

Fractal time in animal behaviour: the movement activity of *Drosophila*

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Abstract. The organization of episodes of activity and inactivity of *Drosophila melanogaster* has a complex structure. Episodes of apparently continuous activity have shorter episodes of inactivity embedded within them. This pattern of activity has a self-similar structure; the activity record appears the same regardless of the time scale used. There is a power law dependence of the rate ‘constants’ that describes how the activity of flies turns on and off. As a consequence no natural time scale for the measurement of the activity level exists, and the amount of activity depends on the time scale of measurement. The observation of fractal time variability in animal behaviour may illuminate the processes that produce activity. Fractal time variation in movement activity can lead to Lévy flight patterns of movement, which produce efficient searches.

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The conventional picture of endogenous behavioural activity is one in which an animal switches between states of activity and inactivity. The transition between inaction and action may be gradual or sudden, but the underlying conceptual model for the activation of an organism is a switch between the states occurring with some probability or under the influence of a timing mechanism. One can measure the amount of time that an animal is active and inactive and calculate the probability of switching between states of activity. These quantities, the probabilities or rates, will not depend on what time units are used to quantify activity, and they provide a scale-independent measure of behaviour.

The recognition of fractal geometry in the natural world has completely changed the way that we describe form and structure in biology (Mandelbrot 1983). The realization that fractal geometry gives a better description of the shapes of blood vessels (Family et al. 1989), trees (Prusinkiewicz & Lindenmayer 1990) or army ant foraging columns (Franks 1989), compels us to derive new explanations for the production of form and allows us to produce a new correspondence between form and function. The potential for

fractal structure in temporal processes has been discussed for a variety of natural phenomena (e.g. active galactic nuclei: McHardy & Czerny 1987; various physical processes associated with glassy materials: Shlesinger 1988; ion channel kinetics: Liebovitch & Sullivan 1987; Liebovitch 1989). Fractal time occurs when the distribution of events is self-similar on a temporal scale; that is, if we measure the pattern of events with equal relative precision over many different time intervals, it is the same regardless of the scale of measurement. One result is the absence of a characteristic time scale for the interval between events.

Here I report the first observation of fractal time variability in animal behaviour. Fractal time variability in behaviour may also compel us to find novel explanations for its production and to develop a new correspondence between timing and the function of animal behaviour. In the present study, I show that the movement activity of *Drosophila melanogaster* is a time fractal and that the traditional portrayal of activity pattern is incomplete. To characterize the activity of *Drosophila*, it is essential to specify the interval with which we are sampling activity. Furthermore, the probability of observing the transition from inactivity to activity also has a power law dependence on the time scale of the measurements. I also show that this pattern of activity can result in a movement pattern called a Lévy flight, which produces efficient searching.

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The activity rate of *D. melanogaster* has often been used to characterize the phenotype of behavioural mutants (e.g. Kaplan & Trout 1969; Hall 1978; Dowse et al. 1987). Over extended periods, the activity of flies is modulated by a circadian pacemaker of which the *per* locus is an integral part (Dushay et al. 1990; Hall 1990; Kyriacou 1990). Mutations at *per* are known that lengthen, shorten or abolish the circadian modulation of activity. Although many studies have shown that the tempo of activity can differ between flies, the results are based on a single signal, breaking a beam of light, and are often summed over 10–60-min intervals. Although these procedures are essential to allow one to observe circadian and other long-term activity patterns, they necessarily obscure shorter temporal patterns. To explore the relation between the time scale of behavioural measurement and the amount of activity, it is essential to observe the pattern of activity at a higher temporal resolution.

METHODS

I obtained the data for *Drosophila* activity with a MicronEye camera to produce a digitized, 640 × 128 pixel image (Cole 1991a, b). I defined movement activity as the number of pixels that had changed between successive images. I placed female flies of a curly-plum stock maintained in a Hoshi R line, in an arena (10 × 6 mm) formed from two microscope slides held apart by a balsa-wood partition. Three walls of the observation arena were of balsawood, and the fourth wall was made of cotton that was moistened with water to prevent desiccation during the experiment. I allowed the flies to acclimatize for at least 30 min in the experimental set-up and then recorded activity for 6–8 h during midday and afternoon. I performed 10 experimental replicates. Data were collected at 2-s intervals.

