat stopping behavior, and possibly its interaction with the complexity of environment, but not its size.

DISCUSSION

There is a constraint on the maximal number of stops per excursion

The special status of the home base in rat locomotor behavior in a novel environment has been established in previous work by focusing on the features of behavior *in* that place[3]. The relative stability of this place suggested it as an appropriate reference place for the examination of rat locomotor behavior throughout the environment. This examination revealed that the total number of stops performed by any of the rats during an excursion — the trip between two successive stops at a home base — did not exceed (but for one case only) the total of 12 stops. Our attempt, in the second part of the present study, to increase this number by increasing the size of the testing environment revealed that although the upper limit on stopping varied from rat session to rat session, the distance covered by the rat had no significant effect on the upper limits average. A constraint on the maximal number of stops per excursion has thus been demonstrated.

The uniform distribution model accounts for the observed constraint on the maximal number of stops

To understand the nature of this constraint we examined the frequency distribution(s) of the number of stops per excursion. These numbers clearly do not cluster about a specific limit, nor do they cluster about each session's upper limit. Instead, we find that a rat performs excursions of varying sizes, spanning the entire range from no stop at all (in excursions between bases) to its maximal size. Therefore, we can not view this upper limit as a 'typical value', but continue to investigate the distribution of the number of stops per excursion. The geometric distribution is also not an appropriate model for the number of stops, because these numbers do not show a trailing tail of ever decreasing frequencies. We are thus led to the uniform distribution over an individual session's range, which was indeed found to be an appropriate model for the number of stops, in each of the excursion types. It describes best the number of stops in round trips of one-base rats and in excursions between bases in two-base rats, and is a good model for the central part of the distribution of the number of stops in round trips of two-base rats.

Two implications of the uniform distribution model

Under this model a rat is equally likely to make one stop as it is to make k stops, as long as k is under the individual session's maximum. While this seems to be a very random behavior, it should be recalled that this is a very structured type of random behavior. First, explicit in the uniform distribution model is the existence of a sharp upper limit. This is the only parameter which defines the entire distribution, and which obviously does not depend on the number of excursions performed in the session. If the estimated upper limit is, say, 8, then 25% of the excursions will include 1–2 stops, another 25% 3–4 stops, etc.

If, on the other hand, the uniform type of distribution has been established as the appropriate model, but the session's upper limit is unknown, it can be estimated right at the beginning of the session. Suppose that two excursions have so far been performed, one of 6 stops and another of 3. Then, because under the uniform distribution these two observations are expected to divide the possible range to 3 equal parts, the estimated upper limit is 9. As additional data come in we shall update our estimate — but the target parameter remains fixed. In other distributions with finite range, other parameters might also need to be estimated and the methods may change, but the upper limit remains fixed.

In contrast, distributions that serve as the 'typical value' model such as the normal and Poison, as well as the geometric distribution, do not have a deterministic upper limit: one may suggest a candidate for an upper limit, but it is a stochastic prediction, its definition should involve some probability statements, and what is even more disturbing, it will depend on the number of excursions to be performed by the rat — and thus be, in contrast to the uniform distribution upper limit, a 'moving target'.

The second implication of the uniform distribution is that under this model the probability of returning to base after a stop increases after each stop, first slowly and then steeply. Consider for example a rat whose maximal number of stops in the session is 7. A priori it may return to base after 1,2,3.. or seven stops, each with equal probability. Suppose we observe the rat in an excursion where it has already made 4 stops and has not yet returned to base. It may therefore return either at the next stop or after the 5th, 6th, or 7th stop. These $4\ (= 7 - 4 + 1)$ possible outcomes are equally likely, they should sum to 1, and thus the probability of each is 1/4. In particular, the probability that the next stop is at base is a 1/4, recalling that it had not done so by the fourth stop. A similar argument shows that if the fifth stop too is not at base, the probability that the next stop is at base increases to 1/3. Casting the argument into the general case, the uniform probability model with upper bound R implies that given the observation that by the kth stop the rat has not yet returned to base, the probability that it would do so in the next stop is: Pr(next stop is at base $|$ by the k's stop is not yet at base) $= 1/R-(k-1)$.

