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A sleeping paradox may extend to the spider

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A scientist slammed his fist on the podium and with a bit of theatricality, decried the fact that no one had yet figured out the function of sleep. The person who immediately followed claimed they "could not disagree more" and calmly, yet defiantly, listed sleep's functions for all attending the sleep conference's special symposium to hear. I was a startled first-year PhD student, and that was the 50th anniversary of the discovery of sleep's most famous stage—rapid eye movement (REM) sleep, when REMs are linked with vivid dreams. The work of Eugene Aserinsky and Michel Jouvet had uncovered a paradox; our immobile, sleeping body is largely paralyzed during episodes of REM, yet the brain appears awake, bristling with electrical activity (1–3). Instead of being idle during this stage of sleep, our brains are engaged in visually rich dreaming. We begin our night of slumber with a sequence of non-REM sleep stages followed by REM, and this cycling of sleep stages continues through the night. During REM sleep, the brain emits fast, low-amplitude waves, electrophysiologically resembling wakefulness far more than it does its sister stages of sleep. The discovery of REM sleep was revolutionary in that it revealed a third state of consciousness or cognitive existence, alongside quiet sleep (characterized by slow, high-amplitude waves) and wakefulness, resulting in a surge of studies that compellingly attribute functions specific to the bizarre state. Although next year marks the 70th anniversary of the discovery of REM sleep and it will have been 20 y since the public display of scientific discord that jolted me back in 2003, such exchanges could just as easily happen today. Sleep science is still shrouded in mystery, and the paradox of REM sleep could benefit from new insights and new comparative investigations. We know that mammals and birds express REM sleep in various forms (4), lizards exhibit similarities to mammalian and bird REM sleep, and that cephalopods show behavioral indications of this state. How much of this is due to shared ancestry? Are REM-related functions products of convergence? Rößler et al. (5) have boldly challenged us to consider a very distant relative of the other REM sleepers by cleverly analyzing the movements of retinal tubes visible through the translucent cuticle of juvenile jumping spiders.

Before I summarize the exhilarating findings of Rößler et al. (5) and consider the provocative implications, it is important to note what this study does not show. With an absence of tests for sleep behavior or physiology, the authors make it clear that they are not definitively demonstrating sleep in their subjects. In fact, no study has ever clearly demonstrated sleep behavior in a species of spider, which is remarkable considering spiders' diversity, ecological impact, cultural allure, and accessibility. Other invertebrate lineages have been subject to sleep studies, including roundworms and molluscs, the recent additions of cnidarians and flatworms, and (non-spider) arthropods contributing thousands of studies of sleep over 39 y, due almost exclusively to studies of insects, with all but a smattering of these studies featuring sleep in Earth's most famous fruit fly. Questions of sleep's evolutionary history motivated Tobler and Stalder (6) to report a suite of sleep characteristics in scorpions (Scorpiones: *Heterometrus longimanus*, *Heterometrus spinnifer*, and *Pandinus* sp.) in the only study of its type for arachnids. The closest anyone has come to establishing sleep in spiders (Araneae) includes reports of circadian activity, resting postures (7) and the study by Rößler et al. (8) of "resting" behavior in the same species of jumping spider as used in the present study (*Evarcha arcuata*). The jumping spiders are sometimes seen within silken retreats, standing, or hanging upside down from a silk thread, motionless through much of the night. This apparent "quiet" sleep state is punctuated by a more active state, with unique posture, twitching, and rapid retinal movements. The spiders' legs stereotypically curl while hanging or partially curl while standing in a manner suggesting muscle atonia. Occasionally, their spinnerets, opisthosoma (the posterior region of the body), or curled legs twitch. Retinae in the two principal eyes jerk around, evoking REM sleep–related queries that have long been restricted to vertebrates. The authors are careful to call the behavior a REM sleep–like state because they have not conducted tests typically designed to define sleep behavior. A sleeping animal, along with being relatively (and reversibly) immobile in a stereotypical posture, exhibits a higher response threshold and a sleep rebound following sleep loss. Having a higher response threshold means it would take a stronger stimulus for the immobile spider to respond than when exhibiting other behavior states, and a sleep rebound means a spider would express more of the state or a deeper version of the state, if deprived of it, suggesting that the state is functionally necessary. Because sleep is a complex behavior with rich mechanistic, developmental, functional, and evolutionary implications, identifying a behavior as sleep and distinct from other states of relative immobility is critical if one wishes to make claims about sleep.

