Chaotic Dynamics Underlying Action Selection in Mice

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In previous papers, we have established, through a functional analysis of the behavioral sequences recorded on laboratory mice over a twelve-hour period, the existence of two independent strategies of action selection. On the one hand, the choice of ultradian alternations of rest and activity bouts makes it possible for every mouse to maximize its net energy gain over a one-day or a one-night interval. On the other hand, the succession of acts performed within an activity bout might serve to precisely fit the metabolic needs of each animal, because the corresponding results present great inter-individual variability, with some mice increasing and others decreasing their net energy gain. To determine what kind of dynamic system could generate these successions of acts within an activity bout, we performed a nonlinear time series analysis of the energy costs related to the acts displayed by the mice during such a period. The results suggest that chaotic dynamics might be involved in action selection in mice. Thus, the variability mentioned above could be a consequence of the sensitive dependence on initial conditions associated with such dynamics, and would allow mice to rapidly adapt their metabolic needs to the ongoing situation.

KEY WORDS: Nonlinear dynamics; chaos; action selection; behavioral sequences; mouse.

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INTRODUCTION

An animal that must survive in its environment has to decide 'what to do next', i.e. to select on-line what action is the most relevant, at a particular time, in a particular environment. That is the problem of *action selection*, long studied in animals by ethologists (Baerends, Drent, Glas, & Groenewold, 1970; Dawkins & Dawkins, 1973; Lorenz, 1950; McFarland, 1977; Tinbergen, 1951; Toates, 1986) and more recently in robots by computer scientists (Beer, 1995; Brooks, 1991; Maes, 1991; Meyer & Guillot, 1994; Pirjanian, 1997 ; Tyrrell, 1993). It is also related to the study of decision-making in humans (Busemeyer & Townsend, 1993; Kahneman, Slovic, & Tversky, 1982; Rachlin, 1989).

Our work deals with the strategies of action selection in laboratory mice, with the goal of implementing them in biologically inspired autonomous robots. Two action selection strategies had already been identified by classical linear analyses: the first - *System I* - concerns the choice of ultradian alternations of rest and activity bouts, and the second - *System II* - concerns the choice of the succession of acts within each activity bout. *System I* seems to allow mice to obtain a high global net energy gain (energy input minus energy output) (Guillot, 1988; Guillot & Meyer, 1995). The functional role of *System II* is not so obvious, as it leads to great inter-individual variability, some mice increasing, but others decreasing, their net energy gain while performing the succession of acts in the activity bouts (Guillot, 1991; Guillot & Meyer, 1995, 1997).

System I exhibits periodic dynamics (Guillot, 1988). The purpose of this paper is to determine, by nonlinear analysis, what kind of dynamics is generated by *System II*, in view of the fact that it is not periodic. Our previous results, relying on ten mice observed in day condition and ten mice observed in night condition, demonstrated that the ‘activity bouts’ controlled by System II were made up of non random and aperiodic transitions of acts. Indeed, n-order sequential analysis showed some deterministic 'melodies' - i.e. successions of acts that appear significantly not to be at random in the sequence (Guillot, 1991; Hazout, Guillot & Meyer, 1989; Meyer & Guillot, 1990). But the computation of power spectra highlighted that neither the acts nor the melodies repeated themselves in the sequence with any apparent regular rhythm (Guillot, 1988).

These characteristics led us to the hypothesis of a chaotic dynamics with regard to System II of action selection. The following analyses were conducted to verify it.

METHOD

Subjects, apparatus and data

Ten C3H male laboratory mice (Mice A to J), four and six weeks old, were isolated in individual transparent 23 x 8 x 8 cm polystyrene cages containing water and food *ad libitum*, together with a cotton ball for nest building, and placed in a dark/light condition of 12:12. These animals are the same ones as those studied previously in night condition.

