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Neuroscience: Kryptonite for half-awake sleepers

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Birds and many marine mammals have the enviable ability to sleep both symmetrically, as humans do, and asymmetrically, with one eye closed and the corresponding hemisphere showing deeper sleep. A new study in birds shows there's a limit to this superpower.

Superheros are endowed with superpowers. Notably, Superman possesses great strength, speed, and hearing; he can fly, and is seemingly invulnerable. From our human perspective, animals have superpowers, too. Caterpillars (*Aglais io*, *Telochurus recens*, *Tyria jacobaeae*) detect and respond to positively charged predatory wasps (*Vespula vulgaris*) by sensing electric fields through the air[1]. Bogong moths (*Agrotis infusa*), at just 2.5 cm long, fly forty million times that length at night to aestivate in cool caves they have never visited before, navigating by the starry night sky and Earth's geomagnetic field[2]. And in a recent issue of *Current Biology*, van Hasselt, Martinez-Gonzalez *et al.*[3] demonstrate that European jackdaws (*Coloeus monedula*) have an elegant superpower allowing them to sleep asymmetrically, and even outright unihemispherically. Yet, just as kryptonite nullifies Superman's power, high sleep pressure forces jackdaws to sleep symmetrically, more like Clark Kent (Figure 1).

Most animals face the daily trade-off between being awake (to eat, move, and be watchful) or asleep (to clean, repair, and restructure the brain)[4–6]. Some animals favour an extreme side of this trade-off, opting for sustained wakefulness while likely enduring the (undescribed) costs of prolonged sleep loss[7,8]. Other animals have apparently side-stepped the trade-off altogether with adaptations that allow 'wake behaviours' to occur during sleep. For example, reindeer (*Rangifer tarandus tarandus*) and other ruminants continue to chew the cud during non-rapid eye movement (non-REM) sleep[9], the main sleep state in mammals and birds. And great frigatebirds (*Fregata minor*) can sleep in the air when soaring and gliding[10]. While aloft, they can engage in symmetric non-REM and REM sleep, but mostly asymmetric non-REM sleep, presumably to watch out for other birds rising in a shared air current. When back at their nest, they engage in less asymmetric sleep, suggesting a hitherto unknown physiological limit to their ability to sleep 'half-awake'.

Hints of this limit can be seen in studies on other birds and marine mammals that share the frigatebird's ability to sleep asymmetrically. When mallard ducks (*Anas platyrhynchos*) sleep in a group, those on the periphery sleep more asymmetrically than the ducks tucked in the centre. In doing so, they keep their open eye aimed away from the others to watch their less protected flank[11]. Conversely, the ducks with neighbours on either side indulge in less-vigilant symmetric sleep, presumably because sleep processes take more time or are less efficient when performed asymmetrically. Accordingly, in a strictly behavioural study on chickens (*Gallus domesticus*), the removal of daytime naps caused a tripling in the occurrence of symmetric sleep during the first hour of the night, which came at the expense of asymmetric sleep[12]. Another example can be seen in northern fur seals (*Callorhinus ursinus*), which can sleep on land and in seawater alike. On land, they favour sleeping symmetrically[13]. While being deprived of sleep on land over three days, mounting sleep pressure caused fur seals to initiate sleep more as the deprivation progressed. When allowed to sleep freely, they showed an acute increase in the amount of deep, symmetric non-REM sleep[13]. In seawater, symmetric non-REM and REM sleep are almost completely abolished, and sleep proceeds mostly as asymmetric non-

