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Sleep: Rock and Swing versus Toss and Turn

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It has been known for centuries that gentle rocking promotes sleep. Two new studies now shed light on the underlying mechanism in both humans and mice.

Since ancient times and across cultures, newly minted parents spend hours cradling their babies in the hope of facilitating their sleep. The vestiges of these childhood experiences might have led the Mayans to invent the hammock some 1,000 years ago, which thereafter spread around the world due to its sleep-promoting effects on children and adults alike. But how exactly does gentle rocking and swinging help induce and maintain sleep? In this issue of *Current Biology*, two exciting new studies reported by Perrault *et al.* [1] and Kompotis *et al.* [2] set out to elucidate the neuronal mechanisms underlying the beneficial effect of rocking for sleep.

The systematic investigation of the impact of rocking on infant sleep dates back to the 1970s and 1980s, using oscillating waterbeds. These early efforts already yielded promising results, indicating that waterbed-mediated rocking accelerated falling asleep and led to more sustained, uninterrupted sleep [3]. More recently, Bayer *et al.* [4] demonstrated that sleeping on a rocking bed not only accelerated sleep onset, but also enhanced the prevalence of two cardinal sleep signatures measured via scalp electroencephalography (EEG), namely slow oscillations and sleep spindles. The <1 Hz slow oscillation is generated in neocortical circuits and comprises alternations between depolarized up states and hyperpolarized down states [5]. Sleep spindles are bursts of oscillatory activity (11–16 Hz) arising from thalamo-cortical networks [6]. These two electrophysiological phenomena not only hallmark non-rapid-eye-movement (NREM) sleep, but recent research has linked them to one of the most intriguing behavioural effects of sleep, namely memory consolidation. It was first shown almost a hundred years ago that sleep after learning leads to better memory performance compared to performance after the same time spent awake [7], and recent neuroimaging work has ascribed a direct role to slow oscillations and spindles in mediating this effect [8,9]. Thus, rocking might not only help induce and maintain sleep, but — by bolstering slow oscillations and spindles — also beneficially impact memory consolidation.

In the first of two related studies published in this issue of *Current Biology*, Perrault and colleagues [1] asked whether rocking-induced sleep oscillations might indeed facilitate memory consolidation. Participants spent two experimental nights in the sleep laboratory. They were continuously rocked during one experimental night, while the bed remained stationary during the other night. To induce rocking motions, an electrical motor gently moved the bed at a frequency of 0.25 Hz, i.e., one full left–right swing every four seconds. Importantly, participants also engaged in a declarative memory task, with performance being tested before and after the sleep interval. In accordance with previous findings by Bayer *et al.* [4], the results first confirmed that rocking accelerated sleep onset and impacted sleep architecture. Specifically, rocking strengthened the depth of sleep by reducing the number of arousals. Also in line with previous findings, rocking broadly increased activity in the sleep spindle range compared to the control night. However, the current study went further to directly link the emergence of sleep oscillations to the rhythm of the rocking bed, i.e., providing evidence for an entrainment function of rocking on sleep oscillations. To this end, the authors added a rocking sensor to their apparatus, sending a marker to their EEG recordings whenever the moving bed reached a turning point. Indeed, both spindles and slow oscillations clustered specifically around time points when the rocking bed changed directions, strongly pointing to entrainment of these brain oscillations by the rocking bed. Back on a behavioural level, the results showed that, firstly, post-sleep memory performance was better after the rocking night compared to the control night and, secondly, spindle power during deep sleep showed a positive correlation with memory benefits across participants. Together, these findings indicate that the rocking bed entrained a boost in spindle activity which in turn improved memory consolidation.

But how exactly can a rocking bed entrain brain oscillations in service of sleep quality and memory formation? One candidate mechanism could be that rocking exerts its beneficial effects by stimulating the vestibular system. This system, considered as the primary sensory organ of movement [10], provides us with the sense of balance and acceleration. Its peripheral parts, located in the inner ear, supply the cerebellum, brainstem and somatosensory cortices with information about our body movement and position in space. Vestibular inputs are also known to send direct projections to the thalamic system [11], which is, as described above, intimately linked to the generation and maintenance of sleep-specific oscillations. Thus, by stimulating the vestibular system, rocking might enhance synchronous activity in thalamo-cortical circuits.