Off-line analysis of videotape, continuously recorded in night condition, made it possible to establish the chronological succession of six general acts (sniffing, locomotion, feeding, drinking, nest building, grooming out of the nest) during the activity bouts. In order to capitalize on as many data points as possible, the behavioral sequences analyzed here corresponded to the longest activity bout, the first, that occurs at the beginning of the night (Figure 1). To assign a common currency to each act, every behavioral sequence was translated into a time series of the metabolic costs associated with the ongoing acts. These energy costs - expressed in J/g/sec - rely upon a previous work (Meyer & Guillot, 1986) and were estimated with data recorded on mice in a respiratory chamber. A 15-sec time-step was chosen in order to avoid too high an autocorrelation between the data and made it possible, for every nonlinear dynamics method used herein, to choose the same time delay of 1. Two sequences out of ten were removed because they turned out to be significantly non-stationary, according to a comparison of means and variances between the first and second half of the data.

Thus, the following analysis called upon eight series of about 1200 to 1800 data points, roughly corresponding to 5 to 7-hrs of continuous observation.

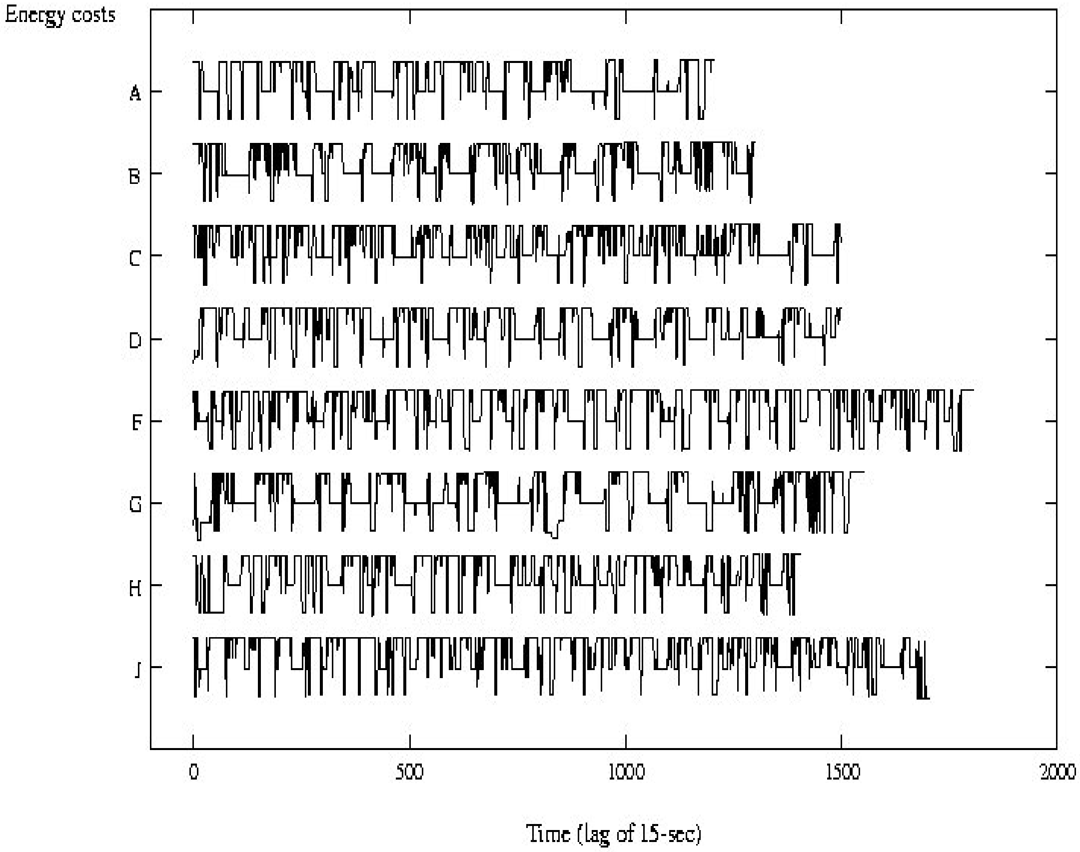


Figure 1. *Experimental time series of metabolic costs in J/g/sec (Y-axis), associated with six acts (sniffing, locomotion, feeding, drinking, nest building, grooming out of the nest), plotted against a 15-sec time step (X-axis), and corresponding to the first nocturnal activity bouts of eight mice.*

Nonlinear dynamics methods

According to Kaplan & Glass (1995), chaotic dynamics are defined as nonlinear processes with *"deterministic dynamics that are aperiodic and display sensitive dependence on initial conditions"*. Rather than proving chaos, which is difficult with non infinite data, an attempt has been made here merely to refute major counter-hypotheses like periodicity, randomness, linearity and long-term predictability. The following classical nonlinear methods were selected for their robustness with regard to our short and probably noisy time series (Scheier & Tschacher, 1996).

