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Review

REM-sleep twitching in adults and the maintenance of specialized sensorimotor systems

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SUMMARY

Twitching, an abundant and spontaneous infant behavior and a defining feature of rapid eye movement (REM) sleep, supports development of the sensorimotor system. For unknown reasons, twitching persists into adulthood. Whereas infantile twitches are distributed across all body parts, adult twitching appears to occur more selectively in those appendages used for active sensing, such as elephant trunks, rat whiskers, pig snouts, and raccoon hands. Notably, these specialized appendages also have disproportionately large representations in sensorimotor cortex, a phenomenon known as cortical magnification. We propose that active sensing and cortical magnification — or, more broadly, neural magnification — helps to explain the persistence of twitching in adults. These associations between twitching, active sensing, and neural magnification are likely a subcategory of a broader need to maintain and update vital sensorimotor functions. We contextualize this proposal within an evolutionary–developmental framework, with the functions of twitching shifting across the lifespans of diverse species, including invertebrates that lack a cerebral cortex. This comprehensive theory of twitching may yield new insights into sleep-dependent processes that support the development, calibration, maintenance, and repair of neuroplastic systems across the animal kingdom, and perhaps even inspire new therapeutic approaches for humans after limb amputation, stroke, or other injuries.

Introduction

Spontaneous neural activity occurs throughout the developing nervous system[1]. Although only a portion of that activity produces behavior, most behavior in fetuses and neonates is spontaneous, that is, it occurs in the absence of any discernible external stimuli[2,3]. In addition to spontaneous movements during wake, spontaneous behavior occurs abundantly during rapid eye movement (REM, or active) sleep in the form of discrete twitches across the body[4,5]. In early life, when REM sleep is the predominant behavioral state, twitches are unique in triggering spatiotemporally precise activity throughout the sensorimotor system; consequently, they function as a primary driver of activity-dependent development[4,6]. For good reason, then, it is generally assumed that twitching is only functionally significant during the neonatal period. However, casual observations of adult animals indicate that twitching continues to occur — often with surprising intensity — during REM sleep. Here we ask: why does twitching persist into adulthood?

To answer this question, one might cite the longstanding view that twitching during sleep is merely a by-product of dreams[7,8]. According to this perspective, dream-related motor commands can sometimes ‘leak’ through an REM-sleep system that normally inhibits movement. This interpretation shaped the field for decades and slowed progress in understanding the functional role of twitching, despite early studies of its neural basis[9–13]. By reconsidering the long-dominant notion that dreams occur in isolation from sensory input and motor output — a concept referred to as ‘cranial envatment’ — twitches and other aspects of motor control during sleep are inspiring new insights into the nature of dream experiences[14]. Moreover, even among those who view dreams as products of a brain isolated from the body, dreams and their associated neural processes have been proposed as opportunities to optimize internal models (e.g., Hobson and Friston[15]). These theoretical connections gain further credibility from empirical evidence linking twitching to the development of internal models[16–19].

As to the mystery of why twitching persists into adulthood, a potential answer materialized as we reviewed videos of twitching in vertebrate and invertebrate species across the lifespan. Patterns emerged that suggested a new integrative framework linking the developmental significance of twitching with its expression in adults[20]. Central to this framework are two distinct but complementary phenomena — active sensing and cortical magnification — that shape how animals perceive and interact with their environment.

Active sensing and cortical magnification: the foundation for a new perspective on adult twitching

Eyes saccade, whiskers whisk, fingers probe. Sensations are gathered, not simply absorbed. *Active sensing* captures this

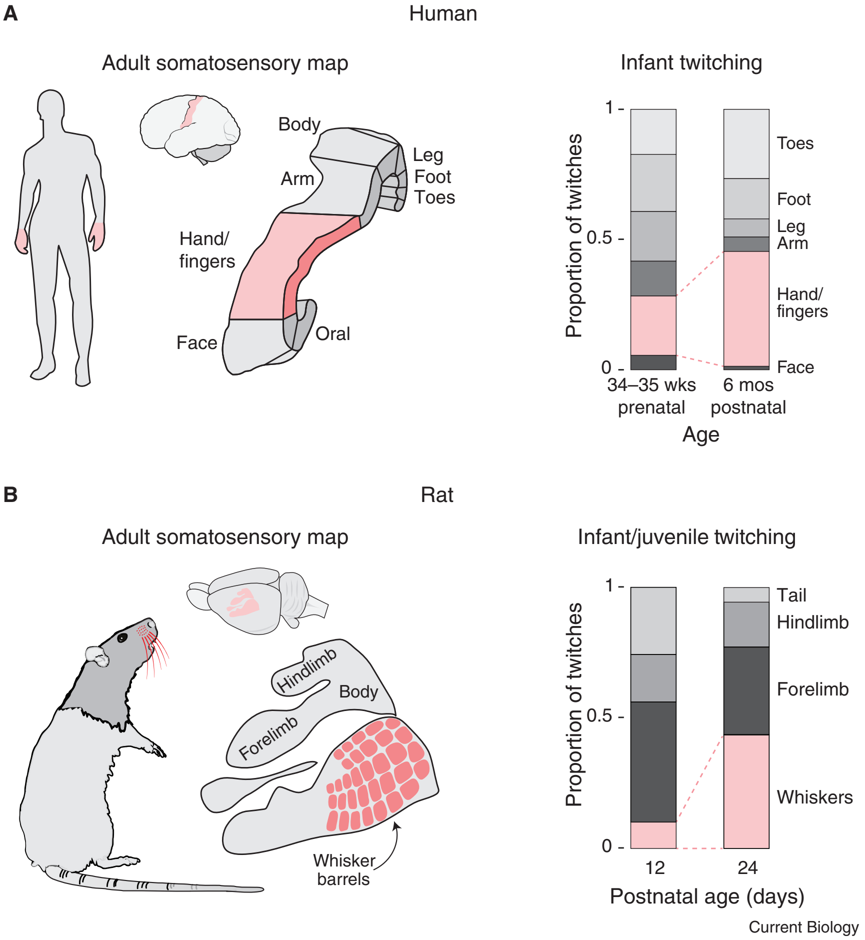

Figure 1. Relations between cortical magnification in adult humans and rats in relation to body-part twitching during REM sleep in early development.

(A) Left: cortical magnification of the hands and fingers (red) in S1 of adult humans. Right: proportion of twitches in the hands and fingers in relation to twitching in other body parts in premature human infants at 34–35 weeks gestational age and in full-term infants at 6 months postnatal age. Human and brain drawings adapted from scidraw.io. Twitching data from Christiansen *et al.*[157] and Sokoloff *et al.*[158]. (B) Left: cortical magnification of the whiskers (red) in barrel S1 of adult rats. Right: proportion of whisker twitches in relation to twitching in other body parts in rats at 12 and 24 days of age. Rat drawing adapted from scidraw.io. Twitching data from Reid *et al.*[31]. Human body (by Zane Mitrevica), human brain and rat body (by Antonis Asiminas) redrawn from Scidraw.io (CC BY 4.0).

process of moving a sensor to shape how sensory information is received and perceived[21–23]. In many species, active sensing demands extraordinarily fast and precise processing, and it often involves exotic appendages — such as elephant trunks — that are morphologically and functionally unique to the species.

Active sensing places enormous computational demands on the nervous system to ensure that the effects of self-motion on sensation are considered. Tracking the movements of a mobile sensor requires sensory input from its muscles (i.e., proprioception) and that the brain informs itself when issuing motor commands (using motor copies, or corollary discharges). *Internal models* enable an animal to predict where its sensors are in space and respond appropriately to salient stimuli in the environment. For example, when a rat uses its whiskers to navigate and identify objects in the dark, it continuously integrates self-motion information from its whiskers, snout, head, and body with the tactile information arising from each whisker as it contacts real-world objects[24].

In addition to providing behaviorally relevant information to the animal, active sensors typically have higher receptor densities than other parts of the body. Together, high receptor densities and behavioral relevance contribute to the disproportionate representation of active sensors in primary somatosensory and motor cortex (S1 and M1, respectively), a phenomenon called *cortical magnification*[25,26]. Using standard brain-mapping techniques, researchers can assess the relative amount of tissue in sensorimotor cortex devoted to each part of the body. When active sensors like human fingers and rat whiskers are mapped, their cortical representations reveal that they are magnified far beyond their actual size (Figure 1). Thus, those body parts that are used for active sensing typically have magnified cortical representations.

As we reviewed videos of twitching in sleeping adult mammals, we noticed that the appendages that seem to twitch the most tend to be those that are used for active sensing and are cortically magnified. Our observations led us to hypothesize that twitching reflects a sleep-dependent system that maintains and calibrates the diverse active sensors that adorn the animal kingdom — from ordinary fingers to the unique elephant trunk.

Central to our hypothesis is the notion that just as REM sleep likely has different functions across the lifespan[27], we should expect the same of a sleep component like twitching. Accordingly, given the prevalence of REM sleep in early life and the abundance of twitch-related neural activity, it is reasonable that twitching would play a critical role in the activity-dependent development, refinement, and maintenance of cortical — and subcortical — maps[4,6]. Later in life, twitching may promote the development of new functions within each limb, as occurs in those species (e.g., humans and other primates) that attain independent use of the fingers for grasping and manipulating objects. An additional role for twitching arises when animals develop cerebellar-dependent internal models that enable movements that are so complex, fast, and precise that reliance on sensory feedback for corrective control is infeasible due to inherent time delays[16–19]. Finally, throughout adulthood as animals learn to use their bodies in new ways and adapt to new circumstances (e.g., weight loss, limb amputation, and stroke), they must update sensorimotor maps and recalibrate internal models. In such circumstances, the ability to recruit a plasticity-promoting mechanism like twitching may be critical.

Twitching in adults and its relation to active sensing and neural magnification

Our understanding of the spatiotemporal patterning of twitching across the body comes from a relatively few detailed studies in infant and adult rats and humans[5,17,28,29]. Developmentally, the rate and patterning of twitching change substantially with age. Whereas twitches in early life are distributed broadly across bouts of REM sleep and across body parts, with age they increasingly concentrate into brief bursts within a select set of body parts. For example, in preterm human infants at 34–35 weeks gestational age, twitching is initially distributed across the entirety of each arm and leg, but in full-term infants at 6 months of age, twitching is largely focused on hands and fingers[5] (Figure 1A). Similarly, in rats over the first postnatal week, twitching is distributed across all four limbs[28,30], but between 12 and 24 days of age, twitching of the limbs and tail decreases as whisker twitching increases[17,31] (Figure 1B).

