SLEEPJ, 2025, 48, 1–3
doi:10.1093/sleep/zsaf300
Advance Access publication 29 September 2025
Perspective

Perspective

The undeniable value of developmental analysis for the science of sleep

Mark S. Blumberg[1,2,*]

[1]Department of Psychological and Brain Sciences, University of Iowa, Iowa City, IA, United States and [2]Iowa Neuroscience Institute, University of Iowa, Iowa City, IA, United States

[*]Corresponding author: Mark S. Blumberg, Department of Psychological and Brain Sciences, University of Iowa, Iowa City, IA 52242, U.S.A. Email: mark-blumberg@uiowa.edu.

To understand sleep, we must understand how it develops. In a field that has largely relegated development to a secondary role, this claim may strike many sleep researchers as excessively bold. But it is not.

Niko Tinbergen famously identified four aspects of any behavior that must be understood: its development, control, functional significance, and evolution [1]. Although sleep is clearly a behavior and thus falls within the purview of Tinbergen's analysis, the field of sleep science has focused primarily on understanding sleep—including its neural mechanisms and functions—in adults. The field's relative inattention to development is particularly perplexing because sleep—in animals from humans to birds to fish to flies—is most prevalent in early life [2–4]. There are many reasons, both historical and pragmatic, for this inattention; no matter the reasons, progress has been impeded.

My aim here is to advocate for the unique insights provided by developmental analyses of sleep, and to also show how investigations of sleep in developing animals can yield benefits even to those who are primarily interested in adults. My guiding perspective is that the development of sleep is a *process* comprising context- and activity-dependent cascades of influences, not the maturation of a predetermined outcome [5]. This perspective derives from the developmental systems approach to understanding the form, functions, and evolution of behavior [6–8].

One critical thing to know about sleep development is that it entails immense qualitative change: Individual sleep components emerge and coalesce over time [9,10]. For example, in newborn rats, active (or REM) sleep is readily identified by the presence of muscle atonia, limb twitching, and irregular breathing (Figure 1,A). Other components, such as rapid eye movements, the hippocampal theta rhythm, and desynchronized cortical activity, emerge over the next two postnatal weeks. The cortical slow waves and sleep spindles indicative of quiet (or non-REM) sleep also emerge over the first several weeks. Thus, sleep is constructed in developmental time through a process that is not yet fully understood.

The qualitative changes in sleep across development reveal a truth that is not apparent with a focus only on adults [9]. Namely, the diminished set of sleep components in early infancy and their gradual emergence over time means that no single component is *essential* to define the state. Of course, one might argue that sleep does not truly exist until a designated essential sleep component has emerged, but on what rational basis do we decide which component is more essential than another? The best option is to accept that no single term like "sleep" is able to accurately capture its complexity in all its forms across developmental (and evolutionary) time. For this reason, I have long favored an approach that de-emphasizes whether a particular animal at a given age *has* sleep, and instead focuses on the real-time dynamics underlying the emergence, expression, and coalescence of individual sleep components [11].

The diversity of components comprising sleep suggest a diversity of sleep functions. But the literature is replete with claims about the function of sleep (for dreaming, synaptic homeostasis, avoiding predators, and so on). When I come across such claims, I routinely ask a simple question: Does that proposed function make sense within a developmental context? More often than not, the answer is *no*. In this way, a developmental perspective constrains functional hypotheses about sleep, encouraging the field to move beyond the narrow and unrealistic quest for singular functions. The more productive approach, I believe, is to seek to understand how the diverse components of sleep individually and jointly contribute to function across the lifespan.