Periodicity and randomness

The aperiodicity of acts within the activity bouts, estimated by the linear method of power spectra, was already mentioned in the introduction. This characteristic was also assessed by the nonlinear method of recurrence plots (Eckmann, Oliffson-Kamphorst, & Ruelle, 1987; Vandenhouten, Goebbels, Rasche, & Tegtmeier, 1996), which reveals the tendency of a trajectory to return to the same points over time. This graphical method consists in placing a point on a plot of coordinates i and j, if two states, Si and Sj, of the system are closer together than a prescribed distance r. Stripes parallel to the diagonal indicate periodicities; points uniformly distributed indicate randomness; patterns between these two extremes indicate aperiodicities (Kaplan & Glass, 1995). Here, a qualitative comparison was made between the recurrence plots for each time series and the recurrence plots for the same time series where data were randomly shuffled, in order to test the null-hypothesis of randomness in the actual data.

Linearity and long-term predictability

We used the ‘Noise Versus Chaos’ algorithm (NVC algorithm) of Kennel & Isabelle (1992) to determine whether the aperiodicity of our data is due to linear stochastic fluctuations or to nonlinear determinism.

This algorithm calls upon the non-parametric comparison (Mann-Whitney rank-sum statistic) between the prediction errors of the actual time series and those of surrogate data sets. Surrogate data are stochastic time series preserving the mean, the variance and some temporal characteristics of the actual sequences (Kantz & Schreiber, 1997; Theiler, Eubank, Longtin, Galdrikian, & Farmer 1992). This algorithm makes it possible to statistically test the null-hypothesis of randomness and, in particular, to test the hypothesis of linearly correlated noise. The surrogate data used here were gaussian random data with the same length and same average power spectral density as the original data sets, so that, if the prediction errors were significantly smaller for the actual data than for the surrogates, the null-hypothesis of linear noise could be rejected. The choice of the NVC algorithm was notably determined by its ability to cope with the observed non-gaussian distribution of our data, because it gaussianizes the data before comparison with the surrogate sets.

We checked the long-term predictability of our data by the forecasting algorithm of Sugihara & May (SM algorithm, 1990) that uses the first part of a given time series as a model to predict the data of the second part. If the correlation between the predicted and the actual data is low and does not decrease with the prediction lag, randomness is assumed. If the correlation between the predicted and the actual data is high and does not decrease with the prediction lag, linear determinism is assumed. If the correlation rapidly decreases with the prediction lag, the hypothesis of nonlinear, deterministic, and chaotic dynamics may be retained.

RESULTS

Recurrence plots

As said before, recurrence plots were computed for each time series, and for the same time series in which data were shuffled. A default embedding dimension of 2 was used, in view of the fact that our data set is too small for this dimension to be estimated with precision. All recurrence plot were computed with a radius of 0.01.

The plots indicate that, for all mice, the null-hypotheses of periodicity and randomness is invalidated. Figures 2b and 2d illustrate this fact in showing the recurrence plots for the longest time series (respectively MouseF and Mouse J). They differ greatly from the recurrence plot corresponding to sinusoïdal data (Figure 2a), and from those corresponding to shuffled data (Figures 2c and 2e), that are uniformly distributed.