I defined movement activity to have occurred when the change between successive images exceeded a threshold value. I determined the threshold by examining a probability plot (Sokal & Rohlf 1981) of the number of pixel changes. The normally distributed noise could easily be identified as a break in the linearity of the probability plot (Cole 1992), and I set the threshold to exclude this noise. I determined the total number of episodes of inactivity that were of a given

length or longer, using two criteria to set the upper and lower cut-off limits for the lengths of inactive periods. Although it is possible to record an inactive period lasting one time unit (2 s), I used only inactive periods that persisted for at least five time units (10 s) to minimize two sorts of error. First, very short intervals can be missed entirely as the length of the inactive interval approaches the resolution of the measurement. Second, the estimated length of the interval has a great deal of error when it is at the limit of the temporal resolution of the instrument. I defined the upper cut-off limit by the minimum sample size to minimize the distortions of very small samples. I required at least five periods of inactivity for each data point and used the longest such interval as the upper cut-off.

RESULTS

The activity of a single fly, in the absence of food, was characterized by seemingly relentless activity (Fig. 1a). A magnification series (Fig. 1b–e) of this activity record showed numerous episodes of activity. Short episodes of inactivity were embedded within each bout of apparently unabated activity. These episodes of inactivity persisted on successively shorter time scales down to the limits of the resolution of the data. This feature suggested a self-similar structure. Apart from the lower data density in Fig. 1e, does the structure of the activity record differ from that of Fig. 1a?

To answer this question and to quantify this phenomenon, I plotted the number of intervals of inactivity of a given length (or longer) as a function of the length of the interval (Fig. 2). The linearity of the log–log plot indicated that the number of intervals of inactivity varies as a power of the length of inactive period. Episodes of inactivity continued to appear at a constant rate, on ever shorter time scales (number of inactive periods = c (length of interval) b , average (\pm se) slope of log–log plot, $b = -1.37 \pm 0.12$, $N = 10$). Thus the temporal distribution of activity has a fractal structure.

One can use the pattern of switching between active and inactive states to derive the rate constant for the transition between activity and inactivity. If the transition between activity and inactivity is a Markov process, then a plot of the rate constant against the time scale of

