

A temporal model of animal behavior and fractal property of the
feeding in Drosophila melanogaster

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Summary

We present a new temporal model of animal behavior, including environmental and internal parameters, based on the ethological idea that the internal states of the individual, not the external stimuli, determine the behavior. This model predicts a fractal property of the behavior, that is, an inverse power law distribution of the duration. Being consistent with the model, we have found a fractal feeding property in Drosophila melanogaster: The dwelling time of starved flies on food showed a clear inverse power law distribution. Predicted change into an exponential distribution and the dependence of the fractal dimension on the intensity of food stimuli have been proved.

Introduction

Temporal analysis of animal behavior has usually been conducted with random models using negative exponential functions (Fagan and Young 1978). However, most behavior consists of a large number of interdependent elementary processes. Such systems, which have no characteristic time scale, are generally said to be 'temporal fractals', which manifest an inverse power law distribution whose exponent is closely related to the fractal dimension of the process (Mandelbrot 1983; West 1990). Based on the ethological idea that the internal states of the individual, not the external stimuli, determine the behavior, we present a fractal model of animal behavior that predicts an inverse power law distribution of the duration. This communication further presents the first evidence of temporal fractal in the feeding behavior of Drosophila melanogaster; the dwelling time of starved flies on food sources shows a clear inverse power law distribution (Shimada and Hara 1988). A change in the distribution into an exponential one and a dependence of the fractal dimension on food stimulus intensity, as predicted by the model, have been revealed under the following experimental conditions.

Methods

Male flies of Drosophila melanogaster (Canton-S), previously starved for 20 hr, were placed on micro-test plates (small plastic boxes with 60 wells) and left to feed for 30 min at 25 C. Ten mM sucrose or 5 mM sucrose mixed with 1 % agar were placed in the wells of the plate (10 ul each, more than sufficient for all the experimental flies; Shimada et al. 1987). Two types of

food distribution were used: (1) dense distribution, in which all 60 wells in the micro-test plate were filled with sucrose solution, and (2) sparse distribution, in which only four symmetrically selected wells were filled with sucrose solution, and the other 56 with water. The movements of five male flies in the micro test plate were recorded on video tape under continuous illumination. With the aid of a personal computer, we monitored the video records played-back at 1/3 normal speed and recorded the entering and leaving times to/from the selected wells by pressing keys correspondingly assigned to the wells. Subsequently, the dwelling times at the wells are calculated based on these data.

Results

Model

Figure 1 shows our basic assumption that even simple animal behavior is determined by a very large number of activated levels N of the internal states in complicated neural networks of the central nervous system (CNS). The internal states are conditioned by various stimuli specified by a parameter β_0 in the environment. The dynamic processes of the CNS probably give rise to the fractal properties of animal behavior. According to statistical considerations, taken from a Boltzmann distribution analogy in statistical mechanics, the simplest expression of the number of internal states $I(N)$ specified by β_0 is expressed by an exponential function;

$$I(N) = I_0 \exp(\beta_0 N) \quad (1)$$

where N denotes the internal state levels and I_0 is the initial

number of states for $N=0$. This expression can also be derived under the assumption of Weber-Fechner's law between the external stimuli and the internal activated levels, N (sensation)(see, Appendix I).

Here, N changes with time from certain levels including zero to a limit expressed as N_c , that is, the critical level for transition to a new state. In this sense, $I(N)$ becomes $I(N, N_c)$. The transition probability, then, is described by the differences between the internal state levels N and N_c (see, Appendix II).

$$\begin{aligned} P_N(\beta_c) &= I(N, N_c) / I(N_c) \\ &= \exp[\beta_c(N - N_c)] \end{aligned} \quad (2)$$