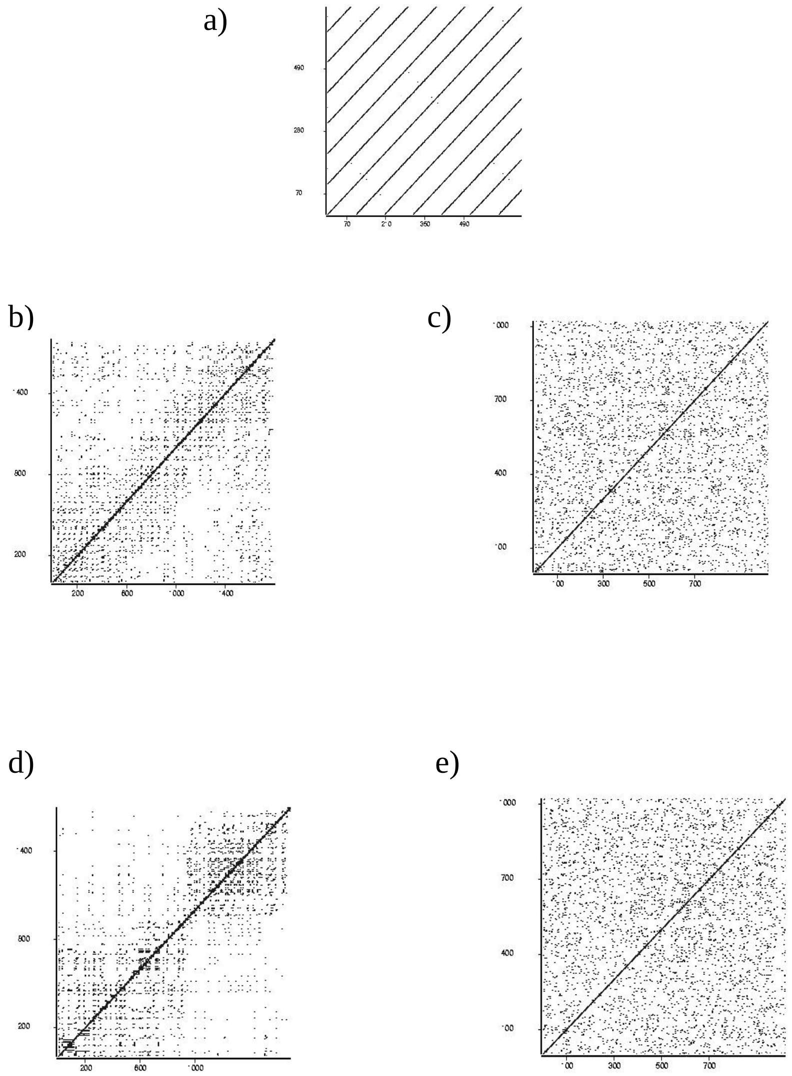
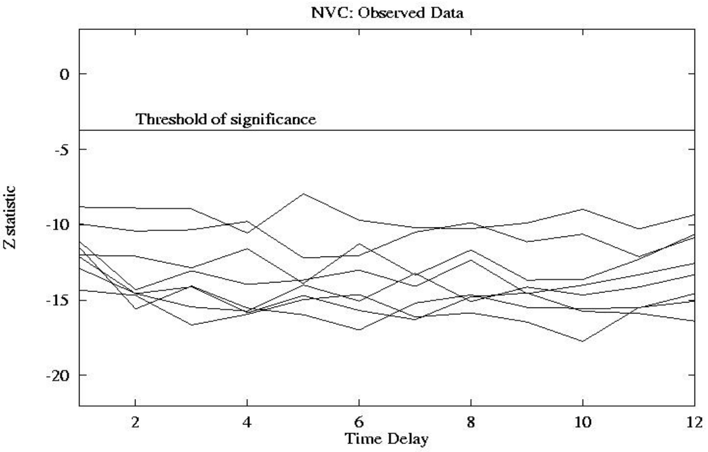


Figure 2. Examples of recurrence plots for sinusoïdal data (a), for actual MouseF and MouseJ time series (b and d) and for shuffled MouseF and MouseJ times series (c and e). Y- and X-axes are scaled from 1 to 1805 (MouseF) and 1 to 1703 (MouseJ) data points.

NVC and SM algorithms

The prediction errors of the actual time series were computed with the NVC algorithm with a time delay from 1 to 12 and an embedding dimension of 2. They were significantly smaller (p<.01) for each mouse than those of a set of 30 surrogate data, as the z-scores were lower than the threshold of significance. In order to validate the method, the same algorithm, run on one surrogate data set built from all the actual time series, but not by the NVC algorithm, gave non-significant z-scores (Figure 3).



