memory traces are components of mental time travel, they can exist without other components in young children and in animals [14]. So I think we can fruitfully use animal models of episodic memory traces. But this should not commit us to concluding, without additional evidence for the other components (or a grand experiment combining them as you mentioned), that rats travel mentally in time.

To make progress we need to combine replicable, empirical approaches like yours, and an open mind to both potential capacities and to limits in nonhuman animals.

JDC: I think we agree that avoiding subjective experiences is a wise approach and that we need to have an open mind to capacities and limits in nonhumans.

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Quick guide

Cannibalism

Chloe Fouilloux[1], Eva Ringler[2,3] and Bibiana Rojas[1,*]

What is cannibalism? Cannibalism is the act of killing and consuming a conspecific in part or as a whole. It is a paradoxical phenomenon widespread across animal taxa. The word 'cannibal' is a modified version of the Spanish word 'caníbal', which in turn comes from the pre-Columbian Taíno word 'caniba'. This was the form with which Christopher Columbus referred to the Caribs, a greatly feared tribe. Previous studies on cannibalism in animals extensively documented the variety of contexts in which it occurs, showcasing the wide range of benefits and costs incurred by cannibals. Consequently, research on cannibalism has increased our understanding of kin selection, sexual conflict, sibling rivalry and parental care.

Which animals are cannibalistic? Although cannibalism has been described in almost every clade in the animal kingdom (Figure 1), the consumption of kin and conspecifics remains a fascinating and, in some instances, inexplicable behavior. Some birds, for example, have evolved asynchronous hatching, where older chicks cannibalize their siblings. In sand tiger sharks, embryos eat their siblings *in utero*. In cases where young consume conspecifics, as seen in some amphibian species, individuals are often morphologically adapted to do so. In fact, some tadpoles born vegetarian undergo morphological transformations after consuming conspecific tissue, exchanging their filter-feeding mouth parts for a keratinized beak and a modified digestive system. For humans, cannibalism is a repulsive act, as it goes against the moral and ethical standards we tend to use to distinguish ourselves from the rest of the animal world. However, humanity has not gone without cannibalism and, in fact, the costs and psychology of this behavior have been extensively studied, particularly with respect to disease transmission.

Figure 1. Cannibalistic animals.
Top left: sexual cannibalism in the Western black widow (*Latrodectus hesperus*; photo: Sean McCann). Top right: non-parental cannibalism in a male lion (*Panthera leo;* photo: Lara Jackson). Bottom left: non-parental cannibalism in the brilliant-thighed poison frog (*Allobates femoralis*; photo: Eva Ringler). Bottom right: sibling cannibalism in the lady bird (*Harmonia axyridis*; photo: Gilles San Martin; CC BY-SA 2.0).

Why cannibalism? Cannibalism occurs in different contexts. Siblings can cannibalize others (sibling cannibalism, intrauterine cannibalism), parents can cannibalize their own progeny (filial cannibalism) or unrelated conspecific offspring (nonparental or hetero-cannibalism), and sexual partners can cannibalize each other (sexual cannibalism). For a long time, there was skepticism about how such destructive behaviour towards conspecifics, and sometimes even close kin, could be adaptive. However, several studies to date have shown that cannibalism may involve ‘obvious’ advantages for the individual and even, in some cases, for the population. For example, when faced with the risk of desiccation, some spadefoot toad tadpoles eat conspecifics— these individuals metamorphose faster, which helps them survive in pools of water that could evaporate at any time. There are many instances where cannibalism is expressed as a result of overcrowding: injured, weak, or diseased individuals who have a slim chance of reproducing or protecting a population are generally the first to be predated. In termites, whose nests can reach huge population densities, the workers eat individuals infected with virulent pathogens, halting the pathogen’s spread and protecting the nest from infection. Leafroller caterpillars, who are preferentially herbivorous in their larval stage, have been observed to exceptionally eat meat when placed next to a parasitized conspecific. These findings challenge the common perception that cannibalism is mostly a route of pathogen transmission, and is always dependent on population-density or resource availability: it may also function in controlling disease spread and maintaining population-wide health.

Who gets cannibalized? Relatedness, or kinship, also plays an important role in determining a cannibal’s prey. Frequently, animals avoid eating their direct relatives when given a choice. Eating unrelated individuals reduces competition and increases the likelihood of a cannibal’s kin reproducing, which increases the cannibal’s indirect fitness. Earwigs, who are very protective of their brood, will sometimes kill nest intruders as a means to protect their offspring from potential conspecific cannibals. In time of low-resource availability, nematodes shift from being oviparous to ovoviviparous, where eggs eat their mother from the inside out. With this said, parents aren’t always their offspring’s protectors: squirrels will consume handicapped or sick individuals to retrieve some of their expended energy (as do several species of teleost fish and salamanders), and frogs have been seen to feed their younger offspring to their older ones.

What makes animals cannibals? Environmental stressors, like food scarcity (in both quantity and quality), high-population density, and a range of abiotic factors can drive individuals to consume conspecifics. Often, cannibals are older and larger, as predation can be costly (or even deadly) when attacking an individual with better developed defenses. Sexual conflict is another driver of cannibalism. In many systems, females invest more energy to produce gametes (anisogamy) and rear offspring; thus, in food-limited conditions where females are unable to hunt or forage during pregnancy, consuming male partners after mating can be a crucial food source contributing to the survival of the mother and her fertilized eggs. For larger vertebrates that live in fragmented habitats, unrelated offspring provide low-risk, high-value food sources which also generate new mating opportunities with otherwise non-receptive parenting mothers; thus, infanticide can also lead to cannibalism for species capable of digesting animal tissue.