Thus, twitching seems to persist in those body parts that, in adults, are active sensors and whose neural representations are magnified. However, detailed assessments of twitching across the body do not exist for adult humans or rats — or, for that matter, the adults of any species. Thus, to bolster our hypothesis that adult twitching persists selectively in active sensors, we collected videos of twitching in the adults of diverse species: from published sleep studies, colleagues and friends, public websites (e.g., YouTube), and user-created online communities (e.g., Reddit).

Although videos collected from public domains are a rich and unique source of information, it is important to note their limitations: These videos are often very brief, they may show only a portion of the body, and they typically lack contextual information about the age and health of the animals and the environmental conditions in which they were filmed. The individuals recording these videos may have inherent biases that lead them, for example, to focus on the face. In addition, it is usually necessary to rely on limited information to infer a subject's behavioral state. Nonetheless, even with these limitations, videos of sleeping adult animals are often remarkably informative.

For many species, only one or two brief videos of sleeping adults exist, although even the briefest of videos can provide proof-of-concept evidence. For a few species, especially domesticated ones that live closely with humans, there is plentiful evidence. In many of these videos, beyond the expression of twitching, other behavioral evidence of REM sleep is clear, including a relaxed body posture with limbs resting on the surface, closed eyes (although animals often sleep with their eyes open, sometimes revealing rapid eye movements), and irregular respiration. Occasionally, snoring can be heard.

Below, we describe video evidence of adult twitching across mammalian species and relate these patterns to the sensory or motor specializations of body parts (all video sources can be found in Table S1, published with this article online). Most of the evidence presented here relates to magnification in S1 because it has been more widely investigated than M1 or subcortical structures. Across taxa, a pattern emerges: the structures that engage in active sensing or fine manipulation — and those with magnified neural representations — appear to be those that twitch most prominently during REM sleep.

Whisker-based tactile specialists

Many mammals rely on mobile whiskers to actively sample their environment, and in species that whisk — such as rats, mice, chinchillas, and opossums[24,32] — these appendages are supported by a specialized musculature that enables independent movement (in contrast, many primates and carnivores have prominent whiskers, but with limited mobility)[33,34]. Whisking involves rapid, coordinated forward (protraction) and backward (retraction) movement of the long whiskers on the snout (macrovibrissae) and is a classic form of active sensing. In whisking rodents, including rats, the somatosensory 'barrel cortex' is highly magnified, with each whisker mapped to a cortical barrel that mirrors the snout's layout[35]. In adult rats, the whisker representation is the most expanded region of S1[36] (Figure 1B), and this magnification appears early in development[37]. Importantly, cortical barrels are not synonymous with whisking: opossums whisk without barrels, whereas guinea pigs have barrels but do not whisk[24,38], suggesting that the evolution of independent whisker control — rather than barrel architecture itself — may be central to this specialization.

Across available videos, whisker twitching is especially prominent during REM sleep in whisking species. Adult rats show intense bouts of collective and individual whisker movements, with comparatively fewer twitches elsewhere on the body (External Video 1); chinchillas display a similar pattern (External Video 2), and work in mice during REM sleep provides additional support[39–41]. These observations raise the possibility that species that possess the capacity to twitch individual whiskers in early life[42] retain that capacity into adulthood in service of calibrating and maintaining this exquisite active-sensing system.

Species that rely on short, dense microvibrissae rather than mobile macrovibrissae, such as capybaras, provide an informative contrast. Capybaras are large South American rodents that exhibit cortical magnification of the perioral region used for fine tactile discrimination[43] but they neither whisk[44] nor possess barrels[38]. The enhanced perioral discrimination may support their semi-aquatic lifestyle that includes the selection of high-quality grasses and other plant material[45]. During REM sleep, their most frequent twitches involve the lips and surrounding perioral area rather than their large limbs, macrovibrissae, or pinnae (External Video 3) — once again linking twitching to a sensory specialization.

Non-whisker tactile specialists

Several species have evolved highly mobile, densely innervated rostral structures used for tactile exploration. Pigs, for example, have a flexible, muscular snout (rostrum) equipped with roughly 900 microvibrissae. The microvibrissae are innervated by 80,000 trigeminal axons projecting to millions of cortical neurons, yielding a disproportionately large representation in S1[46,47] (Figure 2A). As we would predict from such a highly magnified structure, sleeping pigs display conspicuous twitching of the snout during sleep (External Video 4).

The platypus provides another example of extreme cortical magnification. Its bill, equipped with a high density of mechanoreceptors and electroreceptors, accounts for approximately 90% of S1 and large regions of other sensory cortical areas[25,48] (Figure 2B). Platypuses use their bill to guide them toward small

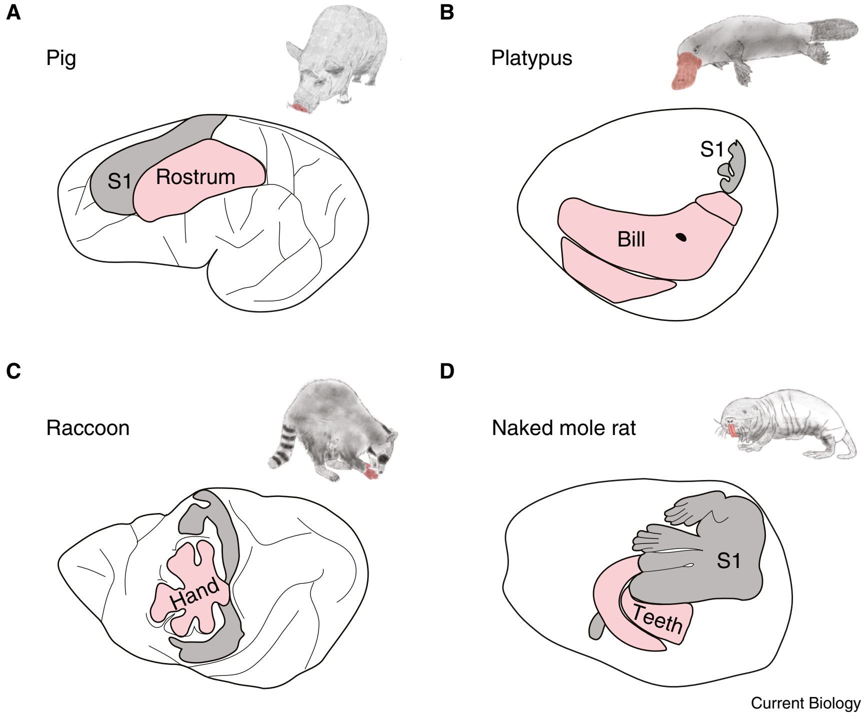

Figure 2. Magnification of the representations in adult S1 for specialized appendages in four mammalian species.
The specialized appendage and its magnified S1 representation are shown in red for (A) the pig's rostrum, (B) the platypus's bill, (C) the raccoon's hand (and fingers), and (D) the naked mole rat's teeth (incisors). S1's representations of other body parts are also shown (grey). Cortical image in (A) adapted from Craner and Ray[47] with additional data from Sauleau *et al.*[159]. Cortical images in (B–D) adapted from Krubitzer and Dooley[141]. Animal drawings by Jacob Horton. Pig brain adapted from Craner and Ray[47] with permission by John Wiley and Sons. Platypus, raccoon, and naked mole rat brains adapted from Krubitzer and Dooley[141] (CC BY 3.0).

invertebrate prey in the water at night when the eyes, ears, and nostrils are shut[49]. These animals are very difficult to observe during sleep, but one study reported very high rates of REM sleep and associated twitching of the bill and head[50] (External Video 5). Thus, despite their evolutionary distance and distinct lifestyles, pigs and platypuses show similar associations between tactile specialization and twitching of the associated body parts.

The star-nosed mole possesses perhaps the most uniquely specialized tactile organ on a snout, sporting 11 pairs of finger-like appendages. All 11 pairs are magnified in S1, but one pair — the one nearest the mouth that is called the 'tactile fovea' — is more magnified than the others[51]. Unfortunately, to our knowledge, no videos of sleeping star-nosed moles exist, but we predict that sleeping adults will show abundant twitching of the star's appendages, especially the pair comprising the tactile fovea. The forelimb claws of this digging species are also oversized and cortically magnified, and so we predict that they will also exhibit prominent twitching.

Manipulative appendages

Many mammals possess specialized appendages adapted for grasping, probing, or digging. Raccoons exemplify fine manual specialization, and their hands and fingers show marked cortical magnification[52,53] (Figure 2C). Like primates, raccoons employ visually guided reaching and grasp food and other objects between their fingers, but their lack of extensive digital manipulation and reliance on bimanual use of their forepaws are typical of carnivores[54]. Videos of sleeping raccoons show clear twitches of the hands and fingers, with fewer twitches occurring in other body parts (External Video 6).

Elephants famously possess a unique and highly specialized manipulative appendage. The trunk is a muscular hydrostat[55] — a non-skeletal structure like the mammalian tongue, the star of star-nosed moles, and cephalopod arms — that provides extraordinary power and dexterity for grasping and manipulating objects, including food. The tip, or 'finger', of the trunk is specialized in both African and Asian elephants[56], with greater dexterity in the former[57]. The trunk and finger have a highly complex system of muscles[58] and is densely innervated by three types of tactile sensors[59,60]. Although cortical magnification of the trunk has not been demonstrated directly, it is strongly suggested by the enormous trigeminal nerve serving the trunk[61] and by the magnified representation of the finger in the principal trigeminal sensory nucleus in the brainstem[62]. Also, the elephant's disproportionately large cerebellum — containing 97.5% of the brain's neurons — likely reflects the trunk's unique motor and sensory demands[63,64]. Consistent with these specializations, twitching of the trunk was observed in Asian elephants, as well as in the legs, tail, and ears, but the movements were not quantified[65]. A video of a sleeping Indian elephant shows trunk twitching, especially near the tip (External Video 7).

Aardvarks are insectivores and expert diggers who use their oversized forelimb claws to search for food and dig extensive tunnel systems[66]. We did not find published research on cortical representations in aardvarks. However, consistent with our other observations, prominent twitching occurs in the claws, including twitches of individual digits (External Video 8).

Echolocating and flying mammals: bats

Bats provide a distinct class of specializations linked to flight and echolocation. Across both microchiropterans (echolocating insectivores) and megachiropterans (primarily frugivores that largely navigate using vision and smell), roughly 20% of S1 is devoted to the wings[67]. Species that rely heavily on acoustic cues, such as the microchiropteran ghost bat, also show enlarged cortical representations of the pinnae[68] (the external projections of ears), and videos of a microchiropteran fringe-lipped bat show REM twitching of the large pinnae and wings (External Video 9). In contrast, Egyptian fruit bats — unique in using tongue clicks for echolocation — display extraordinary cortical magnification of the tongue[69] (41% of S1 and 44% of M1); however, although tongue twitching in this species is plausible, it has not yet been documented.