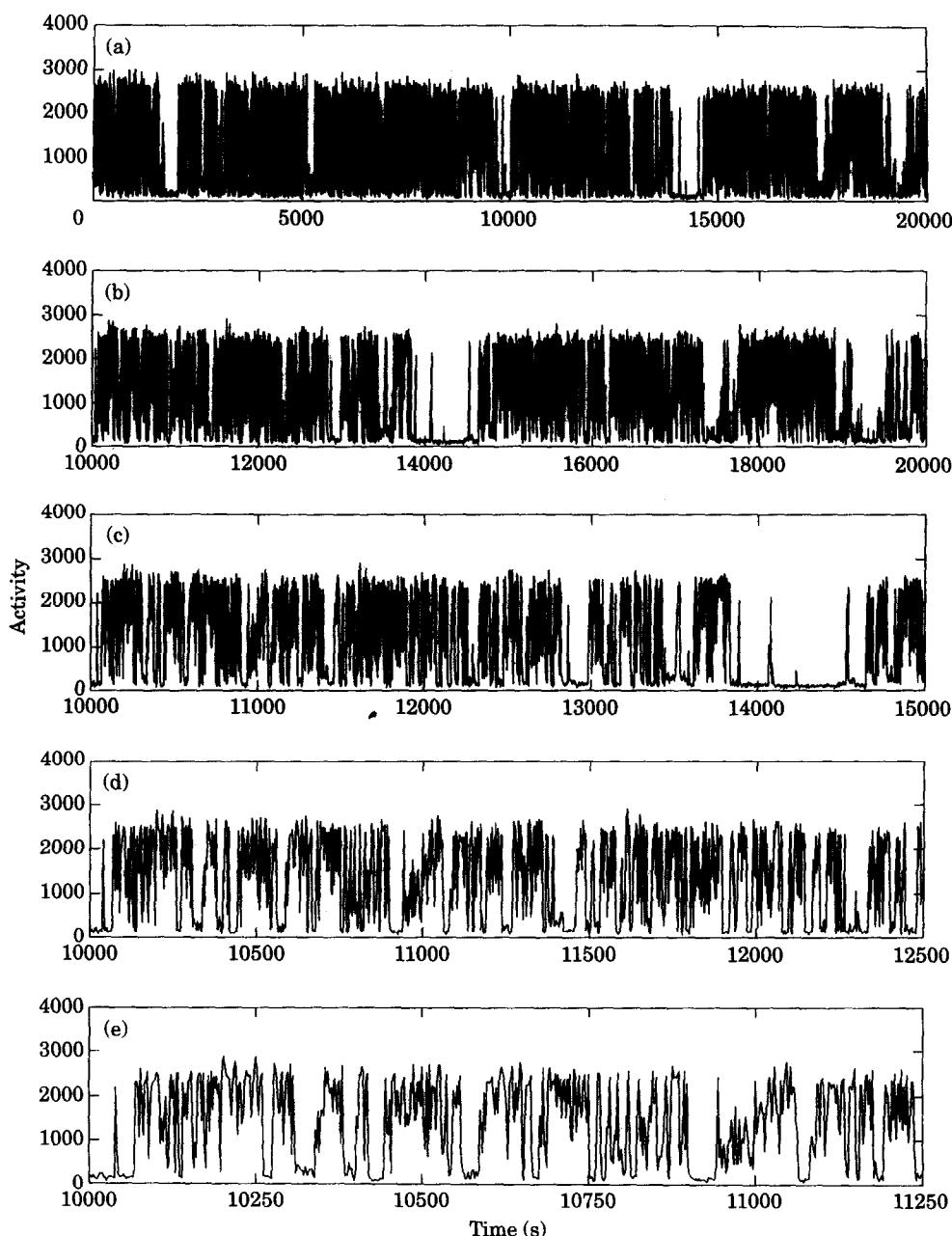


Figure 1. A magnification series of a single *Drosophila* activity record. (a) The entire data record; (b-e) successive two-fold expansions of the time scale. The time is given in 2-s intervals. Activity was measured with an automatic digitizing MicronEye camera. The ordinate is the number of pixels that change between successive images. Notice that an interval of apparently unabated activity has periods of inactivity embedded within it on each time scale. These episodes of inactivity appear with successive magnifications up to the limit of the data density, indicating that there may be self-similarity upon magnification.

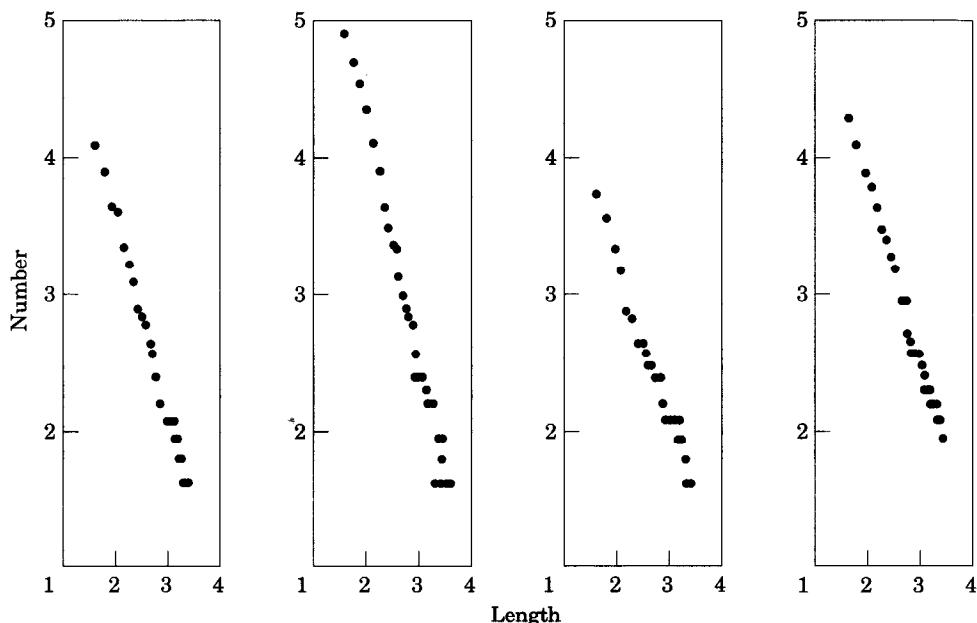


Figure 2. The relationship between the total number of intervals of a given duration as a function of the duration of the inactive interval. Each panel presents data from a single fly. The slopes of these (natural) log-log plots average (\pm SE) -1.37 ± 0.12 . Because the slope is less than -1 , the amount of time that a fly is inactive increases as the amount of time that a fly must be motionless in order to be judged inactive decreases.