If N is very large enough, we can define the continuous level density function $F(N, \beta_c)$ from the above mentioned transition probability as follows;

$$F(N, \beta_c) dN = P_N(\beta_c) dN \quad (3)$$

A fundamental assumption of our model is the relation in which the duration t of the behavior type in question is determined by a reciprocal of the transition probability specified by β ;

$$1/t = W \exp[\beta(N - N_c)] \quad (4)$$

Here, the external parameter β_c of the transition probability of the internal state changes to the internal parameter β since the output of the behavior may be modulated through the transduction process from the internal states . In general, β may be a function of β_c . W is a constant having the dimension of reciprocal time. From the fundamental assumption between t and N , we have

$$dN/dt = -1/\beta t . \quad (5)$$

By the conservation of probability, we can define the probability

density function $\phi(t)$ of the duration of the behavior as follows;

$$\phi(t)dt = F(N, \beta_0)dN \quad (6)$$

After substituting the expression (3) with (2) into the right hand side of (6), we have

$$\begin{aligned} \phi(t)dt &\propto \exp[\beta_0(N - N_c)]dN \\ &= [\exp\{\beta(N - N_c)\}]^{\beta_0/\beta} dN. \end{aligned} \quad (7)$$

Then we can rewrite the expression (7) as follows;

$$\phi(t) \propto [\exp\{\beta(N - N_c)\}]^{\beta_0/\beta} dN/dt. \quad (8)$$

With the aid of (4) and (5), we obtain the result

$$\phi(t) \propto t^{-1 - \beta_0/\beta} [= (1/Wt)^{\beta_0/\beta} (-1/\beta t)]. \quad (9)$$

The cumulative distribution (cd), $\Phi(t)$, defined by integration of $\phi(t)$, is then expressed by the following inverse power law;

$$\Phi(t) \propto t^{-\beta_0/\beta}. \quad (10)$$

If β is small enough, we have a different relation corresponding to (4). By applying the procedures mentioned in (5)~(8), we can approximately express the cd by the exponential form;

$$\Phi(t) \propto \exp[-(\beta_0/\beta)Wt] \quad (11)$$

Our model, then, firstly predicts a temporal fractal behavior, that is, an inverse power law distribution of the duration of the behavior. The following predictions are further deduced: 1) the fractal dimension, that is, the slope of the distribution in log-log plot depends on the stimulus intensity, since it is determined by the environmental parameter β_c . 2) $\Phi(t)$ may change into the exponential distribution of classical random models in (11) under certain experimental conditions for small values of β .

The latter situation indicates the linear relationship between internal states and behavioral output.

These theoretical predictions have been proved by the following experiments.

Inverse power distribution of feeding behavior

Figure 2a shows a typical distribution of the measured dwelling time of 50 flies on 5 mM sucrose wells in a dense food distribution system. The dwelling time frequency histogram is characterized by a long tail distribution. The total number of visits (n) to the wells is 646, and the mean value \pm standard deviation of the dwelling time is 2.9 ± 5.0 sec. The distribution of Fig.2a is rearranged in a log-log plot in Fig.2b and is characterized by a linear section, between 1 and 20 sec, with a slope of -1.5. The ordinate is the ratio R (%) of data that is longer than the dwelling time in question. This inverse power distribution indicates that Drosophila's staying behavior on food can be characterized as a temporal fractal.

Dependence of fractal dimension on food stimuli

The results of three repetitions of the experiments in Fig. 2 are shown in log-log plot in Fig.3a. The slopes of the linear curves, that is, the fractal dimensions, are very stable at -1.5, although data are widely scattered in the three series. Five independent series of 10 mM sucrose dense food distribution experiments are shown in Fig.3b in a log-log plot. The curves are again linear between 1 and 40 sec, where the slopes are stable at -1.1 and are clearly gentler than those of 5 mM sucrose in Fig.3a: i.e., flies stay for a longer time on relatively concen-

trated food. The clear difference between the slopes in Figs.3a and b may reflect the difference in the environmental parameter . . .

Distribution change

The fractal feature of dwelling time disappears when the food distribution is radically changed. Figure 4 shows the log-log and log-linear plots of dwelling time in paired dense and sparse food distribution experiments. The sparse distribution dwelling time is not only much longer, but also does not produce a linear log-log plot. More precisely, the sparse distribution curve has a tendency to become exponential, as clearly shown in the linear section of the log-linear plot curve.

Discussion

The key point of the model (4) is that internal states determine the behavior. We also note the transformation from the internal state levels N to the duration t of the behavior is rewritten into the form

$$N = -\beta^{-1} \ln t + \text{constant}. \quad (12)$$

Based on (12) and under the constraint that $\langle \ln t \rangle = \text{constant}$, the so-called maximum entropy formulation leads to the same inverse power distribution as that in (9), where β^{-1} is a Lagrange multiplier (West 1990) and corresponds to "degree of information" (Hara, 1985; Hara and Okayama, 1988). The logarithm of t may be called a 'fractal' function, since the scaling of a logarithmic variable simply results in an additive constant. In this sense, the transformation in (4) itself is fractal in nature.