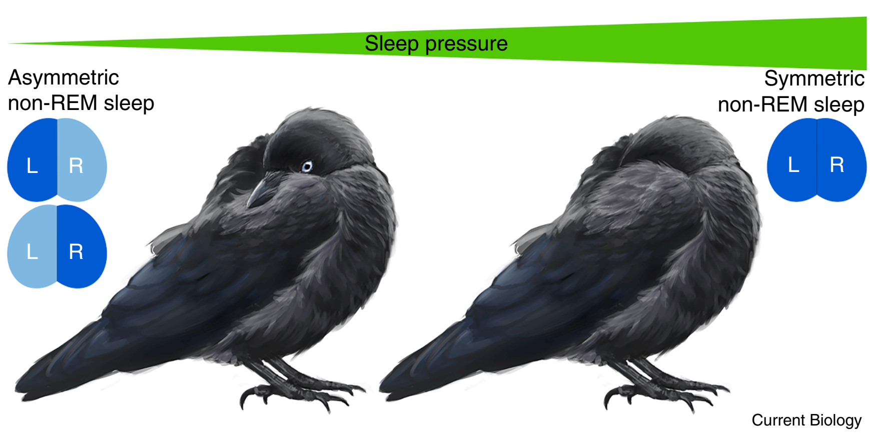

Figure 1. High sleep pressure as a physiological brake on asymmetric sleep.
European jackdaws (*Coloeus monedula*) can use their superpower to sleep asymmetrically with deeper non-REM sleep (*dark blue*) in either the left (*L*) or right (*R*) hyperpallium of each hemisphere but only when sleep pressure is relatively low. When deprived of sleep and most tired, high sleep pressure causes jackdaws to sleep symmetrically. Note, because eye states were not filmed, the open eye shown here is assumed, justified by data from other studies showing a link between asymmetric brain activity and one-eye opening[11]. Nonetheless, even in the absence of visual vigilance, asymmetrically sleeping jackdaws could maintain unilateral auditory awareness of the local environment[15,16]. (Jackdaw illustrations by Laura X. Tan.)

REM sleep[14]. Lastly, when sleeping in an unfamiliar place for the first time, human volunteers were shown to exhibit a lighter form of non-REM sleep in part of their left hemisphere compared to their right hemisphere[15]. This form of asymmetric non-REM sleep wasn't associated with one-eye opening, but did allow for greater auditory vigilance to unusual sounds, which elicited more awakenings with faster reaction times. On the second night, when the venue was more familiar, the hemispheres slept symmetrically.

Asymmetric sleep affords these animals with the ability to sustain visual[10–14] and auditory[15,16] awareness of the local environment. Because absolute safety while asleep is never assured[17,18], if you can sleep asymmetrically, why not *always* sleep asymmetrically? van Hasselt, Martinez-Gonzalez and colleagues shed light on this question using high-density recordings of brain activity from sleeping birds[3].

European jackdaw nestlings were hand-reared so as to be well accustomed to captivity, humans, and handling. Many months later, adolescent jackdaws were fixed with electrodes for recording brain activity over much of the dorsal pallium, including the hyperpallium (a primary visual processing region of the avian brain comparable to the primary visual cortex in mammals), hippocampal formation, and dorsal ventricular ridge. Housed individually, the birds took part in a 72-hour experiment wherein they could sleep freely and undisturbed except for the first 4 or 8 hours of the second night, a period of sleep deprivation. In this way, van Hasselt, Martinez-Gonzalez *et al.*[3] could see how the use of asymmetric and symmetric sleep changed over a 'normal' night, where sleep pressure was greatest at lights-off and declined as sleep accrued, but also on nights with sleep pressure augmented beyond normal. The sleep recordings were scored, and for each 4-second epoch of non-REM sleep, an asymmetry index was calculated between electrode pairs over each hemisphere with a focus on the anterior and posterior hyperpallium, and the hippocampal formation. This index then informed whether the slow brain waves during an epoch of non-REM sleep occurred symmetrically, asymmetrically, or unihemispherically[13].

Most epochs of non-REM sleep occurred symmetrically and few (less than 0.1%) were unihemispheric. Nonetheless, depending on the brain region considered, between 18% and 31% were asymmetric. In the anterior and posterior hyperpallium, sleep pressure influenced the amount of asymmetric non-REM sleep. Specifically, on the undisturbed baseline night, asymmetric non-REM sleep was lowest at lights-off and increased across the night. Furthermore, when deprived of sleep for 4 or 8 hours, the occurrence of asymmetric sleep was lowest when sleep pressure was highest. For reasons that are unclear, this pattern was not found in the hippocampal formation. Nonetheless, in the visual hyperpallium at least, high sleep pressure forces jackdaws, and likely other asymmetrically sleeping animals[10–15], to trade asymmetric sleep for symmetric sleep.