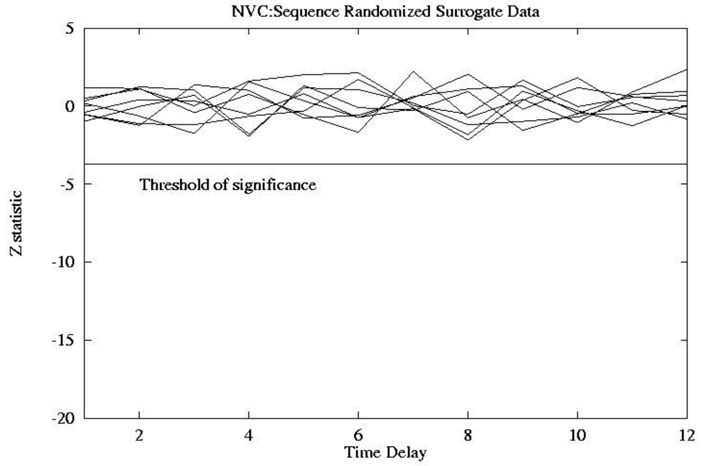


***Figure 3**. Test for 'Noise versus Chaos' (Kennel & Isabelle, 1992). Z scores for each time series (above) and for surrogate data built from each time series (below).*

The SM algorithm, when applied to the data with embedding dimensions varying between 2 to 4, revealed a decrease of the correlation between the predicted and actual data as the prediction lag increased (Figure 4). The forecasts were poorer when the same algorithm was run on one surrogate data set corresponding to each time series, confirming that the actual