Note that the cd function $\Phi(t)$ in (10) has a scaling (fractal) property, $\Phi(at) = \text{constant} \times \Phi(t)$. The scaling property leads us to a relation for the fractal dimension determined by the two parameters, β_c and β . The range of N ($0 \leq N \leq N_c$) gives us the upper and lower limits of the duration of fractal behavior obtained from (4); $t_m = W^{-1} \exp(\beta N_c)$ and $t_o = W^{-1}$.

The fractal nature that we have found, for the first time in the feeding behavior of Drosophila suggests the presence of a simple scaling law in the complex processes of the behavior. The scaling principle may be a useful clue in understanding the complex mechanism of animal behaviors. Furthermore, the inverse power law distribution suggests that error-tolerant systems may be present (West 1990).

Other fractal dimensions, the temporal or spatial ones, can be derived from precise analysis of time series and trajectories in the feeding behavior (Dick and Burrough 1988; Shimada et al, 1990) and would be of use in obtaining additional information.

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Appendix II

In some cases, Weber-Fechner's law may be interpreted as an expression of the relation between external stimuli $S(\tau)$ and internal activated levels N :

$$\beta_c N = \ln S(\tau) \quad (1)$$

where τ is a duration time of the stimuli. When $S(\tau)$ is described by a probability density function (pdf) of stimuli $P(\tau)$

$$S(\tau) = \int_0^{\tau} P(t) dt \quad (2)$$

we have

$$P(\tau) = dS/d\tau = \beta_c \exp(\beta_c N) dN/d\tau \quad (3)$$

from the above two relations. By relating the pdf of the stimuli $P(\tau)$ to the number of internal states $I(N)$, we can define the pdf for the internal states:

$$P(\tau)d\tau = I(N)dN / (\text{total number of internal states}) \quad (4)$$

Expressed differently, we have

$$I(N) \propto P(\tau)d\tau/dN \propto \beta_c \exp(\beta_c N) \quad (5)$$

Appendix II

For Markov process of a probability $W(N_0 t_0, N_1 t_1, \dots, t_c N_c)$ ($t_0 < t_1 < \dots < t_c$), we have a relation for the transition probability $P(N t N_c t_c)$;

$$W(N t; N_c t_c) = P(N t | N_c t_c) W(N_c t_c)$$

we can obtain the equation (2) in the text by multiplying each side of the above equation by the numerical factor (Q) and replacing in the following way;

$$I(N, N_c) = Q W(N t_c ; N_c t_c), \quad I(N_c) = Q W(N_c t_c),$$

$$P_N(\beta_c) = P(N t | N_c t_c).$$

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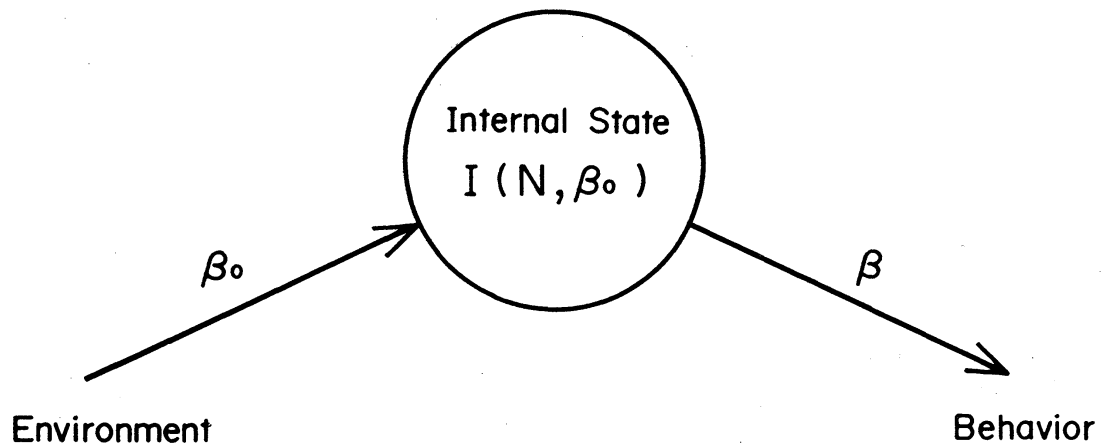


Fig. 1. A model of animal behavior as an internal state input-output system. β_0 is a parameter of information processing from the environment to the internal states, while parameter β specifies the output of the internal states.