The second paper [2] published in this issue used an animal model to investigate the role of the vestibular system in mediating the beneficial effects of rocking on sleep. Mice were continuously rocked for 12 hours by a platform moving in the horizontal plane. To determine the optimal

rocking frequency for mice, the platform moved either at 0.25, 0.5, 1 or 1.5 Hz. During 36 hours before and after the rocking sessions the platform remained stationary, providing baseline and post-rocking measures. In a first step, Kompotis *et al.* [2] tested whether rocking would generally affect sleep in mice as it did in humans. Results revealed that when rocked at the 'optimal' rate of 1 Hz, mice spent more time in NREM sleep relative to time spent awake, while rocking also accelerated sleep onset. Thus, similar to humans, rocking had a considerable impact on sleep architecture, although the difference in effective rocking frequencies (1 Hz in mice, 0.25 Hz in humans) also points to species-specific differences. Another interesting difference to the human study was that rocking did not entrain slow oscillations and sleep spindle activity in mice, but specifically slowed down theta activity (6–10 Hz) during post-rocking wakefulness. This result not only highlights that caution is always warranted when translating from animal models to humans, but also raises the interesting question whether rocking in mice would also impact their memory consolidation even in the absence of spindle entrainment. Further research is clearly needed to answer this question. In any case, having established that rocking also benefits sleep in mice, the remaining question was whether these effects were indeed mediated by the vestibular system. To address this issue, Kompotis *et al.* [2] tested a group of transgenic mice with dysfunctional otolithic organs. The otolithic organs comprise the portion of the vestibular system sensitive to linear acceleration [10]. Thus, otoconia-deficient tilted mice, which were used in the present study, are generally unable to encode linear acceleration. If rocking exerts its effects via vestibular pathways, these mice should be insensitive to the stimulation. Indeed, this is exactly what Kompotis and colleagues observed. Sleep in mice with dysfunctional otolithic organs of the vestibule remained unaffected by rocking at 1 Hz, indicating that an intact vestibular system is necessary for the effects of rocking on sleep (Figure 1).

Taken together the studies by Perrault *et al.* [1] and Kompotis *et al.* [2] highlight several intriguing aspects of rocking.

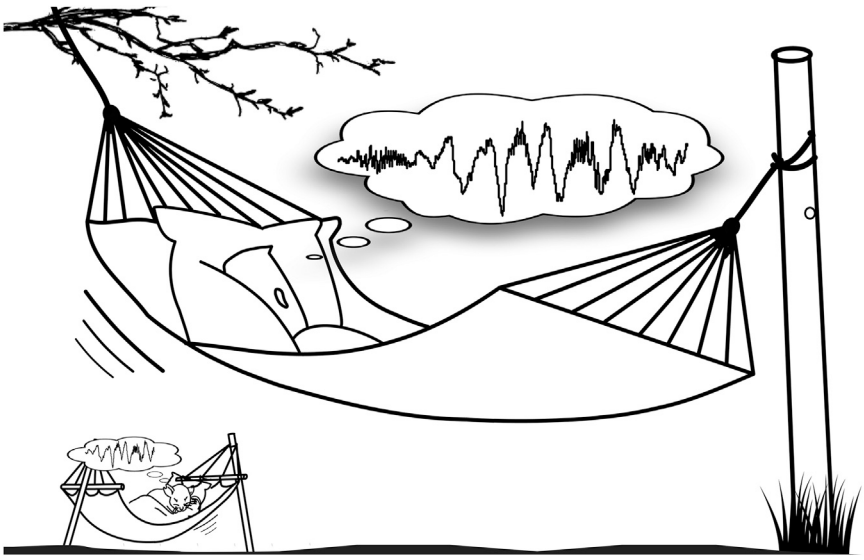

Figure 1. Gentle rocking benefits sleep in both humans and mice.
Rocking impacts sleep architecture and enhances sleep across species. In humans, rocking entrains sleep spindles, which in turn drive memory consolidation. As shown in mice, the sleep-modifying effect of rocking is mediated by the vestibular system.