If we now view the probability that the next stop will be at base as a function of the number k of stops it has so far performed, the probability is increasing in k, slowly for small k and fast for k close to R: the farther the rat is away from base — as measured by the number of stops — the more likely it is to return to base at the next stop. In the extreme cases, if the upper limit is, say, 7, after 6 stops the probability of returning to base at next stop is 1/2; if it continues to the 7th stop, $k=R$ and the probability of returning to base is 1.

A compelling demonstration of the upper bound phenomenon is observable when a rat happens to approach the upper bound range, i.e., perform 10 ± 2 stops, all the while increasing its distance from its home base. Because of the rat's large distance from base, a naive observer familiarized with the home base phenomenon but not with the uniform model, intuitively expects it to perform several stops on the way back to base, spacing them with commonly observed interstop distances. In contrast, an observer having adopted the uniform distribution model expects the rat to progress continuously or almost continuously back to base, *regardless* of the distance to be traversed. As anyone having access to rats can check for himself in real time, it is this last prediction which is fulfilled.

A comparison to the memoryless geometric model

Compare this behavior to the memoryless random model for the behavior of the rat. Under that model, the probability of returning to base at the next stop, given that the rat has not yet returned to base after k stops, is always constant — say p — regardless of the number of stops k it has already performed. p reflects the relative incidence of visits to the home base. Such model leads to the geometric distribution as the model for the number of stops per excursion, where the probability of observing an excursion of k stops is smaller by a factor of p than the probability of observing an excursion of $k-1$ stops.

Unlike the uniform distribution (as well as other distributions with an upper bound), the geometric distribution does not have an intrinsic upper limit. However, the mere fact that an upper limit does seem to be observed is not enough to refute the geometric model: since under this model excursions are likely to be terminated after each stop at an equal probability, the probability that the number of stops will exceed a certain large value is negligible. Therefore, an apparent upper limit on the number of stops per excursion may be observed.

The excursion is a particulate cumulative process having a specific capacity

To refute the possibility that the upper limit is only apparent, it was thus important to establish that the uniform distribution (or some other close distribution) is an appropriate model for the randomness of the number of stops per excursion. Based on the demonstrated appropriateness of this model, it may be concluded that (i) the excursion is a natural particulate process of locomotor behavior in a novel environment, and (ii) the decision to return to base involves some cumulative process which we call, for want of other term, memory, related to the number of stops the rat has already performed after leaving the base. The capacity of this memory in a particular session is related to the rat's estimated maximal number of stops per excursion in that session. Whereas the validation of the excursion as a distinct process could have also been reached had the 'typical value' model been found appropriate, the conclusion that the behavior displays some type of memory is specific to a model with an intrinsic upper bound. Once again, in the present context, the term memory merely expresses a cumulative property of the behavior, which could perhaps even be mediated by a simple cumulative physiological process correlated with the number of stops, without necessarily implying cognition. (The involvement of spatial memory in the excursion process is a different issue, implied by the fact that each of the rats always returns at the end of each excursion to its own preselected home base. Because, in the same testing environment, base locations differ from rat to rat, a base must be established and remembered, and not be selected *de novo*, at the end of every excursion, on the basis of its unique physical features[3].)

What is the quantity which is actually measured by the rat?

(a) Number of stops vs. number of different places

The ratio between the number of different places in which the rat stopped in an excursion, and the total number of stops performed in that excursion could be used as an indication of the presumed amount of novelty to which the rat exposed itself during that excursion. A low ratio would indicate repeated stops in the same places, which could mean a constraint on the amount of managed novel input per excursion. In the present study, the number of stops was equal to the number of visited places in 90% of the excursions; additional 7% included one repeated visit to only one place. It may be concluded, therefore, that if the amount of novelty is managed at all by rats within excursions, then it is almost maximal for the given number of stops.

(b) Number of stops vs. cumulative duration of staying in place and/or number of scanning movements

The predictable increase in the attraction of the home base and the sharp upper bound, do not mean that the rat is actually 'counting' the number of stops it has performed. It might mean that the decision to return to base is mediated by some intervening quantity, correlated with stopping behavior, which is accumulated and 'measured'. Stopping consists of a cessation of forward progression, freezing and/or the performance of lateral and/or vertical scanning movements with some or all of the parts of the trunk, while staying in place (see Materials and Methods). The types and number of these movements, and stopping durations, could be the quantities which are actually evaluated and 'updated' by the rat.

