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On the origin of bursts and heavy tails in animal dynamics

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ABSTRACT

Over recent years there has been an accumulation of evidence that many animal behaviours are characterised by common scale-invariant patterns of switching between two contrasting activities over a period of time. This is evidenced in mammalian wake–sleep patterns, in the intermittent stop–start locomotion of *Drosophila* fruit flies, and in the Lévy walk movement patterns of a diverse range of animals in which straight-line movements are punctuated by occasional turns. Here it is shown that these dynamics can be modelled by a stochastic variant of Barabási's model [A.-L. Barabási, The origin of bursts and heavy tails in human dynamics, Nature 435 (2005) 207–211] for bursts and heavy tails in human dynamics. The new model captures a tension between two competing and conflicting activities. The durations of one type of activity are distributed according to an inverse-square power-law, mirroring the ubiquity of inverse-square power-law scaling seen in empirical data. The durations of the second type of activity follow exponential distributions with characteristic timescales that depend on species and metabolic rates. This again is a common feature of animal behaviour. Bursty human dynamics, on the other hand, are characterised by power-law distributions with scaling exponents close to -1 and $-3/2$.

1. Introduction

Many animal behaviours are characterised by common scale-invariant patterns of switching between two contrasting activities over a period of time. Locomotion in *Drosophila* fruit flies is, for instance, organised into alternating bouts of activity and inactivity [1]. The bouts of inactivity are scale invariant with durations, τ, that are, to good approximation, distributed according to an inverse-square power-law, i.e. according to $P(\tau) \sim \tau^{-\alpha}$ with $\alpha \approx 2$ (Fig. 1(a)). Data analysis is described in the next section. Durations of activity, on the other hand, follow exponential distributions with characteristic timescales that depend on sex and metabolic rate. The stochasticity appears to be innate rather than environmentally cued as the experimental arena used in the study of Martin [1] was featureless and unchanging. The power-law scaling is therefore indicative of the animal's regulatory systems operating far from equilibrium, and that maintaining constancy is not a goal of physiological control. Analogous timings are found in other contexts. For example, the durations of waking episodes during brief sleep–wake transitions in four species of mammal (mice, rats, cats and humans) are power-law distributed with $\alpha \approx 2.2$ whilst sleep episode durations follow exponential distributions with characteristic timescales that change across species in relation to body size and metabolic rate [2–4]. Scale-invariant patterns of switching between two contrasting activities also underlie the movement patterns of many organisms including microzooplankton, jackals, honeybees, *Drosophila* fruit flies and a diverse range of marine predators (e.g. tuna, sharks and turtles) that use a movement strategy well approximated by Lévy walks when they are searching for resources [5–12]. These movement patterns comprise clusters of short move step lengths with longer relocation moves between them. This pattern is repeated across all scales, resulting in scale-free movement patterns in which the step lengths are power-law distributed, $p(l) \sim l^{-\mu}$ with $\mu \approx 2$. Two processes are at play: straight-line movements with durations, τ, drawn from an inverse-square power-law distribution

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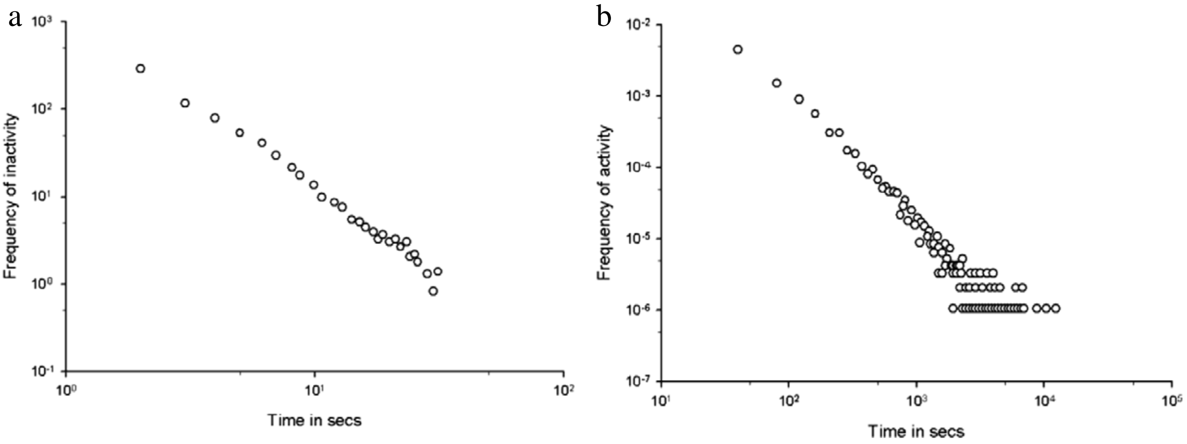