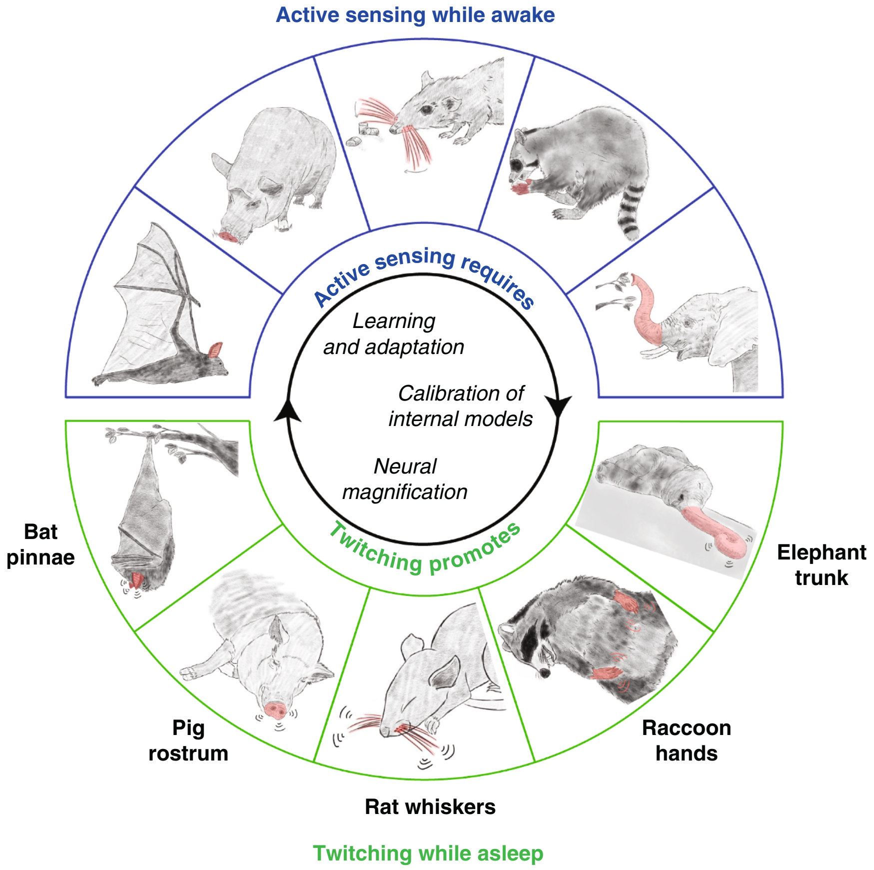

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Figure 3. A comparative framework for understanding the relations between twitching and active sensing in mammals.
Schematic illustration in five mammalian species of how twitching of specialized appendages during sleep (green) relates in an iterative way to the use of those appendages for active sensing during wake (purple). See text for discussion. Animal drawings by Jacob Horton.

Tooth-digging mammals: naked mole rats

The subterranean naked mole rat provides another striking example of anatomical specialization. These small omnivores use their enlarged, externally protruding upper and lower incisors not only for feeding but also for digging, manipulating objects, and relocating young[70]. The lower incisors are uniquely capable of independent movement because the two halves of the lower jaw are flexibly articulated. Remarkably, one-third of their somatosensory cortex represents these incisors[26,71] (Figure 2D). Consistent with this specialization, a video of sleeping naked mole rats shows a brief but clear instance of independent lower-incisor twitching, driven by muscles in the lower jaw (External Video 10).

Twitching beyond active sensing and neural magnification

As striking as the associations are among twitching, active sensing, and neural magnification, they may be a subcategory of a broader phenomenon linking twitching with less specialized forms of species-typical behavior. For example, in ferrets, mapping studies have focused on representations of the forelimbs and digits, but evidence of magnification is lacking[72–74]. Like other burrow-dwelling members of the weasel family, ferrets are prodigious diggers with elongated bodies and short forepaws. Digging is a complex naturalistic behavior that undoubtedly requires complex sensorimotor integration, and videos of sleeping ferrets consistently show long periods of intense forelimb twitching, including twitches of the paws and digits, with seemingly lower rates of twitching in the hindlimbs (External Video 11).

Similar to ferrets, when horses lie down to sleep (which they must do to enter REM sleep) they show vigorous movements of the legs (External Video 12). Leg twitching in these animals may support the maintenance of the precise timing and coordination required for quadrupedal locomotion[75], a requirement shared by all mobile species but especially those carnivores and ungulates that are particularly fast or agile.

In cats, there is some evidence of magnification of the forepaws, including the digits, and face[73,74,76], and dogs appear to show similar patterns of representation[76,77]. Videos of twitching cats (External Video 13) and dogs (External Video 14) reveal movements of the forepaws, including digits, as well as hind legs and face.

These less-exotic — even ordinary — examples of twitching suggest that it plays a role in maintaining spinal and brain circuits that subserve locomotion, digging, and other relatively generic behaviors using non-specialized limbs. Indeed, computational models that incorporate twitch-like activity and Hebbian learning demonstrate that twitching is sufficient to self-organize basic spinal reflex circuits and that, with supraspinal modulation, a diversity of locomotor patterns are produced[78]. As these authors noted, twitch-like activity could be effective for maintaining these sensorimotor circuits across the lifespan and even adapting to morphological changes.

Summary

Across these diverse species, a consistent pattern emerges: the body parts involved in active sensing or fine manipulation — and that exhibit magnified neural representations — seem to twitch most frequently and selectively during REM sleep (Figure 3). Whether the specialization involves whiskers, snouts, hands, trunks, or wings, twitching expresses the sensorimotor priorities of each species. However, as the examples of ferrets, horses, dogs, and cats suggest, these priorities are not limited to active sensing; in such animals, twitching may reflect a broader functional imperative to maintain and update any sensorimotor system that requires high-fidelity control. Thus, at this early stage of understanding — especially given the absence of systematic, quantified analyses of twitching in adults — we should err on the side of caution and remain open to considering a variety of functional roles. Clearly, systematic investigations of species with different morphologies, behaviors, and ecologies will be needed to identify the rules governing the expression of twitching across species.

Twitching and neuroplasticity in humans and other primates across the lifespan

In contrast with what is known about twitching in human infants[5] (Figure 1A), relatively little is known about the rate and patterning of twitching in human adults. Two studies documented the rate of finger twitching[79,80], and several others documented the occurrence of twitching primarily in facial muscles[81–83]. If twitching of the fingers and face are indeed more prevalent than in other body parts, that would align with their cortical magnification[84,85]. It would be especially interesting to know whether facial twitches, particularly of the lips but also — if they occur — of the tongue and other structures specialized for speech, are related to the cortical magnification of speech-related areas in the cortex, including Broca's area[25].

In macaques, the cortical mapping of individual fingers is refined over the first two years[86]. We predict that such refinement will mirror developmental increases in the twitching of individual fingers, as the discreteness of twitching makes it ideally suited to decorrelating sensory input arising from each finger. The significance of decorrelation seems to persist into adulthood: researchers reversibly fused the third and fourth digits of adult owl monkeys and then, months later, mapped their somatosensory cortex[87]. Remarkably, fusing of the two digits produced homologous fusing of their cortical representations, a phenomenon that was attributed to the increased temporal correlation during wake of the sensory information arising from the now-fused digits. However, it may be that twitching during sleep also contributes to this form of neuroplasticity.

There are other aspects of finger and toe twitching that provide insight into the role twitching plays in developmental and experience-dependent neuroplasticity. When animals are born with missing limbs, they become proficient in the use of their remaining limbs in ways that are atypical for the species. The process that makes this dynamic organization possible reflects the inherent plasticity of developing systems[88]. Such species-atypical individuals offer opportunities to probe the relations among anomalous bodies and their neural representations. For example, humans without arms develop the ability to use their feet and toes the way most humans use their hands and fingers. When the cortical map of the toes was assessed in expert foot painters, it exhibited finger-like, individuated somatosensory representations[89]; in contrast, amputation of the arms in adults does not yield individuated toe representations[90]. Because the toes of expert foot painters are enhanced active sensors, we predict that such individuals exhibit toe twitching as infants that persists into adulthood. Further, we propose that the expression of toe twitching in human infants (Figure 1A) contributes to the developmental plasticity that makes expert foot use possible. Perhaps the early expression of toe twitching is a vestige of the evolutionary history of primates and their ability to use feet for grasping[91]. In fact, even in human infants, reaching for objects with feet emerges before reaching with hands[92].

Although rapid eye movements (REMs) are a defining feature of REM sleep in mammals and birds, their functional significance has been investigated most often in human and non-human primates. In human adults, REMs are the most prominent of all sleep-related movements. Although REMs are generally treated separately from twitches, an argument can be made that REMs and twitches are homologous[6]. Indeed, one early hypothesis posited that REMs serve to establish neural pathways involved in the development and evolution of coordinated eye movements for binocular vision[93].

Compelling evidence of a role for REMs in visuomotor plasticity was provided by a study in which human adults wore prisms during the day that severely restricted the visual field to 5 degrees, thereby forcing a decrease in the range of eye movements[94]. Then, at night, subjects exhibited *increased* REMs during sleep without showing changes in the amount of sleep per se; over subsequent nights, the high rate of REMs steadily declined. Other studies in humans[95] and monkeys[96] used behavioral paradigms to alter wake-related eye movements and reported complementary changes in the production of REMs during sleep. Such findings suggest that REMs — and twitches more broadly — are recruited in adults to promote sensorimotor adaptation.

The neural mechanisms related to the production and processing of twitches

The available evidence indicates that the cerebral cortex does not produce twitches in infants[17,30] or adults[10–12]. Accordingly, the brainstem is the primary source of motor control for twitching. In both infant rats[97] and adult cats[10,12], the red nucleus (RN) and its associated rubrospinal tract have received the bulk of the attention, but the reticulospinal and vestibulospinal tracts also contribute significantly[9,11,98,99]. The rubrospinal tract is evolutionarily ancient[100–102]: It is found in cartilaginous fish (e.g., rays) that diverged from the mammalian lineage more than 400 million years ago, and it evolved with the evolution of appendages such as limbs, wings, and fins. In addition to the spinal cord, the RN also projects to the facial motor nucleus[103,104] and thus can drive facial, including whisker, twitching.