To illustrate the points above, consider the twitches of the limbs and whiskers that occur predominantly during active sleep. Based on observations in adults, twitches were long considered functionless by-products of the dreaming brain [12]. This notion never made sense in the context of a newborn animal, but that had little impact on the notion's popularity. However, as is now well established, twitches are particularly abundant in early life, they profoundly shape infant brain activity, and they possess unique spatiotemporal features that make them ideally suited to

Submitted: 23 August, 2025; **Accepted:** 23 September, 2025

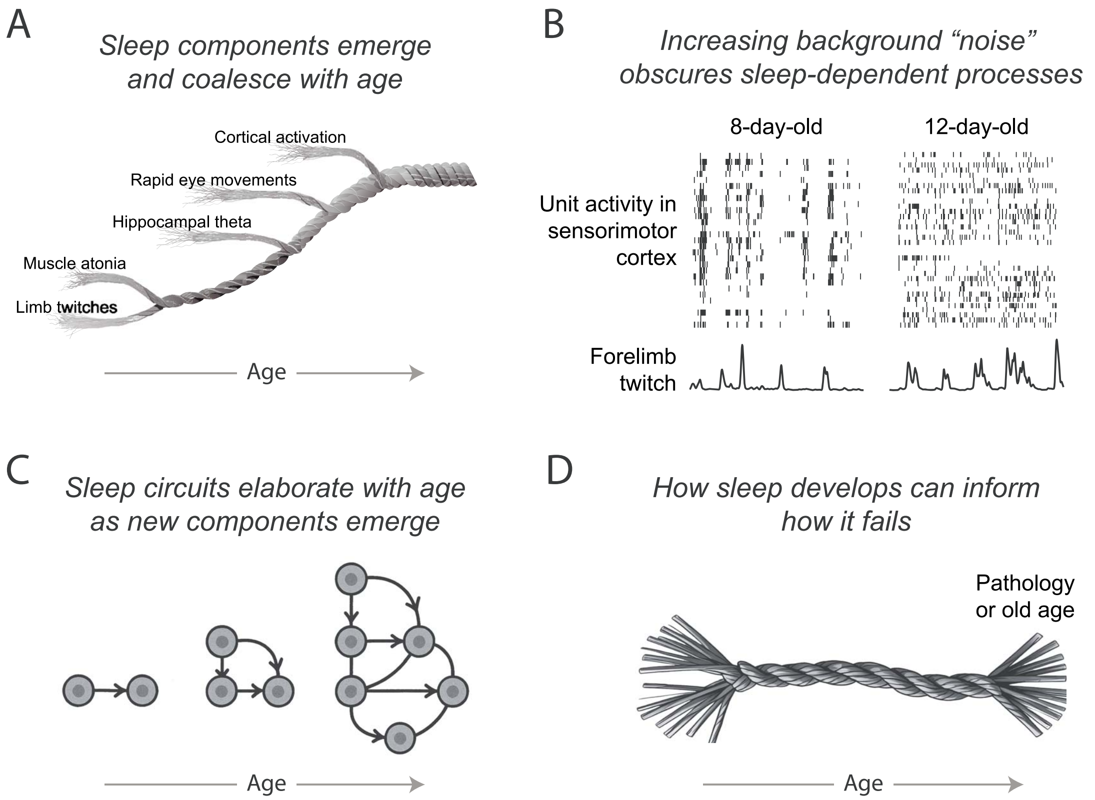

Figure 1. Developmental analysis informs our understanding of sleep. (A) Over the course of development, individual components of active sleep emerge and coalesce, offering an alternative framework for understanding their contributions to sleep regulation and function. The components of quiet sleep exhibit a similar process of developmental emergence. Adapted from [9]. (B) At 12 days of age and into adulthood, continuous cortical activity obscures the relations between twitching and unit activity. But just a few days earlier, cortical activity is discontinuous so that the relations between twitching and neural activity in sensory-responsive cortex is obvious to the naked eye. Adapted from [17]. (C) The neural circuits that regulate sleep elaborate over development, providing unique opportunities to investigate foundational relations among sleep components, their neural control, and their functions. (D) The process by which sleep components develop to form a cohesive state informs how sleep can unravel due to pathology or old age. After [23].

contribute to sensorimotor development—from the refinement of somatotopic maps to the construction of internal models [13,14]. Moreover, insights gleaned from infants can influence interpretations of sleep phenomena in adults. For example, knowledge of the sensory consequences of twitches in infant rats suggests new ways to think about the relations between sleep-related movements and dream activity in human adults with REM sleep behavior disorder [15].