measurement will also be a constant (Liebovitch 1989). On the other hand, if fractal time variability exists in the switch from activity to inactivity, then the rate constant will show a power law relation to the time scale. Given the self-similar structure of activity-inactivity, it is not surprising that the rate of transition between states follows a power law rather than being a constant (Fig. 3; the average (\pm SE) slope of the lines is -1.52 ± 0.13 , $N=10$).

Although the number of periods of inactivity continued to increase, the total amount of time that the flies were inactive did not converge to the total observation period as the time interval approached zero; the activity record of flies did not just consist of ever smaller holes in the activity record. Asymptotically, flies were active for a measurable fraction of the time (under these conditions they are active approximately 80% of the time). If we represent the episodes of activity as line segments and the episodes of inactivity as gaps between the line segments, then the total length of the line segments (even if we imagine carrying out this experiment with ever greater resolution) is positive; i.e. activity has non-zero

measure. These sets, called ‘fat fractals’ (e.g. Farmer 1985; Eykholt & Umberger 1986, 1988) can be characterized by a scaling exponent, β , sometimes termed the ‘fatness exponent’. The value of β is given by: $s(\epsilon) = s(0) + a\epsilon^\beta$, where ϵ is the size of the holes, and $s(\epsilon)$ is the length of all the segments after filling in holes of size ϵ and smaller. The value of β represents the slope of the log-log plot of the total size of the holes of a given size or smaller. The average (± 2 SE) value of β for *D. melanogaster* activity records was -0.31 ± 0.11 .

DISCUSSION

The fraction of time that an animal is active depends upon the temporal scale at which activity is measured. Flies appeared to be more inactive at fine scales than at coarse temporal scales. The total amount of time during which *Drosophila* are inactive increases in a regular manner, as a power function of the measurement interval. The activity of *Drosophila* has a fractal structure, analogous to other fractal patterns of nature, but since

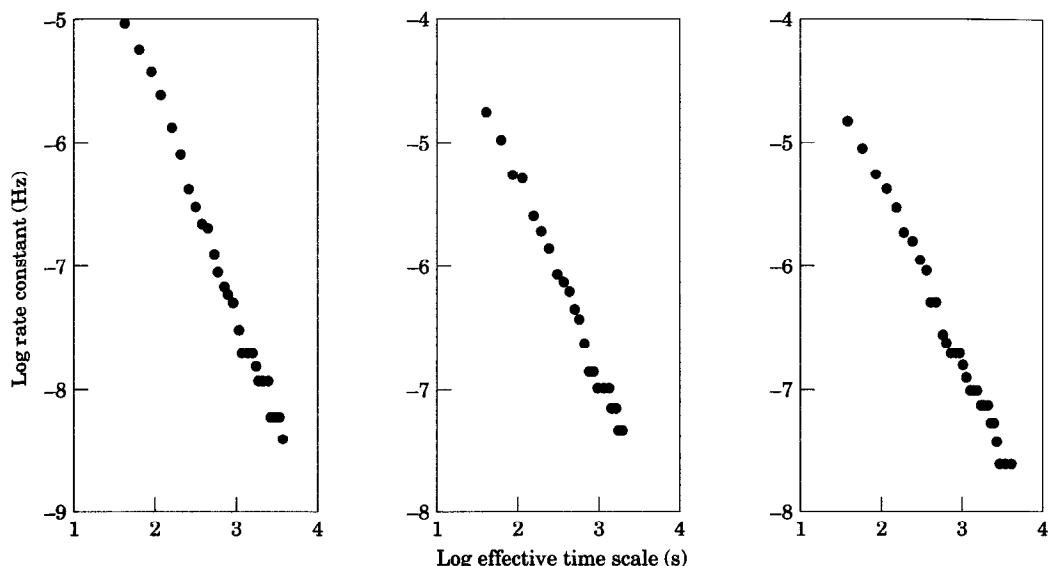


Figure 3. The relation between the effective rate constant (\log_e Hz) of switching between the inactive and active states as a function of the time scale (\log_e s) used to measure the switch between activity and inactivity. Each panel presents data from a single fly.

behaviour has a temporal rather than a spatial dimension, it is fractal in time. The rate measurements that describe the transition between active and inactive states also depend on the temporal scale of measurement.