The RN is part of a larger group of midbrain motor structures within the mesodiencephalic junction (MDJ), including the nucleus of Darkshewitsch, the interstitial nucleus of Cajal, and the nucleus of Bechterew[105]. Of particular interest here is the proposal that the various MDJ nuclei are selectively enlarged depending on the specialized appendages of a given species[106]. For example, in elephants, the nucleus of Darkshewitsch is enlarged and appears to be specifically involved in dexterous movements of the trunk. Such observations raise the possibility that the twitching of specialized appendages in early development is differentially controlled by MDJ nuclei in a species-specific manner.

Beyond driving movement, the RN and associated structures are a source of corollary discharge to the developing cerebellar system[16–19]. In adults, that system compares corollary discharge with actual sensory feedback to minimize 'sensory prediction errors' to enable the calibration of internal models of movement[107,108]. Because twitches are discrete motor events generated against a backdrop of muscle atonia, they function as biological 'test pulses' for associating motor commands with sensory feedback in a low-noise environment[4]. Thus, twitches are ideally suited to both developing internal models in infants and calibrating them in adults, although the latter possibility has yet to be tested.

Finally, it should be noted that many of the specialized appendages that twitch in adult animals — whiskers, trunk, snout, lips, pinnae, and eyes — are located on the face and head. That location is noteworthy as the muscles that control those appendages are not used for postural support and do not exhibit the REM-sleep 'paralysis' that characterizes that state[109,110]. In contrast, neck and limb muscles are inhibited during REM sleep, as is the muscle that controls the lower jaw; thus, sleep paralysis spans the spinal and cranial motor systems. However, as should now be clear, sleep paralysis does not prevent limb twitching in many adult mammals. Thus, although twitches were once explained as epiphenomena of dream-related motor commands 'leaking through' a barrier of muscle inhibition[111], our view is that twitches are products of a system in which motor commands are coordinated to occur against a backdrop of low muscle tone[8].

Twitching beyond mammals

Much of what we have written thus far about sleep and twitching in mammals applies to other vertebrates, especially birds, and to invertebrates such as flies and cephalopods. These non-mammalian species — with their different body plans and neural architectures — afford opportunities to test the generality of our hypotheses regarding the functional significance of twitching. As with mammals, sleep predominates in early life across non-mammalian species[112]. Leaving aside questions regarding the presence of distinct REM and non-REM sleep in such species[113], there is a clear abundance of sleep in developing birds, fish, flies, and worms[114].

Spontaneous movements are ubiquitous in early development across the animal kingdom[3,115,116]. For example, spontaneous movements in flies begin in the larval stage[117] and continue as sleep-related twitches in young adults[118]; the larval movements are implicated in the development of early neural circuits[119,120]. Similarly, newly hatched jumping spiders twitch their limbs and retinal tubes during sleep[121]. Among vertebrates, the observation of spontaneous movements in fish, amphibians, and reptiles inspired the designation of the associated state as rapid-body-movement (RBM) sleep, a primordial expression of what will later in development be designated as REM sleep in mammals and birds[116].

There is evidence in birds that twitching persists into adulthood. For example, during REM sleep, pigeons exhibit REMs along with twitching of the head and bill[122,123]. As with the manipulative appendages of raccoons and elephants, bill twitching in birds may reflect how the bill is used to grasp and manipulate food and other items, similar to how humans use their thumb and index finger[124]. More surprising is that the pigeon's iris exhibits state-dependent activity: during relaxed wakefulness and non-REM sleep, the pupil is dilated, but during REM sleep it constricts and dilates in rapid bursts, which led the discoverers of this phenomenon to call them 'rapid iris movements' (RIMs)[122]. RIMs do not occur in mammals, which makes sense given that the mammalian iris is composed of smooth muscle; however, the iris of birds is uniquely composed of striated (skeletal) muscle, which raises the possibility of active control. Although it has not been established that birds use the iris for communication or to enhance vision in certain contexts (e.g., social interactions), the co-occurrence of RIMs with a striated iris suggests that these unique pupillary events are homologous with other forms of twitching.

There is no compelling evidence of twitching in any adult species of reptile, amphibian, or fish (Box 1); one recent study failed to detect limb or tail twitching in seven lizard species across the main squamate orders and suborders[125]. In contrast, in adult invertebrates there is antennal and tarsal twitching in honeybees[126] and 'rapid antennal movements' (RAMs) in fire ants[127]. But the most spectacular evidence of invertebrate twitching during sleep is found in cephalopods.

Cephalopods such as octopuses and cuttlefish use their eight arms — cuttlefish also have an extra pair of tentacles — in complex ways to move, capture prey, and manipulate objects[128–131]. As muscular hydrostats, arms require complex control mechanisms to manage the immense degrees of freedom that such appendages entail. Unlike mammals, cephalopods rely on neural mechanisms embedded within the arms themselves for much of their control, with the brain able to generate complex movement patterns[128,129]. In addition, feedforward control strategies are used to generate ballistic movements that do not rely on slow, delayed sensory feedback, indicative of internal models similar to those in mammals. Unlike mammals, however, there is no evidence of somatotopic organization of the arms in the octopus's brain, perhaps due to the high degree of neural autonomy within each of the arms[129].

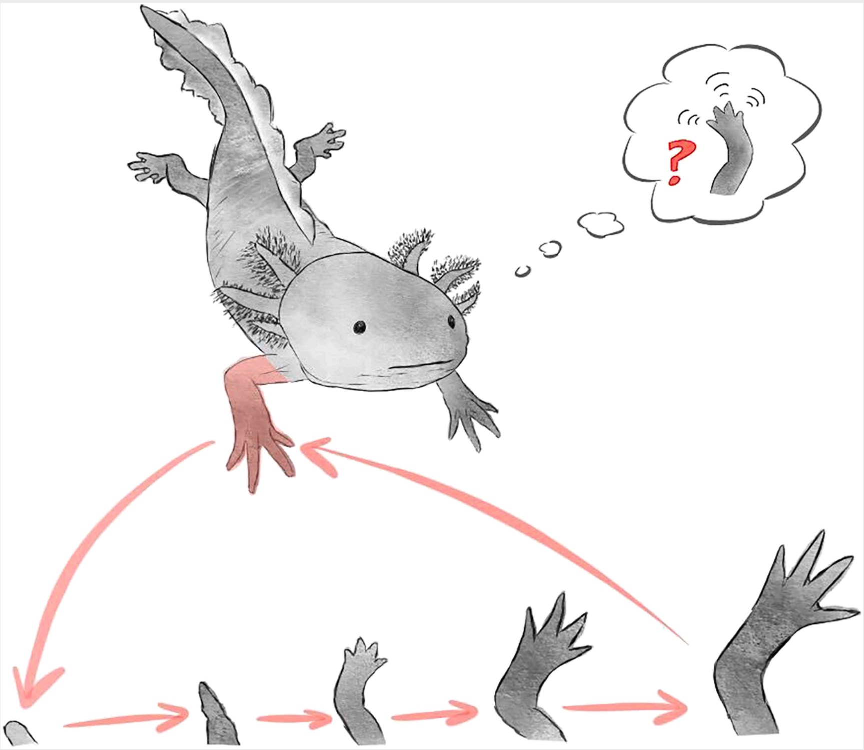
Given the sensorimotor complexity of cuttlefish and octopus behavior, we might expect twitching to occur in these animals — and it does. In cuttlefish before and after hatching, bursts of movements are evident in the arms and head that occur at irregular intervals but at high rates, with twitching persisting into adulthood but at lower rates, reminiscent of the mammalian pattern[132]. In adult cuttlefish and octopuses (External Video 15), twitches of the arms, suckers, and eyes are accompanied by extraordinary displays of phasic-color changes produced by chromatophores, which are pigment-containing sacs controlled by muscle[133–135].

The phasic activity of sleeping cephalopods presents a conundrum for those seeking a straightforward account of the brain circuitry that produces twitches or, indeed, a straightforward evolutionary account of REM sleep itself. On one hand, at least some cephalopod features of sleep seem homologous with REM sleep in mammals. On the other hand, how are we to understand the presence of twitching and other phasic components of REM sleep in invertebrates but their seeming absence in fish, amphibians, and reptiles? One path out of this conundrum is to consider the possibility that twitching has evolved multiple times across diverse species as a mechanism for building and maintaining flexible and adaptive sensorimotor systems. The presence of arm twitching in cephalopods supports such a possibility. So, too, does the fact that roboticists have exploited the unique attributes of twitching to produce behavior that is more flexible and adaptive than when the robot's behavior is hard coded[4,78,136]. Thus, twitching provides a broadly applicable engineering solution to problems shared by complex sensorimotor systems[137].

Conclusions and future directions

The concept of sensory and motor 'maps' emerged in the late 19th century and matured in the 1930s and 1940s with the work of Penfield, Adrian, Woolsey, and others[46,76,138,139]. Although Penfield is credited with the introduction of the 'motor homunculus' based on his work with human patients, what

Box 1. Might twitching help urodele amphibians learn to use regenerating limbs?



Urodele amphibians, including axolotls and salamanders, have the capacity to regenerate lost or injured limbs, thus recruiting in adults a developmental process that occurs when they are embryos[155,156]. Although several invertebrates such as starfish, planarians, and some crustaceans can regenerate complex appendages, urodeles are unique among vertebrates in fully regenerating functional limbs in adulthood. This regenerative capability has intrigued researchers for many decades, in part because of the promise of recreating it in human amputees. Understandably, research in this domain has focused on the molecular mechanisms that enable regeneration.

What remains unexplored, however, is how the limb is functionally integrated with the adult nervous system. One clue regarding that process is that nerve fibers at the site of the wound contribute to regeneration, with the number of nerves at the wound site correlating with the size of the regenerated limb[160]. Whereas experimental manipulations that enhance nerve abundance results in larger regenerated limbs, partial or complete denervation limits growth, suggesting that nerves are active regulators of limb size[160]. Also, urodele limb regeneration goes through a ‘tiny limb’ stage characterized by rapid nerve-dependent growth. Such findings suggest that the central nervous system plays an active role in limb regeneration.