Another relevant item the authors do not experimentally address is the actual paradox that has been used to define REM sleep in other animals. The present study includes no electrophysiological recordings to accompany

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the sleep-like behavior, so we do not know if the brain within a spider's immobile body is firing in a wake-state manner. Behaviorally, REM sleep is defined by REMs in a less responsive animal. There is no reason to think that jumping spiders do not sleep, so if future studies confirm that the stereotyped behavior reported by Rößler et al. (5) is sleep and these REM-like behaviors occur when the spiders are less responsive, an exploration of REM sleep in a species far removed from our usual vertebrate subjects could offer great potential for considering the evolutionary origins and functional nature of this paradoxical state.

Spiders have up to eight eyes, and muscles can move the retina behind each of their two principal eyes so that the spiders are able to redirect their gaze without pivoting their bodies (9, 10). Retinal movement in the jumping spiders is visible with an infrared camera when looking head-on at the otherwise fixed eyes in standing adults and, most easily, when looking dorsally through the temporarily translucent exoskeleton of juveniles. As you can easily see in the movies in the work by Rößler et al. (5), the retinal tubes shift, dart, and jerk about as the body dangles relatively motionless and upside down from a silk thread. At the same time, the spider's legs are curled, and parts of the body occasionally twitch. Rößler et al. (5) discovered that the jerky retinal tube movements were consistent in their duration, with consistent interims between bouts, and that the duration of the bouts increased over the course of the night, as they do in REM-sleeping vertebrates.