The random aspect of the uniform model consists of the fact that within the range demarcated by the upper bound, the number of stops is unpredictable. This randomness could imply that the number of stops influences, but does not determine directly the end of an excursion. For example, if longer stops or stops which include a high number of lateral and vertical scanning movements weigh more than their shorter counterparts in the decision to return to base, then few stops of the first type could be equivalent to many stops of the second type, resulting in apparent randomness. While this specific hypothesis is unlikely because the number of scanning movements varies greatly across excursions, it could be that some types of scanning movement weigh more than others in a hypothetical process of measurement, thus influencing the relative weight of a stop. Alternatively, if stops are assumed to have equal weight, then the randomness would imply a freedom to return to base after any stop, as long as the number of stops has not exceeded the session's upper limit. Such freedom would be intrinsic to the rat's stopping behavior as long as the rat did not reach the individual session's maximum. For the time being, the intervening quantity hypothesis is preferable, because it is both more conservative and testable.

Scaling of interstop distances across environments

On the glass platform there was a positive correlation between the length of an excursion in meters, and the number of stops in that excursion (data not presented). This raised the question — would this correlation be maintained also if the length of an excursion in meters be 'stretched' beyond the range observed on the glass platform? When challenged with a very large environment, will the rat increase the session's upper bound on stops while keeping the same average interstop distance, or will it increase interstop distances without increasing the upper bound on stops? To answer this question we compared the farthest round trips (in terms of covered area) in the small and large outdoor yards. The average distance traversed in the large yard during the performance of the farthest round trips is 2.5 times longer than the distance traversed during the corresponding farthest round trips in the small yard (Fig. 9). But the corresponding averages of the maximal number of stops did not increase with the distance traversed. This implies that the rats must be using some scaling procedure which allows them to modify interstop distances so as to fit stopping capacity to the size of the particular environment. Just how this is done — whether by increasing all interstop distances by a fixed ratio, or by modifying the size of particular interstop distances in the sequence — remains to be examined.

Are upper limits individual-specific?

The uniform model merely characterizes the type of the distribution, without specifying the value of its upper bound. This value might vary and indeed varies greatly, from one rat-session to the next. Furthermore, because each rat was tested only once in each environment, the fact that the upper bounds are not 'increasable' on average, by increasing the size of the area explored, does not tell us whether the estimated upper bound is specific for the rat in the particular session or whether it characterizes the individual across sessions. This question can be solved by, e.g., examining the same individual rats across several novel environments. If the maximal number of stops is specific to the individual, then variance of the same individual across environments should be smaller than variance across individuals exposed to the same environment.

The effect of environmental complexity on stopping

The median estimated maximal excursion sizes across the sessions of individual wild rats on the glass platform ranged between 6.9 and 9.6. In the hooded laboratory rats in the outdoor yards, the six median values of the six groups (three types of excursions in two outdoor yards; Fig. 8) ranged between 7.5 and 14. None of the differences between the glass platform and outdoor groups is significant. Nevertheless, the two outdoor yards, which were much richer in stimuli than the glass platform, seemed to increase the number of stops per excursion. Since the richness of the environment was but one of the differences between the two parts of the experiment, in future studies it would be necessary to examine the effect of environmental complexity on home base attraction. The present study provides a necessary baseline for the answer.

Features of home base attraction and of excursion organization

In summary, in previous work home base attraction was established on the basis of parameters of behavior *in* the home base and on the difference between the time spent and the number of stops performed during locomotion away and locomotion back to base[3]. In the present study we add another feature — the slow and then fast increase in home base attraction with every additional stop, and the existence of an intrinsic upper bound on stops, which does not increase with the size of the explored area. The features of excursion organization — type of distribution of number of stops per excursion, magnitude of upper limits on stopping and on interstop distances, number of bases, and other features such as excursion time — can now be examined in other species and in lesioned and drugged rats. Differential modification of these parameters might not only provide new meaningful measures of brain/behavior relations, but also highlight additional features of excursion organization.

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