Little is known about the emergence of behavior in regenerating limbs, but early development provides clues. Amphibian embryos produce spontaneous movements that begin as uncoordinated bursts before functional swimming behaviors emerge[161]. These embryonic movements may be homologous to the limb twitches that characterize REM sleep in mammals[113]. Although limb twitching has not been observed in most amphibians, including the tiger salamander, it has been reported in one species of frog[161]; perhaps twitching would be more prominent in tadpoles during metamorphosis as they sprout legs and become froglets. A possible developmental role for twitching in embryos raises the possibility that it is recruited in adults to promote the integration of regenerating limbs with spinal and brain circuits.

stands out from this early work is the interest in mapping cortical representations across diverse mammalian species. In the decades that followed, although the concept of cortical maps took hold and shaped neuroscientific thinking, it has had some critics[140]. Regardless, the evolutionary and developmental features of cortical magnification highlight its intimate connection with body parts that play significant roles in the behavior of individuals and the life histories of species[25,26,141], including roles in active sensing.

Twitching may play a critical role in the process of magnifying the neural representations of active sensors in early development and maintaining their optimal function throughout life. Although cortical magnification has received the greatest attention, the process of magnifying the representations of special body parts begins in subcortical structures, including the brainstem and thalamus. For example, the rodent whisker system comprises barrels in the cortex, barreloids in the thalamus, and barrelettes in the principal trigeminal sensory nucleus[142]. The principal trigeminal sensory nucleus is also the site of magnified representations of the elephant's trunk finger[62] and the star of the star-nosed mole[143]. In addition, somatosensory magnification occurs in subcortical structures outside the core sensory-processing stream, including the superior colliculus[144,145]. Thus, cortical magnification should be viewed as only one aspect of a system in which body parts with heightened behavioral significance are overrepresented.

The components of active sensing emerge and integrate over development. For example, in rats, the ability to perform true whisking does not begin until 11 days of age[146]. Similarly, rats are born with sealed eyelids and immobile eyes, and the eyes only begin to move during the second postnatal week[147]. And it is not until three weeks of age in rats that the cerebellum can compute precise internal models of movement[17]. The early emergence of whisker twitches[42] and rapid eye movements and the contributions of twitching to the development of internal models[16–19] suggest multiple roles for twitching in the development of active sensing. It is not difficult to see how such roles could persist into adulthood, but with an emphasis on maintenance and calibration.

Compelling evidence that such maintenance mechanisms persist into adulthood is provided by recent studies of the head-direction system. In adult mice during REM sleep, REMs accurately predict shifts in 'virtual' heading decoded from thalamic activity[148]. These shifts in virtual heading appear to be driven by motor commands originating in the superior colliculus; unilateral silencing of the colliculus alters the virtual heading exhibited during REM sleep[149]. These findings demonstrate that internal models and neural representations remain active and mutable during REM sleep in adults, driven by specific motor commands. Just as collicular activity updates the brain's internal compass via corollary discharge, twitching likely recruits both corollary discharge and associated sensory feedback to calibrate sensorimotor maps and internal models, as it is known to do in early life[6]. A similar process may also occur in sleeping adult songbirds in which fictive song production at night — comprising activation of the syringeal muscles but without the production of sound — may provide opportunities for maintaining the integrity of the songs produced during the day[150,151].

Beyond the maintenance of existing representations, these mechanisms may also support the acquisition of new ones. Realizing that potential will require systematic investigations of twitching across the body and across the lifespan in a diversity of species to quantitatively assess the associations among twitching, active sensing, and neural representations. Such investigations should assess whether developmental changes in the twitching of special appendages track the developmental magnification of their representations, and whether twitching of those appendages persists into adulthood. By studying motor learning in adults, we can begin to ask whether twitches are recruited to support the acquisition, consolidation, and automatization of new skills, including human athletic and musical expertise.

Finally, our perspective also extends to repair: twitching may be recruited in adult nervous systems after amputation, stroke, or other injuries, a possibility that seems plausible given the remapping that takes place in adult humans[152] and owl monkeys[87] after fusing adjacent fingers. Taking inspiration from studies in adult rats[153,154], it may be possible to promote recovery of function in humans by faithfully mimicking twitch-like activity using invasive (i.e., implanted electrodes) or noninvasive (i.e., transcranial ultrasound) brainstem stimulation[155,156], particularly during periods of REM sleep. Thus, we hope the ideas offered here will spark innovative approaches to unraveling the enduring mystery of why twitching continues beyond development, and why it manifests in such a distinctive manner and form.

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DECLARATION OF INTERESTS

The authors declare no competing interests.

SUPPLEMENTAL INFORMATION

Supplemental information including one table can be found with this article online at https://doi.org/10.1016/j.cub.2026.02.048.

REFERENCES

1. Blankenship, A.G., and Feller, M.B. (2009). Mechanisms underlying spontaneous patterned activity in developing neural circuits. Nat. Rev. Neurosci. *11*, 18–29. https://doi.org/10.1038/nrn2759.
2. Narayanan, C.H., Fox, M.W., and Hamburger, V. (1971). Prenatal development of spontaneous and evoked activity in the rat (Rattus norvegicus albinus). Behaviour *40*, 100–134.
3. Corner, M.A. (1977). Sleep and the beginnings of behavior in the animal kingdom — Studies of ultradian motility cycles in early life. Prog. Neurobiol. *8*, 279–295.
4. Blumberg, M.S., Marques, H.G., and Iida, F. (2013). Twitching in sensorimotor development from sleeping rats to robots. Curr. Biol. *23*, R532–R537. https://doi.org/10.1016/j.cub.2013.04.075.
5. Sokoloff, G., Hickerson, M.M., Wen, R.Y., Tobias, M.E., McMurray, B., and Blumberg, M.S. (2020). Spatiotemporal organization of myoclonic twitching in sleeping human infants. Dev. Psychobiol. *62*, 697–710. https://doi.org/10.1002/dev.21954.
6. Blumberg, M.S., Dooley, J.C., and Tiriac, A. (2022). Sleep, plasticity, and sensory neurodevelopment. Neuron *110*, 3230–3242.
7. Blumberg, M.S. (2010). Beyond dreams: Do sleep-related movements contribute to brain development? Front. Neurol. *1*, 140.
8. Blumberg, M.S., and Plumeau, A.M. (2016). A new view of "dream enactment" in REM sleep behavior disorder. Sleep Med. Rev. *39*, 34–42. https://doi.org/10.1016/j.smrv.2015.12.002.
9. Gassel, M.M., Marchiafava, P.L., and Pompeiano, O. (1964). Phasic changes in muscular activity during desynchronized sleep in unrestrained cats. An analysis of the pattern and organization of myoclonic twitches. Arch. Ital. Biol. *102*, 449–470.
10. Gassel, M., Marchiafava, P., and Pompeiano, O. (1966). Rubrospinal influences during desynchronized sleep. Nature *209*, 1218–1220.
11. Pompeiano, O., and Satoh, T. (1967). Vestibular influences on the red nucleus during sleep. Pflugers Arch. Gesamte Physiol. Menschen Tiere *298*, 159–162. https://doi.org/10.1007/bf00364696.

12. Gassel, M.M., Marchiafava, P.L., and Pompeiano, O. (1965). Activity of the red nucleus during deep desynchronized sleep in unrestrained cats. Arch. Ital. Biol. *103*, 369–396.

13. Morrison, A.R., and Pompeiano, O. (1965). Pyramidal discharge from somatosensory cortex and cortical control of primary afferents during sleep. Arch. Ital. Biol. *103*, 538–568.

14. Windt, J.M. (2018). Predictive brains, dreaming selves, sleeping bodies: how the analysis of dream movement can inform a theory of self- and world-simulation in dreams. Synthese *195*, 2577–2625. https://doi.org/10.1007/s11229-017-1525-6.

15. Hobson, J.A., and Friston, K.J. (2012). Waking and dreaming consciousness: Neurobiological and functional considerations. Prog. Neurobiol. *98*, 82–98. https://doi.org/10.1016/j.pneurobio.2012.05.003.

16. Mukherjee, D., Sokoloff, G., and Blumberg, M.S. (2018). Corollary discharge in precerebellar nuclei of sleeping infant rats. eLife *7*, e38213. https://doi.org/10.7554/elife.38213.001.

17. Dooley, J.C., Sokoloff, G., and Blumberg, M.S. (2021). Movements during sleep reveal the developmental emergence of a cerebellar-dependent internal model in motor thalamus. Curr. Biol. *31*, 5501–5511. https://doi.org/10.1016/j.cub.2021.10.014.

18. Richardson, A.M., Sokoloff, G., and Blumberg, M.S. (2024). Developmentally unique cerebellar processing prioritizes self- over other-generated movements. J. Neurosci. *44*, e2345232024. https://doi.org/10.1523/jneurosci.2345-23.2024.

19. Richardson, A., Sokoloff, G., and Blumberg, M. (2025). A transient feature of the inferior olive supports the development of cerebellar internal models. Preprint at bioRxiv, https://doi.org/10.64898/2025.12.06.692744.

20. Blumberg, M.S., and Dooley, J.C. (2017). Phantom limbs, neuroprosthetics, and the developmental origins of embodiment. Trends Neurosci. *40*, 603–612. https://doi.org/10.1016/j.tins.2017.07.003.

21. Schroeder, C.E., Wilson, D.A., Radman, T., Scharfman, H., and Lakatos, P. (2010). Dynamics of active sensing and perceptual selection. Curr. Opin. Neurobiol. *20*, 172–176. https://doi.org/10.1016/j.conb.2010.02.010.

22. Prescott, T.J., Diamond, M.E., and Wing, A.M. (2011). Active touch sensing. Philos. Trans. R. Soc. Lond. B Biol. Sci. *366*, 2989–2995. https://doi.org/10.1098/rstb.2011.0167.

23. Yang, S.C.-H., Wolpert, D.M., and Lengyel, M. (2016). Theoretical perspectives on active sensing. Curr. Opin. Behav. Sci. *11*, 100–108. https://doi.org/10.1016/j.cobeha.2016.06.009.

24. Mitchinson, B., Grant, R.A., Arkley, K., Rankov, V., Perkon, I., and Prescott, T.J. (2011). Active vibrissal sensing in rodents and marsupials. Philos. Trans. R. Soc. Lond. B Biol. Sci. *366*, 3037–3048. https://doi.org/10.1098/rstb.2011.0156.

25. Krubitzer, L. (2007). The magnificent compromise: cortical field evolution in mammals. Neuron *56*, 201–208.

26. Catania, K.C. (2007). Evolution of the somatosensory system — Clues from specialized species. In Evolution of Nervous Systems. Volume 3 — Mammals, J.H. Kaas, and L.A. Krubitzer, eds. (Academic Press), pp. 189–206. https://doi.org/10.1016/b0-12-370878-8/00067-7.