It is no accident that the demise of the by-product hypothesis of twitching came about through investigations in infants. Why? Because infant brains possess unique features that can make it easier to detect phenomena that are obscured in adults. Among these unique features is the discontinuous activity of the infant cerebral cortex, distinguished by population-level bursts of neural activity separated by periods of silence (Figure 1, B). In week-old rats, each bout of limb twitching during active sleep is so obviously related to the intermittent bursts of activity in sensory-responsive cortex that it can be seen with the naked eye [16] (see video here). In contrast, just a few days later when continuous cortical activity has emerged, the relations between twitches and neural activity are now hidden within the background "noise" (see video here); at that age, despite the background activity, nonlinear neural decoding is able to reveal the persistence of the earlier relation [17]. The transition to continuous cortical activity is but one dimension of a process of developmental change that includes the proliferation of inhibitory interneurons [18] and the emergence of brain rhythms, such as delta [19] and theta [20], that promote long-range communication within and between the brainstem and forebrain during quiet and active sleep, respectively.

I am not advocating for an approach that centers on understanding infant sleep at one particular age: The ultimate benefit of developmental analysis for sleep is understanding the processes underlying developmental change. In adults, neuroscientists carefully dissect neural circuits to better understand their contributions to sleep. But infant animals provide a situation in which neural circuits begin in a naturally "dissected" state that can be followed as sleep components emerge, making it possible to reveal how the addition of new components relates to the expression of new behavioral and cognitive capabilities (Figure 1, C). Relatedly, this approach can reveal which neural circuits are necessary and sufficient for the expression of sleep's various components. This appeal to the value of developmental analysis recalls similar arguments for justifying investigations of sleep in relatively "simple" species such as flies, worms, and zebrafish [4,21]. However, investigations of sleep in infant mammals can yield insights into mammalian sleep that investigations in invertebrates and fish cannot.

Finally, a deeper understanding of the processes through which sleep is constructed will also help researchers identify the mechanisms that produce atypical developmental trajectories, including neurodevelopmental and neurodegenerative disorders—because *knowing how sleep is built can provide invaluable insight into how it fails* (Figure 1, D). Central to this approach is identifying those periods of development that are especially sensitive to perturbation [22].

There is still vast and unrealized potential in applying the conceptual and empirical tools of developmental analysis to the science of sleep. I look forward to the day when those tools are fully employed to better understand sleep in all its complexity and diversity.

Acknowledgments

Preparation of this article was made possible by grants from the National Institutes of Health (R01-HD104616; R37-HD081168).

Disclosure statement

Financial disclosure: None.

Non-financial disclosure: No conflicts of interest.

