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Metabolic rate and body size are linked with perception of temporal information[☆]

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Body size and metabolic rate both fundamentally constrain how species interact with their environment, and hence ultimately affect their niche. While many mechanisms leading to these constraints have been explored, their effects on the resolution at which temporal information is perceived have been largely overlooked. The visual system acts as a gateway to the dynamic environment and the relative resolution at which organisms are able to acquire and process visual information is likely to restrict their ability to interact with events around them. As both smaller size and higher metabolic rates should facilitate rapid behavioural responses, we hypothesized that these traits would favour perception of temporal change over finer timescales. Using critical flicker fusion frequency, the lowest frequency of flashing at which a flickering light source is perceived as constant, as a measure of the maximum rate of temporal information processing in the visual system, we carried out a phylogenetic comparative analysis of a wide range of vertebrates that supported this hypothesis. Our results have implications for the evolution of signalling systems and predator–prey interactions, and, combined with the strong influence that both body mass and metabolism have on a species' ecological niche, suggest that time perception may constitute an important and overlooked dimension of niche differentiation.

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All biological systems, from organisms to ecosystems, are shaped by universal constraints. For example, body size and metabolic rate act as important constraints on several characteristics of organisms such as life history and behaviour, making them a particularly common and well-studied aspect of species' ecology (Brown et al. 2004; Woodward et al. 2005; Sibly et al. 2012). However, constraints imposed by the organism's sensory limitations are probably equally important and yet frequently overlooked (McGill & Mittelbach 2006; Pawar et al. 2012).

In animal species, the limitations of sensory systems are crucial in shaping both intra- and interspecific interactions. For example the ability to spot and accurately predict the motion of the opposite

party can be pivotal in determining the outcome in both predator–prey interactions (Fig. 1; Cronin 2005; Stevens 2007; Stevens et al. 2011; Clark et al. 2012; De Vries & Clandinin 2012) and the locating of mates (Land & Collett 1974; Hornstein et al. 2000). While the links among sensory limitations, foraging and spatial acuity have been studied in detail (e.g. in the use of search images for prey detection; Cronin 2005), the temporal resolution at which dynamic information can be perceived has received considerably less attention, in particular within a general ecological and evolutionary context.

The ability to integrate information over fine timescales, that is, at high temporal resolution, is thus fundamental to many aspects of an organism's ecology and behaviour. Furthermore, temporal resolution is also directly linked to the perception of the passage of time itself for humans, in particular when tracking fast moving stimuli (Hagura et al. 2012). From an evolutionary perspective, a trade-off exists between the demand for information at high temporal resolution and the costs of its acquisition given the energetic demands associated with increased rates of neural processing in

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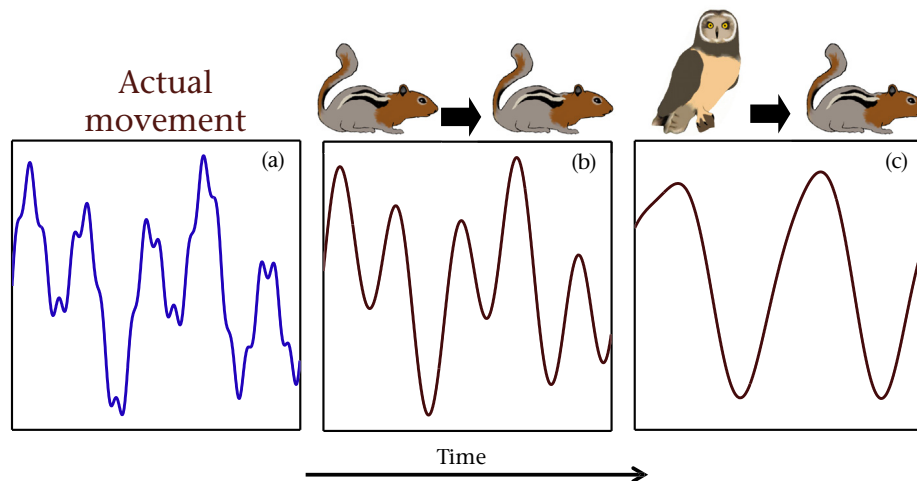


