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In Focus

# Featured Articles in This Month's *Animal Behaviour*

*Time is in the Eye of the Beholder**

Sight, like all senses, shapes the manner in which an animal interacts with other organisms and the environment. For example, to meet a mate, to evade a predator or to catch a prey item, an animal needs the ability to spot an individual from the same or another species and predict its movement accurately. The spatial resolution of sight has been studied in detail as, for example, in the way sensory limitations shape how foraging animals use search images to detect prey. By contrast, temporal resolution of sight is much less well understood particularly in the context of how sensory limitations shape the ecological and evolutionary aspects of behaviour.

The ability of an animal to track a moving object depends on the temporal scale at which it can acquire visual information about the object's movement. Species capable of high temporal resolution can integrate information over finer scales and perceive more movement detail. Species with a low temporal resolution integrate information over more course-grained scales and perceive a smoother version of the original movement. Clearly, such differences in temporal resolution capabilities have a fundamental influence on the ability of animals to react to dynamical environments. For example, owing to the relatively low temporal resolution of their visual system, some tiger beetles have to stop and start during hunting in order to recalibrate their perception of prey position. Intriguingly, in humans temporal resolution is linked to the perception of the passage of time itself with time appearing to slow down during the tracking of fast-moving stimuli.

Higher levels of visual temporal resolution come at the cost of greater energy expenditure because they are mediated by higher rates of neural processing in the visual system. Therefore, in evolutionary terms, there is a trade-off between the benefits of the extra information provided by higher temporal resolution and the costs of the neural processing required for the supply of this information. In addition to environmental factors such as light level, this trade-off is likely to be shaped by the behaviour and ecology of the species. For example, predators of fast-moving prey such as raptors or cheetahs would be expected to be capable of higher visual temporal resolution than predators of slower prey. However, intrinsic factors may also shape the trade-off between the benefits and costs of an animal's ability to integrate visual information over fine timescales. Body size and metabolic rate are two likely candidates. The former is related to manoeuvrability: the larger the animal, the less manoeuvrable it is. By contrast, the higher the metabolic rate, the greater is the manoeuvrability and the physiological ability of an animal to process information.

The hypothesis that smaller animals with higher metabolic rates perceive temporal changes on finer timescales is tested by Kevin Healy (Trinity College Dublin, Ireland), Luke McNally (University of Edinburgh, U.K.), Graeme Ruxton (University of St Andrews, U.K.), Natalie Cooper and Andrew L. Jackson (both from Trinity College Dublin) in the present issue (pp. 685–696). Although many earlier studies have demonstrated a positive relationship between body mass and metabolic rate and a negative relationship between body mass and mass-specific metabolic rate (that is the metabolic rate per unit mass; a shrew has a much higher mass-specific metabolic rate than an elephant, for example), to the best of our knowledge this is the first study to test a hypothesis about their relationship with temporal visual resolution in the context of behavioural ecology.

The first issue the authors had to address was how to quantify the degree to which animals are able to resolve temporal information. In fact, owing to the binary, all-or-nothing nature of neural firing, temporal resolution in the visual system must be encoded as a discrete variable. Given that the temporal and spatial information received by their visual organs is continuous, animals must have a mechanism for discretizing it and subsequently integrating it over a period of time. Such 'integration time' can be quantified by the critical flicker fusion frequency (abbreviated as CFF). This is defined as the lowest frequency of flashing at which an animal perceives a flickering light source as constant. Therefore, animals with higher CFF can resolve temporal information at a finer scale.

Using phylogenetic comparative methods and controlling for light levels (because light intensity can increase CFF), Healy and coauthors used CFF to compare the temporal resolution of the visual system of a wide range of vertebrate species among fish, amphibians, reptiles, birds and mammals. They tested whether species' maximum temporal resolution of the visual system is positively related to species' average mass-specific metabolic rate and negatively related to species' average body mass. Data on 34 species were obtained from the literature. The authors corrected for the phylogenetic nonindependence of species by using published molecular phylogenies and evolutionary divergence times as well as applying a statistical modelling approach, which accounts for such nonindependence. In addition to the effect of body mass and the temperature-corrected mass-specific resting metabolic rate (to account for the effect of temperature on the metabolic rate of cold-blooded species), their analysis of CFF took into account the light level under normal conditions for each species (as mentioned earlier, light intensity can increase CFF) and whether CFF was quantified using a behavioural method or as a direct

* After David Kelly who came up with this phrase as acknowledged by the authors of the featured paper (Fig. 1).