References

1. Tinbergen N. On aims and methods of ethology. *Z Tierpsychol*. 1963;**20**(4):410–433. https://doi.org/10.1111/j.1439-0310.1963.tb01161.x
2. Roffwarg HP, Muzio JN, Dement WC. Ontogenetic development of the human sleep-dream cycle. *Science*. 1966;**152**(3722):604–619. https://doi.org/10.1126/science.152.3722.604
3. Jouvet-Mounier D, Astic L, Lacote D. Ontogenesis of the states of sleep in rat, cat, and guinea pig during the first postnatal month. *Dev Psychobiol*. 1970;**2**(4):216–239. https://doi.org/10.1002/dev.420020407
4. Kayser MS, Biron D. Sleep and development in genetically tractable model organisms. *Genetics*. 2016;**203**(1):21–33. https://doi.org/10.1534/genetics.116.189589
5. Blumberg MS, Dooley JC, Tiriac A. Sleep, plasticity, and sensory neurodevelopment. *Neuron*. 2022;**110**(20):3230–3242. https://doi.org/10.1016/j.neuron.2022.08.005
6. Oyama S, Griffiths PE, Gray RD. *Cycles of Contingency: Developmental Systems and Evolution*. Cambridge, MA: MIT Press; 2003.
7. Blumberg MS. Development evolving: the origins and meanings of instinct. *Wiley Interdiscip Rev Cognitive Sci*. 2016;**8**(1-2):1–9. https://doi.org/10.1002/wcs.1371
8. Johnston T. Developmental systems theory. In: Freeman MS, Freeman JH, Robinson JH, eds. *Oxford Handbook of Developmental Behavioral Neuroscience*. New York: Oxford University Press; 2010: 12–29.
9. Blumberg MS, Lesku JA, Libourel P-A, *et al*. What is REM sleep? *Curr Biol*. 2020;**30**(1):R38–R49. https://doi.org/10.1016/j.cub.2019.11.045
10. Blumberg MS, Gall AJ, Todd WD. The development of sleep–wake rhythms and the search for elemental circuits in the infant brain. *Behav Neurosci*. 2014;**128**(3):250–263. https://doi.org/10.1037/a0035891
11. Blumberg MS, Lucas DE. A developmental and component analysis of active sleep. *Dev Psychobiol*. 1996;**29**(1):1–22. doi:10.1002/(sici)1098-2302(199601)29:1<1::aid-dev1>3.0.co;2-y
12. Blumberg MS. Beyond dreams: do sleep-related movements contribute to brain development? *Front Neurol*. 2010;**1**:140. https://doi.org/10.3389/fneur.2010.00140
13. Blumberg MS, Dooley JC, Sokoloff G. The developing brain revealed during sleep. *Curr Opin Physio*. 2020;**15**:14–22. https://doi.org/10.1016/j.cophys.2019.11.002
14. Dooley JC, Sokoloff G, Blumberg MS. Movements during sleep reveal the developmental emergence of a cerebellar-dependent internal model in motor thalamus. *Curr Biol*. 2021;**31**(24):5501–5511. https://doi.org/10.1016/j.cub.2021.10.014
15. Blumberg MS, Plumeau AM. A new view of “dream enactment” in REM sleep behavior disorder. *Sleep Med Rev*. 2016;**39**:34–42. https://doi.org/10.1016/j.smrv.2015.12.002
16. Glanz RM, Dooley JC, Sokoloff G, *et al*. Sensory coding of limb kinematics in motor cortex across a key developmental transition. *J Neurosci*. 2021;**41**(32):6905–6918. https://doi.org/10.1523/jneurosci.0921-21.2021
17. Glanz R, Sokoloff G, Blumberg MS. Neural decoding reveals specialized kinematic tuning after an abrupt cortical transition. *Cell Rep*. 2023;**42**(9):113119. https://doi.org/10.1016/j.celrep.2023.113119
18. Butt SJ, Stacey JA, Teramoto Y, *et al*. A role for GABAergic interneuron diversity in circuit development and plasticity of the neonatal cerebral cortex. *Curr Opin Neurobiol*. 2017;**43**:149–155. https://doi.org/10.1016/j.conb.2017.03.011
19. Ahmad M, Kim J, Dwyer B, *et al*. Coincident development and synchronization of sleep-dependent delta in the cortex and medulla. *Curr Biol*. 2024;**34**(12):2570–2579.e5. https://doi.org/10.1016/j.cub.2024.04.064
20. Rio-Bermudez CD, Kim J, Sokoloff G, *et al*. Theta oscillations during active sleep synchronize the developing rubro-hippocampal sensorimotor network. *Curr Biol*. 2017;**27**(10):1413–1424. https://doi.org/10.1016/j.cub.2017.03.077
21. Hendricks JC, Sehgal A, Pack AI. The need for a simple animal model to understand sleep. *Prog Neurobiol*. 2000;**61**(4):339–351. https://doi.org/10.1016/S0301-0082(99)00048-9
22. Aton SJ, Seibt J, Dumoulin M, *et al*. Mechanisms of sleep-dependent consolidation of cortical plasticity. *Neuron*. 2009;**61**(3):454–466. https://doi.org/10.1016/j.neuron.2009.01.007
23. Corner MA. Ontogeny of brain sleep mechanisms. In: McGinty DJ, Drucker-Colín R, Morrison A, *et al*., eds. *Brain Mechanisms of Sleep*. New York, NY: Raven Press; 1985:175–197.

SLEEPJ, 2025, **48**, 1–3
https://doi.org/10.1093/sleep/zsaf300
Perspective