Fig. 1. (a) Frequency distribution of times spent by male *Drosophila* fruit flies during bouts of inactivity. The data is taken from Ref. [1]. A similar distribution (not shown) of inactivity durations was reported for females. The Akaike weight for a power-law is 0.99 which is indicative of near complete support for a power-law ($a = 3.0$ s). The maximum likelihood estimate for $\mu = 2.09 \pm 0.08$ (95% CI). (b) Frequency distribution of times spent by Large White × Landrace gilts during bouts of 7 distinguishable behaviours whilst nest building within pens, the most common of which are long cyclic sequences of 'nosing the ground' and 'alertness'. The Akaike weight for a power-law is 1.00 which is indicative of complete support for a power-law ($a = 150$ s). The maximum likelihood estimate for $\mu = 2.17 \pm 0.02$. The data is taken from Ref. [14].

and; turning events those durations are exponentially distributed. The turns may be associated with changes in the animal's physiological or behavioural state that are capable of breaking apart previous directional persistence [13]. Finally, the behaviour records of Large White × Landrace gilts (a species of the wild boar *Sus scrofa*) when nest building within pens show random sequences of 7 types of distinguishable behaviours: scratching; 'nosing' the environment (exploratory or manipulative behaviour directed at fixed features at or above the ground level); excretion; resting; feeding; nosing the floor and alertness (all other behaviours not defined above) [14]. The durations of these distinct activities are, to good approximation, distributed according to an inverse-square power-law (Fig. 1(b)).

The apparent ubiquity of $\alpha \approx 2$ power-law scaling in animal dynamics appears not to have been reported on in the literature. Here it shown that such 'burstiness' can be modelled by a stochastic variant of Barabási's [15] model of bursts and heavy tails in human dynamics. Barabási [15] proposed that the bursty nature of human activity is a consequence of a decision-based queuing process in which individuals execute activities based on some perceived priority. In the original model of Barabási [15], an agent operates with a priority list of L tasks. Each task on the list has a randomly assigned priority, x, drawn from a distribution $\rho(x)$. At each time step the agent selects the highest-priority task from the list and executes it. That task is then removed from the list and a new task is added to the list and given a random priority. In accordance with empirical evidence for email traffic, the model of Barabási [15] predicts that the times, τ, that tasks spend on the list are heavy tailed, i.e. distributed according to $P(\tau) \sim \tau^{-\alpha}$ with $\alpha \approx 1$. Two variants of this basic model have been reported on. In one, the rate at which new tasks are added to the priority list outstrips the rate at which tasks are executed. In accordance with the letter correspondence patterns of Darwin and Einstein, this model predicts that $\alpha \approx 3/2$ [16]. In the second, the probability to choose a task with priority, x, for execution in unit time is $\Pi(x) = x^{\gamma}$ [15]. When implemented with a fixed-length priority list this model predicts that $P(\tau) \sim \rho\left(\tau^{-1/\gamma}\right) \tau^{-(1+1/\gamma)}$. The strict priority-based *deterministic* choice corresponds to $\gamma \to \infty$. Neither of these variants of Barabási's [15] basic model captures the particular kind of burstiness seen in animals.

2. Analysis of inactivity bouts in *Drosophila* locomotion and analysis of nest building behaviours of Large White × Landrace gilts

Maximum likelihood estimates and the Akaike information criterion were used to test whether the observational data of Martin [1] and Harnos et al. [14] for behavioural bouts with durations $\tau \geq a$ is better modelled as a power-law distribution, $P_1(\tau) = (\mu - 1)\, a^{\mu-1} \tau^{-\mu}$, as an exponential distribution, $P_2(\tau) = \lambda e^{-\lambda(\tau - a)}$ or as a stretched exponential, $P_3(\tau) \propto e^{-(\lambda\tau)^{\beta}}$. The latter is a phenomenological description of relaxation in disordered systems. Maximum likelihood estimates for μ are more accurate than estimates obtained using other methods (e.g. linear regressions of log-transformed distributions with either linear or logarithmic binning, and fittings to cumulative frequency distributions) [17,18]. The Akaike weight for the power-law can be considered as the weight of evidence in favour of the power-law being the better model. The Akaike weight, w_1, for a power-law can vary from 0 (no support) to 1 (complete support). The Akaike weights are not, however, indicative of the actual distance between model fits. Here this distance was quantified following an approach advocated by Clauset et al. [19] that is related to the Anderson–Darling Test [20]. An observed distribution is extremely unlikely to follow a power-law form exactly as there will always be some small deviations because of the random nature of the sampling process. The approach of Clauset et al. [19] distinguishes deviations of this type from those that arise because the data are in actuality not power-law distributed. This is achieved by sampling many synthetic data sets from a true power-law distribution,