Although the activity of flies had a fractal structure when measured every 2 s for 20 000 s, this pattern is unlikely to persist if extended over very long time intervals. Circadian modulation of activity seems likely to interfere with this pattern. For very brief episodes of activity and inactivity, there will at least be a limit to the rate at which a fly can switch muscular activity on and off. Entry into a different temporal domain should be characterized by a sudden change in the slope of the relationships in Figs 2 and 3 at critical time scales.

Animal behaviour often has a temporal component. Although it may be useful to characterize the behaviour of an organism by some long-term average measure, this procedure ignores its temporal structure. For example, in *Drosophila*, a long-term average measure of the fraction of time active or inactive gives a result that depends on the time scale. It is not possible to answer the simple question: 'how much of the time is a fly active?' without also specifying the temporal scale that defines inactivity. If we ignore the temporal

pattern of behaviour, we will have, at best, an incomplete understanding of behavioural complexity. At worst we can make mistakes concerning the validity of an interpretation. As a hypothetical example, suppose we were investigating the effect of a mutant allele or a drug on the activity level of an organism. If we averaged activity over a time interval, we may conclude that the mutant allele decreases the level of activity of the organism. Because we know that the average activity level is a function of the time scale of measurement, we need to say more about this change. We could obtain this result by either changing the slope of the relation between activity and measurement interval or by a change in the elevation of the relationship.

When possible, rather than measuring the fraction of activity, it would be more appropriate to characterize activity using the relation between the time scale of measurement and the amount of activity. The dimension of a fractal provides an obvious index to describe the relation between the scale and measurement. However, because the fractal is 'fat', the dimension of the activity does not reflect the fractal structure (Farmer 1985). The fatness exponent better characterizes the relation between the amount of activity and the temporal scale of observation.

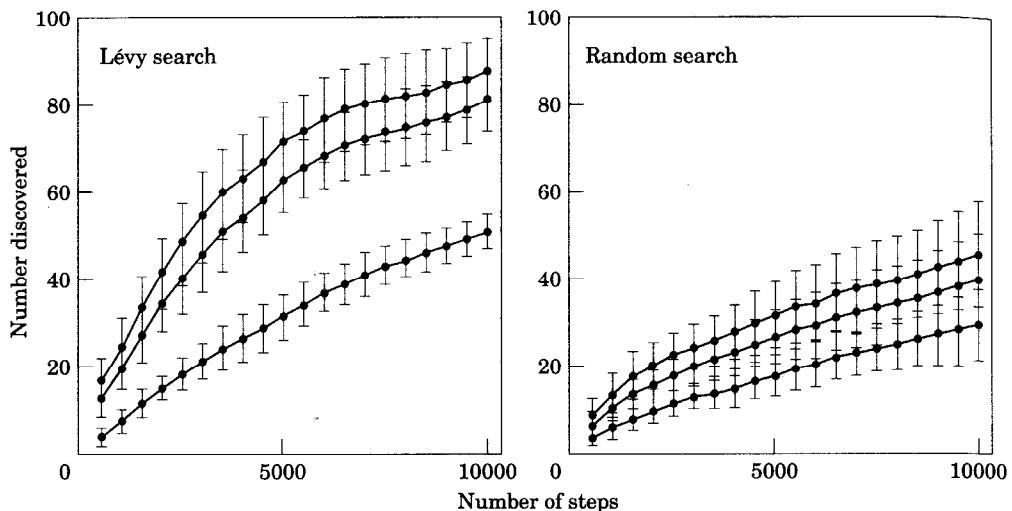


Figure 4. A plot of the mean (± 2 SE) number (for 20 replicates) of food items discovered in a random search and a Lévy search. One hundred food items were randomly scattered on a 950 by 950 grid and considered to be discovered when the searcher passed within a given radius of the food item. Search radii of 10, 30 and 50 units are shown. The random search had a step size of 9.5 units which was the mean step size in the Lévy search. The minimum and maximum step sizes in the Lévy search were 1 and 100 units, respectively. The exponent relating frequency of steps to step size was -1.37 , the average exponent from Fig. 2.