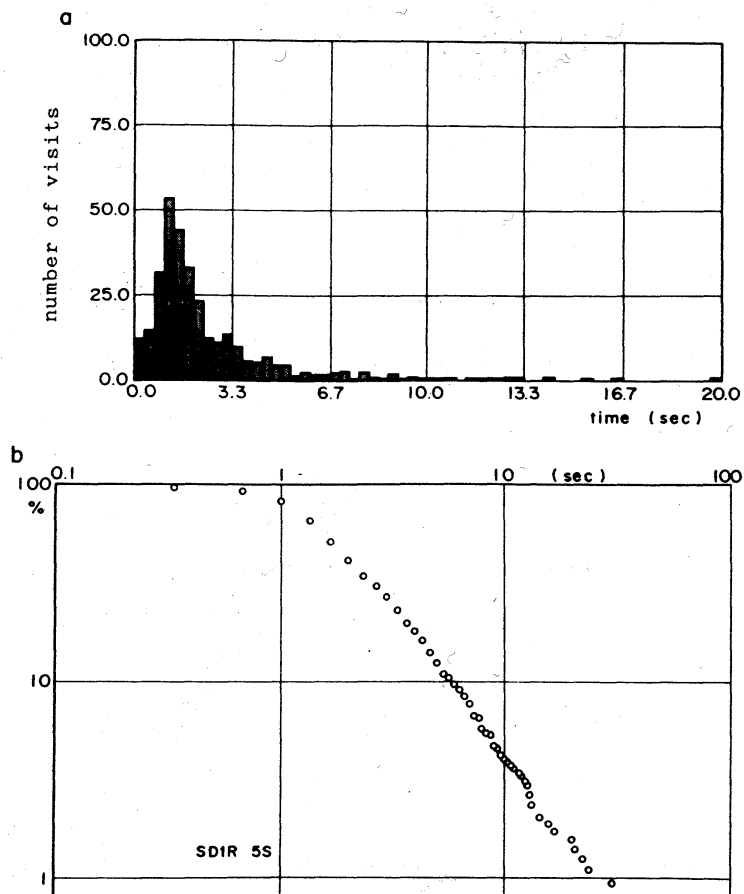


Fig. 2. Measured dwelling time distribution on 5 mM sucrose .

(a) This figure represents summed results obtained from 10 runs of an experiment in which five male *Drosophila* flies were starved for 20 hr, put on a micro-test plate at 25 °C, and videotape recorded for 30 min. To analyze the feeding behavior of *Drosophila*, the recorded videotape was played back and the dwelling time on the symmetrically selected four representative wells filled with sucrose solution was measured with the use of a personal computer. Number of visits of *Drosophila* to each well (frequency) is plotted in 1/3 sec unit. (b) Dwelling time distribution in log-log plot. The ordinate is the ratio R (%) of data that is longer than the dwelling time in question. The plot is obtained from rearrangement of data in Fig.2a.