27. Cao, J., Herman, A.B., West, G.B., Poe, G., and Savage, V.M. (2020). Unraveling why we sleep: Quantitative analysis reveals abrupt transition from neural reorganization to repair in early development. Sci. Adv. *6*, eaba0398. https://doi.org/10.1126/sciadv.aba0398.

28. Blumberg, M.S., Coleman, C.M., Gerth, A.I., and McMurray, B. (2013). Spatiotemporal structure of REM sleep twitching reveals developmental origins of motor synergies. Curr. Biol. *23*, 2100–2109. https://doi.org/10.1016/j.cub.2013.08.055.

29. Sokoloff, G., Dooley, J.C., Glanz, R.M., Wen, R.Y., Hickerson, M.M., Evans, L.G., Laughlin, H.M., Apfelbaum, K.S., and Blumberg, M.S. (2021). Twitches emerge postnatally during quiet sleep in human infants and are synchronized with sleep spindles. Curr. Biol. *31*, 3426–3432.e4. https://doi.org/10.1016/j.cub.2021.05.038.

30. Kreider, J., and Blumberg, M.S. (2000). Mesopontine contribution to the expression of active ‘‘twitch’’ sleep in decerebrate week-old rats. Brain Res. *872*, 149–159.

31. Reid, M.R., Sattler, N.J., and Dooley, J.C. (2025). Subcortically generated movements activate motor cortex during sleep and wake in rats through postnatal day 24. Preprint at bioRxiv, https://doi.org/10.1101/2025.01.26.634890.

32. Grant, R.A., Breakell, V., and Prescott, T.J. (2018). Whisker touch sensing guides locomotion in small, quadrupedal mammals. Proc. R. Soc. B *285*, 20180592. https://doi.org/10.1098/rspb.2018.0592.

33. Dörfl, J. (1982). The musculature of the mystacial vibrissae of the white mouse. J. Anat. *135*, 147–154.

34. Mitchinson, B., Martin, C.J., Grant, R.A., and Prescott, T.J. (2007). Feedback control in active sensing: rat exploratory whisking is modulated by environmental contact. Proc. R. Soc. B Biol. Sci. *274*, 1035–1041. https://doi.org/10.1098/rspb.2006.0347.

35. Petersen, C.C.H. (2007). The functional organization of the barrel cortex. Neuron *56*, 339–355.

36. Chapin, J.K., and Lin, C. (1984). Mapping the body representation in the SI cortex of anesthetized and awake rats. J. Comp. Neurol. *229*, 199–213. https://doi.org/10.1002/cne.902290206.

37. Seelke, A.M.H., Dooley, J.C., and Krubitzer, L.A. (2012). The emergence of somatotopic maps of the body in S1 in rats: The correspondence between functional and anatomical organization. PLoS One *7*, e32322. https://doi.org/10.1371/journal.pone.0032322.t006.

38. Woolsey, T., Welker, C., and Schwartz, R. (1975). Comparative anatomical studies of the SmI face cortex in special reference to the barrels. J. Comp. Neurol. *164*, 79–94.

39. Dong, Y., Li, J., Zhou, M., Du, Y., and Liu, D. (2022). Cortical regulation of two-stage rapid eye movement sleep. Nat. Neurosci. *25*, 1675–1682. https://doi.org/10.1038/s41593-022-01195-2.

40. Bueno-Junior, L.S., Ruckstuhl, M.S., Lim, M.M., and Watson, B.O. (2023). The temporal structure of REM sleep shows minute-scale fluctuations across brain and body in mice and humans. Proc. Natl. Acad. Sci. USA *120*, e2213438120. https://doi.org/10.1073/pnas.2213438120.

41. Boscher, F., Jumel, K., Dvořáková, T., Gentet, L., and Urbain, N. (2024). Thalamocortical dynamics during rapid eye movement sleep in the mouse somatosensory pathway. J. Neurosci. *44*, e0158242024. https://doi.org/10.1523/jneurosci.0158-24.2024.

42. Tiriac, A., Uitermarkt, B.D., Fanning, A.S., Sokoloff, G., and Blumberg, M.S. (2012). Rapid whisker movements in sleeping newborn rats. Curr. Biol. *22*, 2075–2080. https://doi.org/10.1016/j.cub.2012.09.009.

43. Campos, G.B., and Welker, W.I. (1976). Comparisons between brains of a large and a small hystricomorph rodent: Capybara, hydrochoerus and guinea pig, cavia; Neocortical projection regions and measurements of brain subdivisions. Brain Behav. Evol. *13*, 243–266. https://doi.org/10.1159/000123814.

44. Welker, W.I. (1964). Analysis of sniffing of the albino rat. Behaviour *22*, 223–244.

45. Pineda, C.R., Bresee, C., Baldwin, M.K.L., Seelke, A.M.H., Krubitzer, L., and Krubitzer, L. (2025). Organization of the perioral representation of the primary somatosensory cortex in prairie voles (Microtus ochrogaster). Brain Behav. Evol. *100*, 139–155. https://doi.org/10.1159/000543248.

46. Adrian, E.D. (1943). Afferent areas in the brain of ungulates. Brain *66*, 89–103. https://doi.org/10.1093/brain/66.2.89.

47. Craner, S.L., and Ray, R.H. (1991). Somatosensory cortex of the neonatal pig: I. Topographic organization of the primary somatosensory cortex (SI). J. Comp. Neurol. *306*, 24–38. https://doi.org/10.1002/cne.903060103.

48. Krubitzer, L., Manger, P., Pettigrew, J., and Calford, M. (1995). Organization of somatosensory cortex in monotremes: In search of the prototypical plan. J. Comp. Neurol. *351*, 261–306. https://doi.org/10.1002/cne.903510206.

49. Pettigrew, J.D. (1999). Electroreception in monotremes. J. Exp. Biol. *202*, 1447–1454. https://doi.org/10.1242/jeb.202.10.1447.

50. Siegel, J.M., Manger, P.R., Nienhuis, R., Fahringer, H.M., Shalita, T., and Pettigrew, J.D. (1999). Sleep in the platypus. Neuroscience *91*, 391–400. https://doi.org/10.1016/s0306-4522(98)00588-0.

51. Catania, K.C. (2011). The sense of touch in the star-nosed mole: from mechanoreceptors to the brain. Philos. Trans. R. Soc. Lond. B Biol. Sci. *366*, 3016–3025. https://doi.org/10.1098/rstb.2011.0128.

52. Herron, P. (1978). Somatotopic organization of mechanosensory projections to SII cerebral neocortex in the raccoon (Procyon lotor). J. Comp. Neurol. *181*, 717–727. https://doi.org/10.1002/cne.901810403.

53. Welker, W.I., and Seidenstein, S. (1959). Somatic sensory representation in the cerebral cortex of the raccoon. J. Comp. Neurol. *111*, 469–501.

54. Iwaniuk, A.N., and Whishaw, I.Q. (1999). How skilled are the skilled limb movements of the raccoon (Procyon lotor)? Behav. Brain Res. *99*, 35–44. https://doi.org/10.1016/s0166-4328(98)00067-9.

55. Kier, W.M., and Smith, K.K. (1985). Tongues, tentacles and trunks: the biomechanics of movement in muscular-hydrostats. Zool. J. Linn. Soc. *83*, 307–324. https://doi.org/10.1111/j.1096-3642.1985.tb01178.x.

56. Racine, R.N. (1980). Behavior associated with feeding in captive African and Asian elephants. Elephant *1*, 57–71. https://doi.org/10.22237/elephant/1521731845.

57. Kaufmann, L.V., Schneeweiß, U., Maier, E., Hildebrandt, T., and Brecht, M. (2022). Elephant facial motor control. Sci. Adv. *8*, eabq2789. https://doi.org/10.1126/sciadv.abq2789.

58. Longren, L.L., Eigen, L., Shubitidze, A., Lieschnegg, O., Baum, D., Nyakatura, J.A., Hildebrandt, T., and Brecht, M. (2023). Dense reconstruction of elephant trunk musculature. Curr. Biol. *33*, 4713–4720.e3. https://doi.org/10.1016/j.cub.2023.09.007.

59. Rasmussen, L.E.L., and Munger, B.L. (1996). The sensorineural specializations of the trunk tip (finger) of the asian elephant, elephas maximus. Anat. Rec. *246*, 127–134. https://doi.org/10.1002/(SICI)1097-0185(199609)246:1<127::AID-AR14>3.0.CO;2-R.

60. Deiringer, N., Schneeweiß, U., Kaufmann, L.V., Eigen, L., Speissegger, C., Gerhardt, B., Holtze, S., Fritsch, G., Göritz, F., Becker, R., *et al.* (2023). The functional anatomy of elephant trunk whiskers. Commun. Biol. *6*, 591. https://doi.org/10.1038/s42003-023-04945-5.

61. Purkart, L., Tuff, J.M., Shah, M., Kaufmann, L.V., Altringer, C., Maier, E., Schneeweiß, U., Tunckol, E., Eigen, L., Holtze, S., *et al.* (2022). Trigeminal ganglion and sensory nerves suggest tactile specialization of elephants. Curr. Biol. *32*, 904–910.e3. https://doi.org/10.1016/j.cub.2021.12.051.

62. Reveyaz, N., Schneeweiß, U., Heise, O., Gerhardt, B., Gui, A.M., Kaufmann, L.V., Alfken, J., Reichmann, J., Salditt, T., Hildebrandt, T., *et al.* (2024). A myelin map of trunk folds in the elephant trigeminal nucleus. eLife *13*, RP94142. https://doi.org/10.7554/elife.94142.

63. Herculano-Houzel, S., Avelino-de-Souza, K., Neves, K., Porfírio, J., Messeder, D., Feijó, L.M., Maldonado, J., and Manger, P.R. (2014). The elephant brain in numbers. Front. Neuroanat. *8*, 46. https://doi.org/10.3389/fnana.2014.00046.

64. Maseko, B.C., Spocter, M.A., Haagensen, M., and Manger, P.R. (2012). Elephants have relatively the largest cerebellum size of mammals. Anat. Rec. Adv. Integr. Anat. Evol. Biol. *295*, 661–672. https://doi.org/10.1002/ar.22425.

65. Tobler, I. (1992). Behavioral sleep in the Asian elephant in captivity. Sleep *15*, 1–12. https://doi.org/10.1093/sleep/15.1.1.

66. Melton, D.A. (2008). The biology of aardvark (Tubulidentata-Orycteropodidae). Mammal Rev. *6*, 75–88. https://doi.org/10.1111/j.1365-2907.1976.tb00204.x.

67. Calford, M.B., Graydon, M.L., Huerta, M.F., Kaas, J.H., and Pettigrew, J.D. (1985). A variant of the mammalian somatotopic map in a bat. Nature *313*, 477–479. https://doi.org/10.1038/313477a0.