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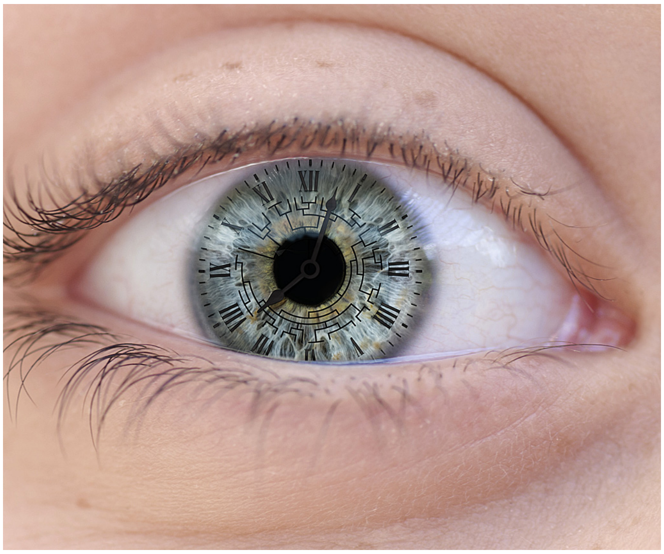

**Figure 1.** Depiction of time perception through the visual system. The study found that the ability to perceive temporal information is linked with both metabolic rate and body mass across a range of vertebrates as represented by the phylogeny in the clock face image. Image credit: Creative Cargo.

measurement of the electrical response of the retina in reaction to a light source. Furthermore, the authors ran sensitivity analyses, which included brain mass data on 28 of the species, to account for any possible effects of the amount of brain tissue on the value of CFF.

The results clearly demonstrate that small animals with high mass-specific metabolic rates in well-lit environments have the highest CFF, meaning that they have the ability to resolve dynamic visual information at the finest temporal scales. Conversely, large animals with low mass-specific metabolic rates in low light environments have the lowest CFF. Whether CFF was measured behaviourally or as a direct electrical response did not have any effect and phylogeny had only a minimal influence. The results were also robust to the sensitivity analyses.

The findings by Healy and coauthors demonstrate for the first time the existence of a general trend among vertebrates for body mass and mass-specific metabolic rate to act as constraints on the ability of animals to resolve temporally dynamic visual information. This is important because it links quantitatively sensory adaptations to fundamental constraints and trade-offs imposed on animals across taxa and over magnitudes in scale. Future studies on whether this relationship applies to invertebrate animals and whether it is qualitatively the same would add to the generality of these findings. Further work is needed to establish the underlying mechanisms for this generality and its ecological consequences.

**Ana Sendova-Franks**
**Executive Editor**

*The Sweet Smell of Success*

Chemical signals used for social communication are both ancient and widespread. Early attention was focused on these as cues for species recognition. Female silk moths send their pheromones wafting on the breezes and males might detect them downwind from as far away as 10 km. To be useful as a mate attractant, these pheromones should vary between species and between the sexes. Only recently has it been appreciated that these volatile chemicals might vary between individuals and therefore could potentially provide information about mate quality. Animals from spiders to humans (even fungi for that matter) have been shown to use chemical cues to assess potential mates. However, a recent review on the importance of odour in mate choice makes no mention of any bird (Johansson & Jones 2007); after all, birds are thought to rely on visual and acoustical cues for social communication.

Dark-eyed juncos (Fig. 2) are a socially monogamous songbird with biparental care and a considerable level of extrapair fertilizations. Like most birds, they have uropygial (preen) glands that secrete oil. The birds spread it on their feathers, which helps to keep them waterproof, clean and flexible. The preen oil contains small amounts of volatile and semivolatile compounds that have been shown to vary and change in abundance during the breeding season, by sex, population of origin and relatedness. Furthermore, measurements of relative abundance are repeatable for individuals in both the short and long term. As such, these preen compounds are perfect candidates to contain information not only about individual identity but also individual quality. Studies on other species of birds have hinted that this might be so.

In this issue (pp. 697–703), Danielle Whittaker and colleagues from the Universities of Michigan State and Indiana asked whether these chemical cues could be used in mate assessment. They examined whether the abundance or profile of the volatile secretions covaried with quality, measured by reproductive success (genetic and social), and with visual cues (plumage and wing length) known to be involved in female mate preference. They collected preen oil early in the breeding season and several times thereafter. They also took blood samples for paternity analysis, made several morphological measurements and estimated the proportion of white on the tail. Later they took blood from, counted and measured the nestlings and identified the social parents.

The preen volatiles of interest were linear alcohols, carboxylic acids and methyl ketones chosen because they change in abundance during the breeding season, peaking about the time of egg laying. Whittaker et al. used the sample of greatest abundance from each individual; for most birds this was closest to the start

**Figure 2.** Female dark-eyed junco collecting material for her nest. Photo: Nicole Gerlach.