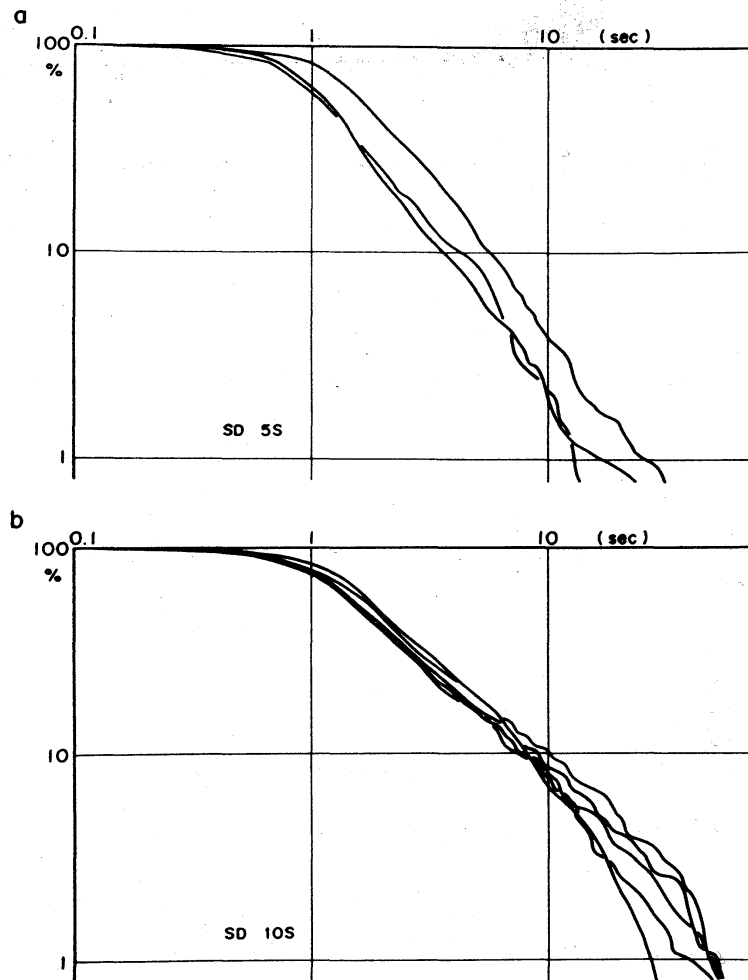


Fig. 3. Dwelling time distribution in log-log plot. The ordinate is the ratio R (%) of data that is longer than the dwelling time in question. (a) Three different series of the experiment shown in Fig. 2. Each point of one series is smoothly connected by a solid line. (b) Five series of similar experiments with 10 mM sucrose. The log-log coordinates are the same as in a.

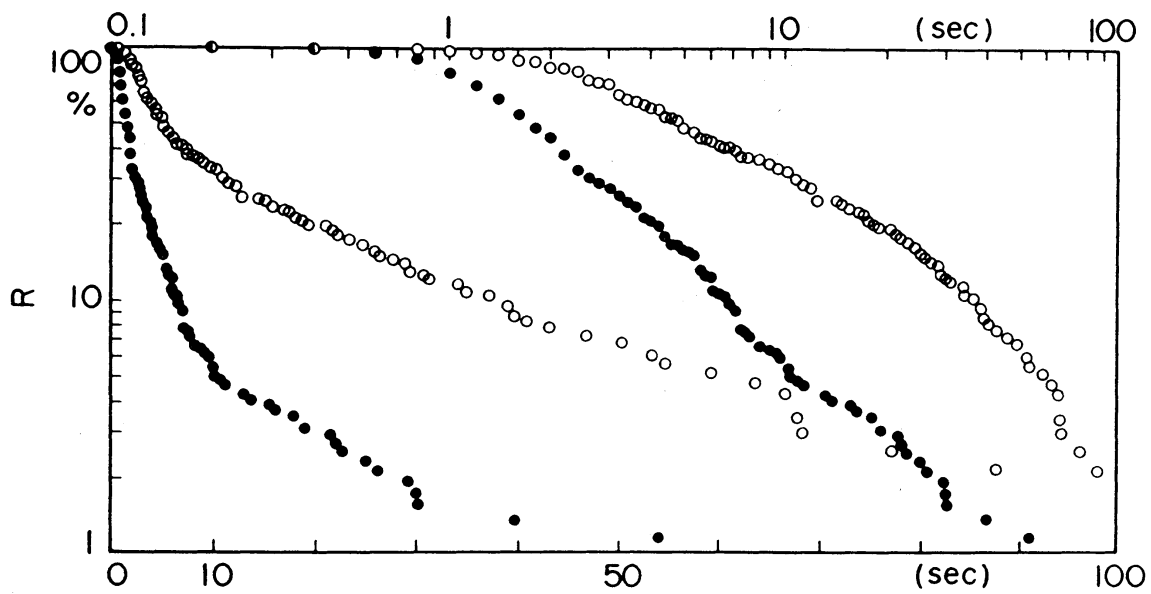


Fig. 4. Dependence of dwelling time distribution on the food distribution of 10 mM sucrose; ● = dense food distribution (60 wells) and ○ = sparse distribution (4 wells). The upper abscissa is a log time scale and the lower is a linear scale. The ordinate is the same as in Fig.3.