Figure 1. The ability of an organism to track a moving object depends on the time integral over which the individual can obtain its information. This is determined by its ability to resolve temporal information. In cases where an animal, such as a ground squirrel, displays complex movement (a), conspecifics may perceive the individual as moving according to a first-order integral of its actual movement owing to its high temporal resolution abilities (b). However a species with lower temporal resolution abilities, such as a short-eared owl, may perceive the motion as an even higher order derivative of the actual motion, meaning information of prey motion at finer temporal scales is not available to it (c).

the visual system (Laughlin 2001). This trade-off is likely to be shaped by various ecological (e.g. mode of predation) and environmental factors (e.g. light levels) as well as intrinsic factors (e.g. morphology) that will ultimately shape an organism's optimal temporal resolution for sensory perception. For example, predators of slow-moving prey may require less temporal resolution than predators that engage in active pursuit of fast-moving prey, such as raptors catching prey during flight.

This ability to perceive and react to a dynamic environment is a key behavioural and ecological trait. Ecologically, interaction strengths can be affected by the ability to identify and track fast-moving objects such as prey or mates (Fig. 1; Land & Collett 1974; Fritsches et al. 2005). The necessity of this ability to perceive one's environs accurately is perhaps best demonstrated in cases where temporal resolution is too coarse to allow the observer to follow the motion of a moving target accurately. A stark demonstration of this can be seen in the tiger beetle, *Cicindela hudsoni*, which, owing to the relatively low temporal resolution of its visual system, must take a stop–start approach in order to recalibrate the position of its prey when hunting (Gilbert 1997). In humans, the limitations of our temporal perception are apparent when tracking fast-moving objects such as the curving trajectory of a ball in soccer (Dessing & Craig 2010) and baseball (Bahill & Baldwin 2004).

Two intrinsic factors that may shape the costs and benefits of the temporal resolution of the sensory system, in particular with respect to their effects on an individual's ability to interact with the environment on short timescales, are body size and metabolic rate. As larger body sizes decrease manoeuvrability (Heglund & Taylor 1988; Dudley 2002; Biewener 2003; Sato et al. 2007; Vogel 2008; Hedrick 2011; Watanabe et al. 2012) and higher metabolic rates increase both manoeuvrability and the physiological ability to process information (Laughlin 2001; Franz & Ronacher 2002), we hypothesized that smaller organisms and those with higher metabolic rates perceive temporal change on finer timescales.

To quantify the temporal perceptual abilities of a range of species we took advantage of the all or nothing nature of neural firing in the visual system. Owing to this binary firing, temporal resolution must be encoded in terms of discrete units, as biological visual systems must discretize the continuous-time and continuous-space information reaching the retina and then

integrate this information over some time period. This 'integration time' of visual systems can be quantified using the critical flicker fusion frequency (CFF): the lowest frequency of flashing at which a flickering light source is perceived as constant (D'Eath 1998; Schwartz 2009). As light intensity can increase the number of flashes that can be observed per second, the maximum CFF value, as measured in a response curve of CFF against light intensity (Ferry 1892; Porter 1902), can be used as a proxy for the temporal resolution of the sensory system.

We used CFF to compare the temporal resolution of the visual system in a wide range of vertebrate species including representatives from Mammalia, Reptilia, Aves, Amphibia, Elasmobranchii and Actinopterygii. Using phylogenetic comparative methods and controlling for the light levels each species typically experiences, we tested whether the temporal resolution of the sensory system increases with mass-specific metabolic rate and decreases with body mass.

METHODS

Data Collection

To test our prediction that CFF increases with mass-specific metabolic rate and decreases with body size (when controlling for light levels), we collated data on CFF values of vertebrate species from the literature (Table 1). We only included values from studies that measured CFF using either behavioural or electroretinogram (ERG) procedures. In behavioural studies, CFF is measured through conditional training with the subject trained to respond to a change in its perception of a light flashing (D'Eath 1998; Rubene et al. 2010). For example, Lisney et al. (2011) conducted behavioural tests in domestic chickens, *Gallus gallus*, through choice experiments using flickering and nonflickering stimulus windows with choice of the correct stimulus rewarded with food. This is repeated over a range of light intensities and flicker frequencies until individuals can no longer distinguish between the stimuli. In ERG studies, a direct measurement of the electrical response of the retina in reaction to a flashing light source is used as a measure of CFF (D'Eath 1998; Schwartz 2009). As there may be further processing of temporal information after it reaches the retina that may cause behavioural studies to measure lower CFF values (D'Eath 1998), we included the

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