What does the observation of fractal time variability in *Drosophila* behaviour suggest about the mechanism and nature of animal behaviour? If a fly randomly switches off and on, then the frequency distribution of the lengths of inactivity would be a negative exponential rather than the observed power function scaling of periods of inactivity. If there is more than one active or inactive state, with a probability of switching between each of them, then this will produce more than one time scale over which the transitions between activity and inactivity are a constant. If several independent Markov processes govern the switch from inactivity to activity, then there will be more than one region of constancy in the measurement of the rate constant corresponding to the time scale of each of the switches (Liebovitch & Sullivan 1987; Liebovitch et al. 1987; Liebovitch & Toth 1991). Fractal time can result if there is a continuum of states of activity that are achieved by activating a continuum of triggers. The observation of fractal ion channel kinetics (Liebovitch & Sullivan 1987; Liebovitch & Toth 1991) may even provide the beginning of a plausible mechanistic connection between this phenomenon and the actions of the nervous system. Liebovitch & Toth (1991) have shown that

fractal time variability in ion channel kinetics can result from chaotic ion channel dynamics. In a perfectly analogous way one can produce fractal time variability in *Drosophila* activity by a chaotic process governing movement activity. Behavioural chaos has been suggested previously in the activity of *Leptothorax* ants (Cole 1991b, 1994).

Fractal time switching between activity and inactivity may have implications for the pattern of movement in the environment. Fractal switching of movement activity translates into fractal space use by producing a type of random walk known as a Lévy flight. Fractal random walks have been demonstrated in the search behaviour of clownfish larvae, *Amphiprion perideraion* (Coughlin et al. 1992). Lévy flights are produced as a random walk with a power function distribution of distances between turning points (Shlesinger 1988; Takayasu 1989). If we assumed that the flies moved at a constant rate when they were active, a Lévy flight would be the natural result of fractal time variability in movement.

A simulation of this type of movement helps to illustrate its importance (Fig. 4). The Lévy flight and the random walk had the same mean distance travelled between points. In the Lévy search, the exponent describing the frequency distribution of

the step sizes was the same as found in the fly activity (Fig. 2). In both cases a new direction was chosen completely at random at each turning point. Although this is unrealistic for the movement patterns of animals, presumably it is equally unrealistic for both types of search. In each case movement took place on a 950 by 950 grid and reflection occurred at the boundaries. The search efficiency was measured by the number of randomly scattered points (i.e. food sources) that were discovered after a number of steps. A point was taken to be discovered when it fell within a given radius of a turning point. I plot the mean number of points discovered (\pm SE for 20 simulations) for three search radii (10, 30 and 50 units). The Lévy flight clearly outperforms a simple random walk at all times and for all search radii. The high variance in the travel distances in the Lévy flight simulation produces a search path that can take an organism into new regions. The relative performance of a Lévy search and a random walk may depend on the pattern of dispersion of the food sources in the environment (e.g. clumped, random or fractal patterns) and on the distribution of turning angles in the search paths.

Although the precise relation between relative search efficiencies will depend on numerous factors, a Lévy search yields a surprisingly efficient search path. The correspondence between the fractal pattern of activity and a fractal search pattern in the environment can provide a mechanism to translate activity patterns into efficient foraging. Fractal time variability in movement activity naturally generates Lévy flight movement patterns, and these may in turn be produced naturally by the actions of the nervous system.

Division of observational data into bouts and inter-bout intervals (e.g. Slater 1975; Machlis 1977; Sibly et al. 1990; Speakman et al. 1992) has been a consistent behavioural problem to those quantifying the temporal patterns of animal behaviour. The recognition that temporal patterns may be naturally organized in fractal patterns may provide a more powerful and broadly applicable mechanism for understanding the temporal structure of behaviour.

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