Do humans practice cannibalism? Humanity has had its own relationship with cannibalism throughout time. Most frequently cited is the case of Kuru, a neurodegenerative condition popularized by western doctors who studied the disease and inevitable deaths of Papua New Guinean cannibals in the 1950s. In the 17th century, Europe was full of ‘medicinal cannibalism’, which was prescribed to peasants and the elite alike, and a direct correlate to the increase in executions in the 17th century to meet the demand for human body parts. Cannibalism persists to this day: well-documented ‘survival cannibalism’ in China is recorded throughout Mao Zedong’s disastrous rule in the late 1950s, but also spiritual cannibalism continues to exist in the Amazon jungle. Dark shamans, known as Kanaimà in Guyana, are human cannibals whose spirit is said to transform into jaguars after consuming the fermented juices of their buried prey. Western culture continues to be fascinated with cannibalism, where cases of cannibalistic serial-killers and popular television shows persist in daily life; the fascination, as described by Lewis Petrinovich, is core to the human experience, “The cannibal is within all of us, and all cannibals are within all cultures, should the circumstances demand the appearance.”

What can we learn from cannibalism? Research in the past three decades has uncovered unexpected trends and consequences of cannibalism. With the advent of novel molecular, neurochemical, and mathematical approaches, researchers from different sub-disciplines are reviving their interest in the study of cannibalism, which is currently focused on the ecological factors that have shaped its evolution and the underlying cognitive processes within single individuals. Another potential exciting future field of research might focus on the role of disease transmission for the evolution of cannibalistic behaviours across animal taxa. While it is known that in some species the threats and risks associated with disease transmission might have impeded the expression of cannibalism, in other species, cannibalism is even used as a measure to prevent disease transmission across siblings or populations. The investigation of mechanisms that make animals more or less susceptible to pathogens transmitted via cannibalism will be an important step towards understanding the proximate mechanisms driving cannibalistic behaviour in animals.

Where can I find out more?

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No evidence for an S cone contribution to acute neuroendocrine and alerting responses to light

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Exposure to even moderately bright short-wavelength light in the evening can strongly suppress the production of melatonin and delay our circadian rhythm. These effects are mediated by the retinohypothalamic pathway, connecting a subset of retinal ganglion cells to the circadian pacemaker in the suprachiasmatic nucleus (SCN) in the brain. These retinal ganglion cells express the photosensitive protein melanopsin, rendering them intrinsically photosensitive (ipRGCs). But ipRGCs also receive input from the classical photoreceptors — the cones and rods. Here, in human participants, we examined whether the short-wavelength-sensitive (S) cones contribute to the neuroendocrine response to light by using stimuli which differed exclusively in the amount of S cone excitation by almost two orders of magnitude (ratio 1:83), but not in the excitation of long-wavelength-sensitive (L) and medium-wavelength-sensitive (M) cones, rods, and melanopsin. We specifically examined the S cones since the previously published action spectra for melatonin suppression [1,2] pointed to a possible role of S cones in addition to melanopsin. We find no evidence for a role of S cones in the acute alerting and melatonin-supressing response to evening light exposure.

To probe the role of S cones in circadian responses to light, we generated a pair of stimuli providing either minimal S cone stimulation, S-, or maximal S cone stimulation, S+ (Figure 1A). The stimuli were designed to produce no differential stimulation of the L and M cones, the rods, and melanopsin. We employed a spectrally tuneable light source consisting of ten different LED lights, which were individually adjustable in intensity, thereby producing complex mixtures of light which differed in the amount of S cone stimulation by a factor of ~83, or equivalently, ~1.92 units at moderate photopic light levels (168–173 lux; Figure 1A). The S cones play an important role in colour vision, encoding the blue–yellow dimension of colour vision. As a consequence, our S-cone isolating stimuli appeared different in colour (but not luminance, or ‘brightness’), with S- corresponding to an orangish, and S+ corresponding to a pinkish colour (Figure S1E, published in Supplemental Information with this article online).

With these stimuli, we probed the human circadian timing system using acute melatonin suppression. Melatonin, which rises in concentration approximately two hours prior to habitual bedtime, can be strongly suppressed by short-wavelength light [1,2]. In an in-laboratory within-subject protocol under controlled lighting conditions, we found no difference in salivary melatonin production when participants (n = 15) were exposed to our two stimuli differing in S cone activation (Figure 1A) from 150 to 30 minutes prior to their habitual bedtime. While a change in light stimulus by almost two orders of magnitude (1:100) is known to move the neuroendocrine response to light from no response to saturation, a change of size in only the S cones produced no difference in the production of evening melatonin (Figure 1B; Bayes factor (BF) comparing full model with lighting condition as factor versus model without lighting condition: 0.71 ± 0.019). We also examined if our stimuli affected subjective sleepiness (measured using the Karolinska Sleepiness Scale; Figure 1C) and vigilant attention (measured using reaction time to beeps, averaged over ~50 trials; Figure 1D). Neither sleepiness (BF: 0.43 ± 0.068) nor vigilant attention (median reaction time BF: 1.4 ± 0.029; fastest 10% reaction time BF: 0.32 ± 0.031; slowest 10% reaction time BF: 0.44 ± 0.053) were modulated by S cones alone.

Earlier studies located the peak spectral sensitivity for melatonin suppression near 460 nm [1,2], i.e. between the S cones and melanopsin. This spectral sensitivity cannot be described by a combination of L and M cones (‘luminance’) and a recent