First, the sleep-enhancing effect of rocking manifests across species. Second, in humans, rocking entrains sleep spindles which in turn mediate both the sleep-promoting and memory-enhancing effects. Finally, on a mechanistic level, the mouse model suggests that this effect is mediated by the vestibular system. Both studies open up an array of exciting practical implications: in recent years, several experimental procedures have been employed in an effort to non-invasively bolster sleep, including transcranial direct current stimulation (tDCS) [12] or auditory stimulation [13]. While some of these studies reported success in inducing sleep oscillations and in enhancing memory consolidation [14], they did not show general improvements on sleep architecture/quality. Thus, rocking might represent a promising non-pharmacological intervention to accelerate sleep onset and improve sleep quality by reducing arousals, especially in patients suffering from sleep disorders. Also, might it be feasible to use rocking in combination with other experimental methods to strengthen memories during sleep? For instance, recent work has shown that playing auditory reminders during sleep can improve memory consolidation ('targeted memory reactivation', TMR) [15,16]. Importantly, this effect again seems to be mediated by sleep spindles [16–18], and the timing of the reminders with respect to sleep spindles seems to be critical [18]. As Perrault *et al.* [1] now demonstrate that rocking entrains spindles at predictable time-points, sending memory reminders during anticipated spindle onsets might further enhance the efficacy of TMR. In other words, the combined effects of rocking and TMR might constitute a powerful tool for memory-enhancement in both educational and clinical settings. And finally, memories not only benefit from sleep, but also from awake rest periods [19]. This begs the question whether another iconic piece of furniture can be used to improve memories during everyday life rest periods: the rocking chair.

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Symbiosis: Wolf Lichens Harbour a Choir of Fungi

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Identification of the fungus *Tremella* as a consistent fourth component of wolf lichens further challenges the conventional view of lichen symbiosis as a mutualistic interaction between two players.

Lichens, along with corals and root-dwelling fungi, are traditionally presented as quintessential models for mutualistic interactions [1]. These systems are often depicted as stable two-player interactions between a phototroph and a heterotroph, in which fixed carbon, produced by the phototroph, is exchanged for metabolites, water, and physical housing fashioned by the heterotroph. However, recent studies have shown that many macrolichens (that is, those lichens possessing leaf-like, hair-like, or shrubby structures) are consistently composed of not one, but two fungal heterotrophic players: an ascomycete and a basidiomycete [2], in addition to a phototrophic algal partner. Yet in a further twist, work reported in this issue of *Current Biology* complicates the matter once again by demonstrating that wolf lichens — *Letharia vulpina*, the yellow-green macrolichens found throughout Europe and western North America — are composed of an alga and at least three fungal heterotrophs: an ascomycete and two phylogenetically distinct basidiomycetes [3].

This newly identified second basidiomycete partner is a member of the *Tremella* fungi. Such fungi had previously been found to form gall-like structures — composed of polarised cell forms known as hyphae — associated with these lichens [4] (Figure 1A,C). These hyphal cells were described as being representative of a parasitic infection, and the gall was interpreted as an invasive tissue resulting in fitness costs to the lichen [5]. In the new study, Tuovinen *et al.* [3] first used an untargeted genome-sequencing approach that sampled total DNA from wolf lichens to identify a signature of *Tremella*-like genes in lichens that had no evidence of galls. The authors' interest was piqued and thus a large-scale survey of wolf lichens was undertaken, making use of samples from across North America and Europe. This work revealed that 273 (86%) of the samples studied consistently demonstrated the presence of *Tremella* fungal genes within the wolf-lichen DNA samples.

The authors went on to develop specific DNA fluorescent probes to identify and