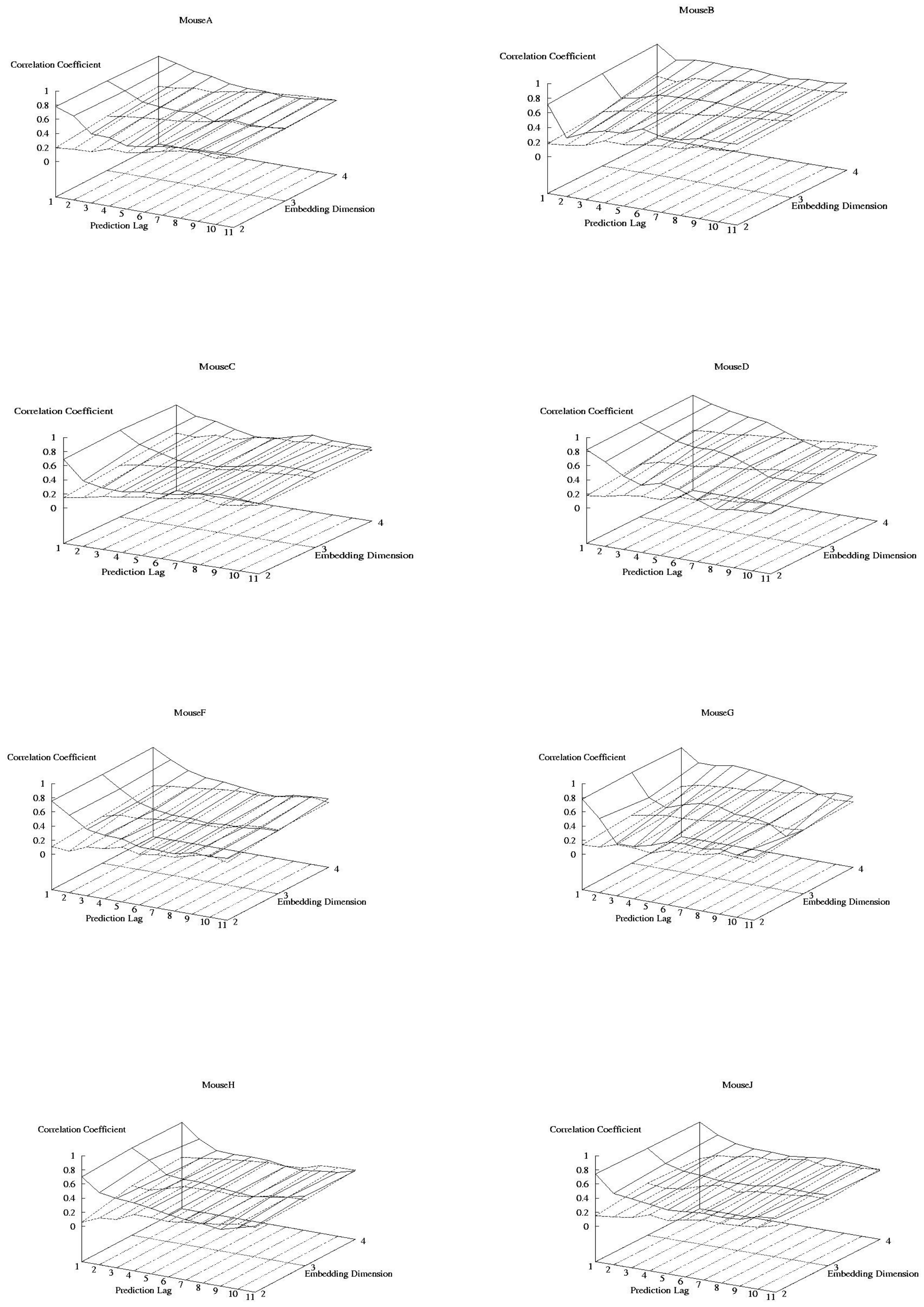


Figure 4. *Nonlinear forecasting (Sugihara & May, 1990). Correlation coefficients (Z-axis) for prediction time from 1 to 12 (X-axis) and embedding dimensions from 2 to 4 (Y-axis), corresponding to each time series (solid lines) and one surrogate data (dashed lines).*

sets were deterministic with a short-term predictability.

Thus, both the NVC and SM methods invalidate the null-hypotheses of linearity and long-term predictability.

DISCUSSION

The conclusion of the dynamic analysis is that the sequences of metabolic costs in the nocturnal activity bouts are aperiodic, non-random, nonlinear, and have a short-term predictability. Thus, the assumption of a chaotic dynamics underlying System II of action selection can be retained.

For several years physiologists have been aware that rodents - and other species - might actively regulate their body weights over both the short- and the long-term. This regulation is not a homeostatic one, because it does not call upon a fixed reference value. In fact, rodents can dynamically maintain a high body weight as well as a low one, according to the specific conditions of their environmental context (Le Magnen, 1985).

Such an action selection mechanism characterizes what McFarland & Bösser (1993) term a ‘motivationally autonomous’ animal, i.e. an animal that is able to decide which action it will perform next according not only to its past and present states, but also because it is able to take into account the expected consequences of its future actions. This planning is not always expressed, and often depends on the resolution at which the features of the environment are examined. For example, an animal can predict its future states according to some repetitive characteristics of the environment, like temperature, that will be warmer in spring than in winter, or light, that will be greater by day than by night. But it will have difficulties in predicting the micro-variabilities of the context and their impact on its state like, for example, the ongoing fluctuations of temperature or of light that occur over one hour or one minute.

The two independent systems of action selection may serve to accommodate these prediction discrepancies, according to which some features of the future context can be predicted, but not their precise details.

Within such a perspective, *periodic System I* may be a system adapted to the roughly repetitive or constant features of the environment. It does not take into account the details of the context and provides all the animals experiencing the same general environment with a high value net gain, by selecting their rest and activity states.

On the contrary, *chaotic System II* may be a system adapted to the unpredictable details of the ongoing specific context. It is able to dynamically adjust, under internal and external constraints, the metabolic needs of the animal. Because each animal is in - or starts from - a different precise situation, this system generates different behavioral trajectories for each animal, with different consequences with respect to energy. Chaotic dynamics is a good candidate for this kind of task, because it allows rapid transitions to be displayed from act to act, because it makes it possible to escape from a given attractor, and because it facilitates non-perseveration (Lloyd & Lloyd, 1995; Kelso, 1995; Port & van Gelder, 1993). It also may improve awareness of the ongoing novelties of the situation (Skarda & Freeman, 1987; Freeman, 1995). Furthermore, this kind of dynamics has already been brought up in relation to a closely related topic, that of decision-making in humans (Guastello, 1995).