68. Wise, L.Z., Pettigrew, J.D., and Calford, M.B. (1986). Somatosensory cortical representation in the Australian ghost bat, Macroderma gigas. J. Comp. Neurol. *248*, 257–262. https://doi.org/10.1002/cne.902480208.

69. Halley, A.C., Baldwin, M.K.L., Cooke, D.F., Englund, M., Pineda, C.R., Schmid, T., Yartsev, M.M., and Krubitzer, L. (2022). Coevolution of motor cortex and behavioral specializations associated with flight and echolocation in bats. Curr. Biol. *32*, 2935–2941.e3. https://doi.org/10.1016/j.cub.2022.04.094.

70. Catania, K.C., and Remple, M.S. (2002). Somatosensory cortex dominated by the representation of teeth in the naked mole-rat brain. Proc. Natl. Acad. Sci. USA *99*, 5692–5697. https://doi.org/10.1073/pnas.072097999.

71. Henry, E.C., Remple, M.S., O'Riain, M.J., and Catania, K.C. (2006). Organization of somatosensory cortical areas in the naked mole-rat (Heterocephalus glaber). J. Comp. Neurol. *495*, 434–452. https://doi.org/10.1002/cne.20883.

72. McLaughlin, D., Sonty, R.V., and Juliano, S.L. (1998). Organization of the forepaw representation in ferret somatosensory cortex. Somatosens. Mot. Res. *15*, 253–268. https://doi.org/10.1080/08990229870673.

73. Dykes, R.W., and Gabor, A. (1981). Magnification functions and receptive field sequences for submodality-specific bands in SI cortex of cats. J. Comp. Neurol. *202*, 597–620. https://doi.org/10.1002/cne.902020411.

74. Morse, R.W., Adkins, R.J., and Towe, A.L. (1965). Population and modality characteristics of neurons in the coronal region of somatosensory area I of the cat. Exp. Neurol. *11*, 419–440. https://doi.org/10.1016/0014-4886(65)90057-9.

75. Dickinson, M.H., Farley, C.T., Full, R.J., Koehl, M.A.R., Kram, R., and Lehman, S. (2000). How animals move: An integrative view. Science *288*, 100–106. https://doi.org/10.1126/science.288.5463.100.

76. Adrian, E.D. (1941). Afferent discharges to the cerebral cortex from peripheral sense organs. J. Physiol. *100*, 159–191. https://doi.org/10.1113/jphysiol.1941.sp003932.

77. Hamuy, T.P., Bromiley, R.B., and Woolsey, C.N. (1956). Somatic afferent areas I and II of dog's cerebral cortex. J. Neurophysiol. *19*, 485–499.

78. Marques, H.G., Bharadwaj, A., and Iida, F. (2014). From spontaneous motor activity to coordinated behaviour: A developmental model. PLoS Comput. Biol. *10*, e1003653. https://doi.org/10.1371/journal.pcbi.1003653.

79. Reiter, A.M., Roach, G.D., Sargent, C., and Lack, L. (2020). Finger twitches are more frequent in REM sleep than in non-REM sleep. Nat. Sci. Sleep *12*, 49–56. https://doi.org/10.2147/nss.s233439.

80. Stoyva, J.M. (1965). Finger electromyographic activity during sleep: Its relation to dreaming in deaf and normal subjects. J. Abnorm. Psychol. *70*, 343–349. https://doi.org/10.1037/h0022511.

81. Gennaro, L.D., Ferrara, M., and Bertini, M. (2000). Muscle twitch activity during REM sleep: Effect of sleep deprivation and relation with rapid eye movement activity. Psychobiology *28*, 432–436.

82. Rivera-García, A.P., RamÍres-Salado, I., Corsi-Cabrera, M., and Calvo, J.M. (2011). Facial muscle activation during sleep and its relation to the rapid eye movements of REM sleep. J. Sleep Res. *20*, 82–91. https://doi.org/10.1111/j.1365-2869.2010.00853.x.

83. Baldridge, B.J., Whitman, R.M., and Kramer, M. (1965). The concurrence of fine muscle activity and rapid eye movements during sleep. Psychosom. Med. *27*, 19–26. https://doi.org/10.1097/00006842-196501000-00003.

84. Saadon-Grosman, N., Loewenstein, Y., and Arzy, S. (2020). The 'creatures' of the human cortical somatosensory system. Brain Commun. *2*, fcaa003. https://doi.org/10.1093/braincomms/fcaa003.

85. Sutherling, W.W., Levesque, M.F., and Baumgartner, C. (1992). Cortical sensory representation of the human hand: Size of finger regions and nonoverlapping digit somatotopy. Neurology *42*, 1020. https://doi.org/10.1212/wnl.42.5.1020.

86. Arcaro, M.J., Schade, P.F., and Livingstone, M.S. (2019). Body map proto-organization in newborn macaques. Proc. Natl. Acad. Sci. USA *116*, 24861–24871. https://doi.org/10.1073/pnas.1912636116.

87. Allard, T., Clark, S., Jenkins, W., and Merzenich, M. (1991). Reorganization of somatosensory area 3b representations in adult owl monkeys after digital syndactyly. J. Neurophysiol. *66*, 1048–1058.

88. Blumberg, M.S. (2009). Freaks of Nature: What Anomalies Tell Us About Development and Evolution (Oxford University Press).

89. Dempsey-Jones, H., Wesselink, D.B., Friedman, J., and Makin, T.R. (2019). Organized toe maps in extreme foot users. Cell Rep. *28*, 2748–2756.e4. https://doi.org/10.1016/j.celrep.2019.08.027.

90. Schone, H.R., Maimon-Mor, R.O., Kollamkulam, M., Szymanska, M.A., Gerrand, C., Woollard, A., Kang, N.V., Baker, C.I., and Makin, T.R. (2025). Stable cortical body maps before and after arm amputation. Nat. Neurosci. *28*, 2015–2021. https://doi.org/10.1038/s41593-025-02037-7.

91. Patel, B.A., Wallace, I.J., Boyer, D.M., Granatosky, M.C., Larson, S.G., and Stern, J.T. (2015). Distinct functional roles of primate grasping hands and feet during arboreal quadrupedal locomotion. J. Hum. Evol. *88*, 79–84. https://doi.org/10.1016/j.jhevol.2015.09.004.

92. Galloway, J.C., and Thelen, E. (2004). Feet first: object exploration in young infants. Infant Behav. Dev. *27*, 107–112. https://doi.org/10.1016/j.infbeh.2003.06.001.

93. Berger, R.J. (1969). Oculomotor control: A possible function of REM sleep. Psychol. Rev. *76*, 144–164. https://doi.org/10.1037/h0027235.

94. Herman, J., and Roffwarg, H. (1983). Modifying oculomotor activity in awake subjects increases the amplitude of eye movements during REM sleep. Science *220*, 1074–1076.

95. Gennaro, L.D., Casagrande, M., Violani, C., Giovanni, M.D., Herman, J., and Bertini, M. (1995). The complementary relationship between waking and REM sleep in the oculomotor system: an increase of rightward saccades during waking causes a decrease of rightward eye movements during REM sleep. Electroencephalogr. Clin. Neurophysiol. *95*, 252–256. https://doi.org/10.1016/0013-4694(95)00090-l.

96. Berger, R.J. (1968). Characteristics of REM sleep following different conditioned rates of waking eye movement in the monkey. Percept. Mot. Ski. *27*, 99–117. https://doi.org/10.2466/pms.1968.27.1.99.

97. Rio-Bermudez, C.D., Sokoloff, G., and Blumberg, M.S. (2015). Sensorimotor processing in the newborn rat red nucleus during active sleep. J. Neurosci. *35*, 8322–8332. https://doi.org/10.1523/jneurosci.0564-15.2015.

98. Pompeiano, O., and Morrison, A.R. (1965). Vestibular influences during sleep. I. Abolition of the rapid eye movements of desynchronized sleep following vestibular lesions. Arch. Ital. Biol. *103*, 569–595.

99. Morrison, A.R., and Pompeiano, O. (1966). Vestibular influences during sleep. II. Effects of vestibular lesions on the pyramidal discharge during desynchronized sleep. Arch. Ital. Biol. *104*, 214–230.

100. Donkelaar, H.T. (1988). Evolution of the red nucleus and rubrospinal tract. Behav. Brain Res. *28*, 9–20.

101. Olivares-Moreno, R., Rodriguez-Moreno, P., Lopez-Virgen, V., Macías, M., Altamira-Camacho, M., and Rojas-Piloni, G. (2021). Corticospinal vs rubrospinal revisited: An evolutionary perspective for sensorimotor integration. Front. Neurosci. *15*, 686481. https://doi.org/10.3389/fnins.2021.686481.

102. Basile, G.A., Quartu, M., Bertino, S., Serra, M.P., Boi, M., Bramanti, A., Anastasi, G.P., Milardi, D., and Cacciola, A. (2021). Red nucleus structure and function: from anatomy to clinical neurosciences. Brain Struct. Funct. *226*, 69–91. https://doi.org/10.1007/s00429-020-02171-x.

103. Pong, M., Horn, K.M., and Gibson, A.R. (2008). Pathways for control of face and neck musculature by the basal ganglia and cerebellum. Brain Res. Rev. *58*, 249–264. https://doi.org/10.1016/j.brainresrev.2007.11.006.

104. Isokawa-Akesson, M., and Komisaruk, B.R. (1987). Difference in projections to the lateral and medial facial nucleus: anatomically separate pathways for rhythmical vibrissa movement in rats. Exp. Brain Res. *65*, 385–398. https://doi.org/10.1007/bf00236312.

105. Onodera, S., and Hicks, T.P. (2009). A comparative neuroanatomical study of the red nucleus of the cat, macaque and human. PLoS One *4*, e6623. https://doi.org/10.1371/journal.pone.0006623.

106. Onodera, S., and Hicks, T.P. (1999). Evolution of the motor system: Why the elephant's trunk works like a human's hand. Neuroscientist *5*, 217–226. https://doi.org/10.1177/107385849900500411.

107. Wolpert, D.M., Miall, C.R., and Kawato, M. (1998). Internal models in the cerebellum. Trends Cogn. Sci. *2*, 338–347.

108. Shadmehr, R., Smith, M.A., and Krakauer, J.W. (2010). Error correction, sensory prediction, and adaptation in motor control. Annu. Rev. Neurosci. *33*, 89–108. https://doi.org/10.1146/annurev-neuro-060909-153135.