Why might this be? The fastest way to erase a physiological deficit is to perform the restorative process at the fastest rate, often to the exclusion of everything else. For example, a hungry animal will feed at the maximal rate, even foregoing anti-predator vigilance[19]. Yet, as the animal eats and energy is restored, they take fewer risks and look around more. The same appears to be true for the physiological deficits wrought by prolonged wakefulness[3]. Being awake causes metabolic waste, molecular damage, synaptic changes, and energy expenditure that are redressed during sleep[4–6,20]. Sleep pressure motivates the animal to sleep so those restorative processes can be carried out. Such processes seem to be accomplished best by sleeping symmetrically when the animal is most tired and the deficit is the greatest[3,12,13]. The shift towards more vigilant, asymmetric sleep occurs only after sufficient symmetric sleep has accrued. This shift allows the animal to still achieve some benefits of sleep, but concurrent with greater environmental awareness. And so, by keeping sleep pressure low, jackdaws maintain unconstrained use of their superpower.

What remains unclear, however, is the identity of the sleep processes that are impaired by sleeping asymmetrically. Is the preference for symmetric sleep simply a matter of minimizing the time needed to achieve sleep functions for both hemispheres? Or do some functions, such as waste clearance or memory consolidation[4,6], require between-hemisphere state symmetry? By answering these questions, the study of asymmetrically sleeping animals[10–14], including humans[15], can provide new testimony on the purposes and processes of sleep.

DECLARATION OF INTERESTS

The author declares no competing interests.

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Biotremology: Spider webs are not just a lazy way to capture prey

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The funnel-weaving spider *Agelenopsis pennsylvanica*, tested in urban vs. rural habitats under quiet vs. loud noise treatments, was found to be able to influence information reception in the presence of environmental noise carried through the external sensory surface of its web.

Biotremology is a rather new biological discipline, which was only given a name in 2016. It deals with all sorts of behaviors and interactions with the environment by organisms through use of non-sound mechanical waves. Technically, sound waves, or acoustic waves, are also mechanical, but they are restricted by definition to those compressional waves that are detected by some sort of ear…a pressure receiver or pressure-difference receiver[1]. Vibrational waves are detected by a broad array of mechanical receiving organs across taxa, best known in the Arthropoda. This diversity gives us some sense of how ancient vibrational behavior must be in organisms for this level of diversity to have evolved. Most of the biotremology community members first studied the biological use of vibrational waves with respect to animal communication but then had to consider that many of the animal interactions did not correspond to the strict definition of communication. Further, we now also know that plants respond to stimuli carried in vibrational waveforms, as do vertebrate animals, but also non-arthropod invertebrates such as nematodes…and we continue to discover a range of vibration-based behaviors across biological systems.

One of the groups that has gained increased focus in recent years since the expansion of biotremology is the web-building spiders. These spiders interact with each other and their prey in a unique landscape because the substrate through which vibrations travel is constructed from biological materials the spiders produce, rather than being soil, or plant or water surfaces. Most of us who enjoy being outside in regions where web-building spiders live naturally will remember learning as small children that the web is a structure, built by the adult resident, that is used for capturing and even storing prey items. Indigenous people in North America have spider stories that are likely similar to others from any region of the world that has web-builders. In these stories the spider is often revered for its patience, its perseverance and its efficiency in capturing prey in the web it makes for itself[2]. The web constructed by spiders has been studied since the early 1980s for its functions other than prey-capture and storage. Web residents can gain information about location and characteristics of various disturbances in their web[3] and can distinguish vibrations produced by prey from those of male and female adults and juvenile members of their own species[4]. Many web-building species have poor visual acuity but send and receive information via vibrations through the web threads during courtship and care of offspring[5]. Spiders that prey on web residents can exploit this behavior by mimicking the resident's prey or creating disturbance vibrations that distract the web resident and mask the movement of the predator species[6]. Yet, web-building spiders exist as part of a larger ecosystem beyond their web, and modern technology has allowed us access to broader questions about the potential roles of the web itself. A study by Pessman and Hebets[7] published in a