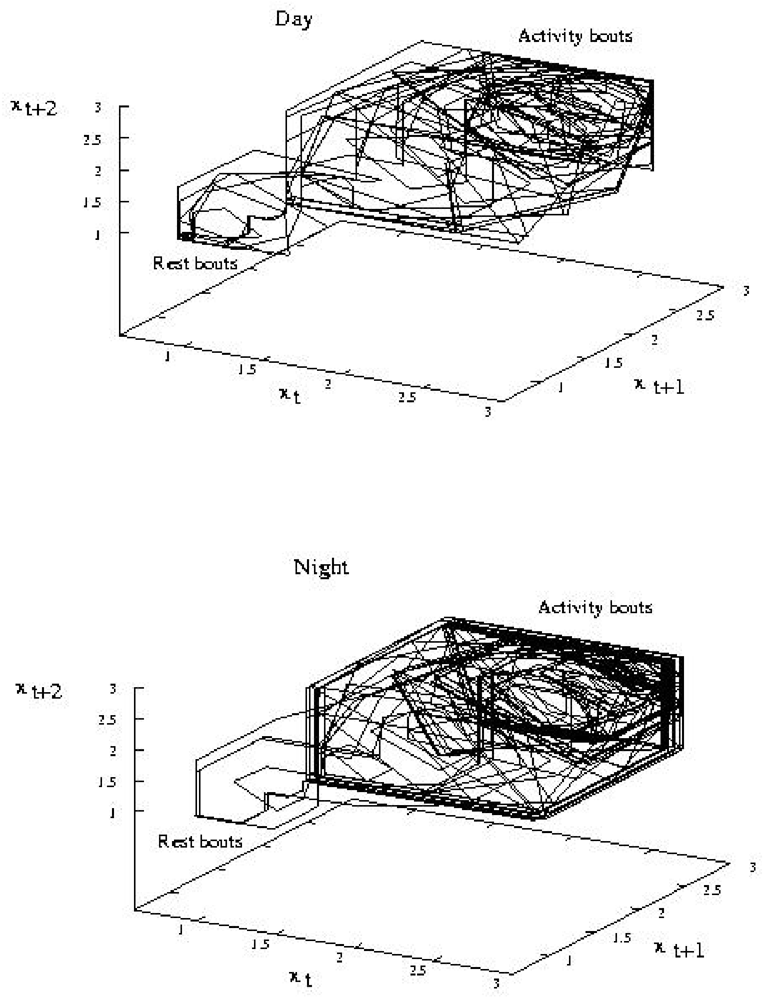


Figure 5. *Reconstructed 3-D trajectories (Takens, 1981) of an entire diurnal (above) and nocturnal (below) behavioral sequence, with rest and activity bouts. X-axis corresponds to* x_t *, Y-axis to* x_{t+1}*, and Z-axis to* x_{t+2}*.*

CONCLUSION AND PROSPECTS

As exemplified in the 3-D reconstructed trajectory (Takens, 1981) of an entire behavioral sequence including rest and activity bouts (Figure 2), the control architecture of action selection in mice is a complex system where the global attractor could be a limit cycle, itself constituted by two attractors corresponding to the rest and activity states. The data set is too limited to allow the precise dynamics of the rest state to be studied, but it may be simple, because there is little interaction between the animal and the environment in this situation. Interaction is greater during activity, and this is why the corresponding dynamics is more complex. We hypothesize that one possible function of this architecture is that it makes it possible to globally, but also precisely, satisfy the metabolic needs of the animals, in order to dynamically adjust their body weights.

One prospect of this study will be - in addition to quantifying the complexity of the dynamics highlighted here - to investigate biologically plausible hypotheses concerning an architecture for both System I and System II, such as multiple interacting oscillators at different time scales (Barrio, Zhang & Maini, 1997; Lloyd, 1997). This architecture should satisfy both the periodic nature of alternations of rest and activity and the chaotic nature of the succession of the acts.

Another prospect will be to integrate such a biologically inspired architecture into autonomous robots of the next generation - or 'animats' (Guillot & Meyer, 1998). As of today, some of these robots are efficient at executing single tasks, such as gathering scattered material at a given spot. Unlike actual mice, they nevertheless still encounter difficulties carrying out several, sometimes conflicting, tasks in an unpredictable environment, not to mention the vital necessity they will face - that of dynamically maintaining a sufficient energy level.

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