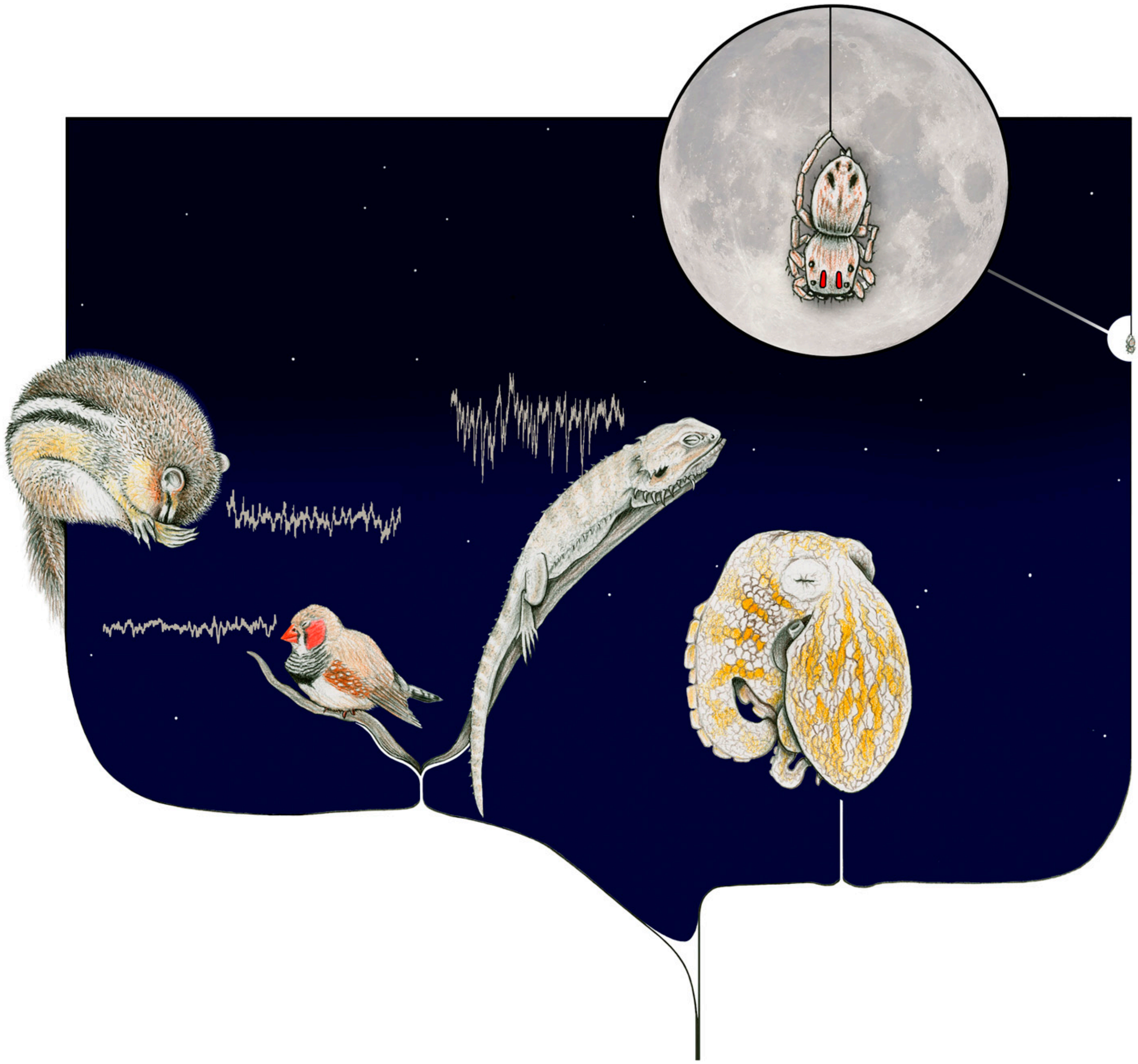

Fig. 1. Animal taxa, from left to right, known to exhibit REM sleep [mammals: chipmunk (17); birds: zebra finch (18)], REM-like sleep [lizards: bearded dragon (11); cephalopods: octopus (14)], and REM-like, sleep-like behavior [jumping spider (5)]. Electroencephalogram traces from REM sleep were extracted and modified from source publications about chipmunks and zebra finches, and graciously supplied by Mark Shein-Idelson from a bearded dragon; they are each 3 s and matched for amplitude (in microvolts). *Inset* features a magnified view of the jumping spider suspended from a silk thread at the far right of the phylogeny. Retinae, dorsally hidden in adults but visible in juveniles, are highlighted in red.

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Are these episodic retinal tube movements REM? This is a surprisingly deeply complicated question that exacerbates an already muddied enterprise. Identifying REM sleep began with Aserinsky's human subjects, and now, it is generally assumed that all mammals exhibit it (perhaps excluding the curious case of cetaceans). The hunt for REM sleep in other vertebrates has been mixed. Unequivocal REM sleep is restricted to birds, and a REM-like state has been shown in lizards. Notably absent are birds' closest living relatives, the crocodilians. As argued by Blumberg et al. (4), a binary REM/non-REM label oversimplifies a phenomenon often defined by components that do not overlap perfectly across or even within lineages. Some birds exhibit REM sleep while standing (leg muscles are not paralyzed), and the tegu lizard shows no wake-like brain activation during periods of REM. Even the name can be a misnomer for owls, whose eyes are largely set, unmoving, within their skulls. Do we ask the question in terms of phylogeny and ancestry? If so, we can begin with the fact that all animals, whether visually endowed or primitively eyeless, share deep homology with respect to the molecular underpinnings of eye development (e.g., PAX6 gene). The evolution of the eye itself is one of convergence across multiple animal lineages, and the question of how deeply homologous sleep is remains a mystery. If REM sleep described in the Australian bearded dragon is homologous with the stage in birds and mammals, the origins of REM sleep harken back to early amniote evolution, at least 300 Mya (11). A far deeper ancestry would require ample evidence of REM sleep in invertebrates. Although some invertebrates twitch in a REM-like fashion during sleep, scant precedent exists for seriously speculating about REM sleep's invertebrate origins. The most compelling evidence exists in the dynamic display of REM-like sleep behavior in cephalopods. Octopuses and cuttlefish twitch, their eyes move, and their chromatophores flicker and flash in suggestive bouts of what may be paradoxical sleep (12–14) (Fig. 1).

Equally exciting would be to address the question of REM in jumping spiders by considering the current utility of the phenomenon. If REM sleep evolved convergently, explanations of its origins and maintenance would confirm its functional importance. It is possible that the expression of REM sleep across lineages indicates a need that is instrumental in aspects of the consolidation of emotionally rich memories, learning, and other fitness-relevant factors. It would be difficult to deny the importance of a trait that renders one vulnerable if it is performed even by a bird in flight (15).

Studying something as strange as sleep or dreaming benefits from new technologies, new insights, and new study systems. To appreciate its biological relevance, more wild animals observed in the wild and studied under naturalistic conditions are key. The true triumph of the study of Rößler et al. (5) is in experimentally investigating an obscure but long-known natural phenomenon (retinal movement in spiders) to lend insight to one of science's great mysteries (the nature of REM sleep) (16). This fundamental insight is the hallmark of great comparative biology, and recognizing and empirically investigating something as quirky as episodes of jumping spiders' retinal movements during the brief window within which they are visible may cultivate or catalyze fertile new directions for REM research and our understanding of sleep and dreaming.

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