109. Rivera-García, A.P., Ramírez-Salado, I., Corsi-Cabrera, M., and Calvo, J.M. (2011). Facial muscle activation during sleep and its relation to the rapid eye movements of REM sleep. J. Sleep Res. *20*, 82–91. https://doi.org/10.1111/j.1365-2869.2010.00853.x.

110. Bliwise, D., Coleman, R., Bergmann, B., Wincor, M.Z., Pivii, R.T., and Rechtschaffen, A. (1974). Facial muscle tonus during REM and NREM sleep. Psychophysiology *11*, 497–508. https://doi.org/10.1111/j.1469-8986.1974.tb00578.x.

111. Chase, M., and Morales, F. (1990). The atonia and myoclonia of active (REM) sleep. Annu. Rev. Psychol. *41*, 557–584.

112. Blumberg, M.S., Ungurean, G., and Rattenborg, N. (2025). Developmental and comparative insights into the origins and functions of sleep. In Evolution of Nervous Systems, third edition, J.H. Kaas, and S. Herculano-Houzel, eds. (Academic Press), pp. 269–297.

113. Blumberg, M.S., Lesku, J.A., Libourel, P.-A., Schmidt, M.H., and Rattenborg, N.C. (2020). What Is REM sleep? Curr. Biol. *30*, R38–R49. https://doi.org/10.1016/j.cub.2019.11.045.

114. Kayser, M.S., and Biron, D. (2016). Sleep and development in genetically tractable model organisms. Genetics *203*, 21–33. https://doi.org/10.1534/genetics.116.189589.

115. Corner, M.A. (2013). Call it sleep — what animals without backbones can tell us about the phylogeny of intrinsically generated neuromotor rhythms during early development. Neurosci. Bull. *29*, 373–380. https://doi.org/10.1007/s12264-013-1313-3.

116. Corner, M.A., and Schenck, C.H. (2015). Perchance to dream? Primordial motor activity patterns in vertebrates from fish to mammals: their prenatal origin, postnatal persistence during sleep, and pathological reemergence during REM sleep behavior disorder. Neurosci. Bull. *31*, 649–662. https://doi.org/10.1007/s12264-015-1557-1.

117. Crisp, S., Evers, J.F., Fiala, A., and Bate, M. (2008). The development of motor coordination in Drosophila embryos. Development *135*, 3707–3717. https://doi.org/10.1242/dev.026773.

118. Dilley, L.C., Vigderman, A., Williams, C.E., and Kayser, M.S. (2018). Behavioral and genetic features of sleep ontogeny in Drosophila. Sleep *152*, 604–611. https://doi.org/10.1093/sleep/zsy086.

119. Zeng, X., Komanome, Y., Kawasaki, T., Inada, K., Jonaitis, J., Pulver, S.R., Kazama, H., and Nose, A. (2021). An electrically coupled pioneer circuit enables motor development via proprioceptive feedback in Drosophila embryos. Curr. Biol. *31*, 5327–5340.e5. https://doi.org/10.1016/j.cub.2021.10.005.

120. Carreira-Rosario, A., York, R.A., Choi, M., Doe, C.Q., and Clandinin, T.R. (2021). Mechanosensory input during circuit formation shapes Drosophila motor behavior through patterned spontaneous network activity. Curr. Biol. *31*, 5341–5349. https://doi.org/10.1016/j.cub.2021.08.022.

121. Rößler, D.C., Kim, K., Agrò, M.D., Jordan, A., Galizia, C.G., and Shamble, P.S. (2022). Regularly occurring bouts of retinal movements suggest an REM sleep–like state in jumping spiders. Proc. Natl. Acad. Sci. USA *119*, e2204754119. https://doi.org/10.1073/pnas.2204754119.

122. Ungurean, G., Martinez-Gonzalez, D., Massot, B., Libourel, P.-A., and Rattenborg, N.C. (2021). Pupillary behavior during wakefulness, non-REM sleep, and REM sleep in birds is opposite that of mammals. Curr. Biol. *31*, 5370–5376.e4. https://doi.org/10.1016/j.cub.2021.09.060.

123. Ungurean, G., Behroozi, M., Böger, L., Helluy, X., Libourel, P.-A., Güntürkün, O., and Rattenborg, N.C. (2023). Wide-spread brain activation and reduced CSF flow during avian REM sleep. Nat. Commun. *14*, 3259. https://doi.org/10.1038/s41467-023-38669-1.

124. Wild, J.M. (2022). The avian somatosensory system: A comparative view. In Sturkie's Avian Physiology, sixth edition, C.G. Scanes, and S. Dridi, eds. (Academic Press), pp. 55–69. https://doi.org/10.1016/b978-0-12-407160-5.00005-1.

125. Bergel, A., Schmidt, J.M., Barrillot, B., Arthaud, S., Averty, L., Blumberg, M.S., Carachet, C., Clair, A., Filchenko, I., Froidevaux, C., *et al*. (2026). Sleep-dependent infraslow rhythms are evolutionarily conserved across reptiles and mammals. Nat. Neurosci. *29*, 543–550.

126. Klein, B.A., Olzsowy, K.M., Klein, A., Saunders, K.M., and Seeley, T.D. (2008). Caste-dependent sleep of worker honey bees. J. Exp. Biol. *211*, 3028–3040. https://doi.org/10.1242/jeb.017426.

127. Cassill, D.L., Brown, S., Swick, D., and Yanev, G. (2009). Polyphasic wake/sleep episodes in the fire ant, Solenopsis invicta. J. Insect Behav. *22*, 313. https://doi.org/10.1007/s10905-009-9173-4.

128. Sumbre, G., Gutfreund, Y., Fiorito, G., Flash, T., and Hochner, B. (2001). Control of octopus arm extension by a peripheral motor program. Science *293*, 1845–1848. https://doi.org/10.1126/science.1060976.

129. Hochner, B., Zullo, L., Shomrat, T., Levy, G., and Nesher, N. (2023). Embodied mechanisms of motor control in the octopus. Curr. Biol. *33*, R1119–R1125. https://doi.org/10.1016/j.cub.2023.09.008.

130. Wu, J.J.-S., and Chiao, C.-C. (2023). Switching by cuttlefish of preying tactics targeted at moving prey. iScience *26*, 108122. https://doi.org/10.1016/j.isci.2023.108122.

131. Wu, J.J.-S., Hung, A., Lin, Y.-C., and Chiao, C.-C. (2020). Visual attack on the moving prey by cuttlefish. Front. Physiol. *11*, 648. https://doi.org/10.3389/fphys.2020.00648.

132. Corner, M.A. (2013). Postnatal persistence of episodic spontaneous rapid-body-movement bursts and twitches in the cuttlefish, Sepia officinalis. Behaviour *150*, 939–950. https://doi.org/10.1163/1568539x-00003091.

133. Frank, M.G., Waldrop, R.H., Dumoulin, M., Aton, S., and Boal, J.G. (2012). A preliminary analysis of sleep-like states in the cuttlefish Sepia officinalis. PLoS One *7*, e38125. https://doi.org/10.1371/journal.pone.0038125.t001.

134. Duntley, S.P., and Morrissey, M.J. (2004). Sleep in the cuttlefish. Ann. Neurol. *56*, S68.

135. Pophale, A., Shimizu, K., Mano, T., Iglesias, T.L., Martin, K., Hiroi, M., Asada, K., Andaluz, P.G., Dinh, T.T.V., Meshulam, L., *et al*. (2023). Wake-like skin patterning and neural activity during octopus sleep. Nature *619*, 129–134. https://doi.org/10.1038/s41586-023-06203-4.

136. Dujany, M., Hauser, S., Mutlu, M., van der Sar, M., Arreguit, J., Kano, T., Ishiguro, A., and Ijspeert, A. (2020). Emergent adaptive gait generation through Hebbian sensor-motor maps by morphological probing. In IEEE/RSJ International Conference on Intelligent Robots and Systems (IROS) (IEEE), pp. 7866–7873. https://doi.org/10.1109/iros45743.2020.9341211.

137. Franklin, D.W., and Wolpert, D.M. (2011). Computational mechanisms of sensorimotor control. Neuron *72*, 425–442. https://doi.org/10.1016/j.neuron.2011.10.006.

138. Penfield, W., and Boldrey, E. (1937). Somatic motor and sensory representation in the cerebral cortex of man as studied by electrical stimulation. Brain *60*, 389–443. https://doi.org/10.1093/brain/60.4.389.

139. Marshall, W.H., Woolsey, C.N., and Bard, P. (1937). Cortical representation of tactile sensibility as indicated by cortical potentials. Science *85*, 388–390. https://doi.org/10.1126/science.85.2207.388.

140. Weinberg, R.J. (1997). Are topographic maps fundamental to sensory processing? Brain Res. Bull. *44*, 113–116. https://doi.org/10.1016/s0361-9230(97)00095-6.

141. Krubitzer, L., and Dooley, J.C. (2013). Cortical plasticity within and across lifetimes: how can development inform us about phenotypic transformations? Front. Hum. Neurosci. *7*, 620. https://doi.org/10.3389/fnhum.2013.00620.

142. Erzurumlu, R.S., Murakami, Y., and Rijli, F. (2010). Mapping the face in the somatosensory brainstem. Nat. Rev. Neurosci. *11*, 252–263.

143. Catania, K.C., Leitch, D.B., and Gauthier, D. (2011). A star in the brainstem reveals the first step of cortical magnification. PLoS One *6*, e22406. https://doi.org/10.1371/journal.pone.0022406.

144. Dräger, U.C., and Hubel, D.H. (1976). Topography of visual and somatosensory projections to mouse superior colliculus. J. Neurophysiol. *39*, 91–101.

145. Meredith, M.A., Clemo, H.R., and Stein, B.E. (1991). Somatotopic component of the multisensory map in the deep laminae of the cat superior colliculus. J. Comp. Neurol. *312*, 353–370. https://doi.org/10.1002/cne.903120304.

146. Grant, R.A., Mitchinson, B., and Prescott, T.J. (2012). The development of whisker control in rats in relation to locomotion. Dev. Psychobiol. *54*, 151–168.

147. Someren, E.J.W.V., Mirmiran, M., Bos, N.P.A., Lamur, A., Kumar, A., and Molenaar, P.C.M. (1990). Quantitative analysis of eye movements during REM-sleep in developing rats. Dev. Psychobiol. *23*, 55–61. https://doi.org/10.1002/dev.420230106.

148. Senzai, Y., and Scanziani, M. (2022). A cognitive process occurring during sleep is revealed by rapid eye movements. Science *377*, 999–1004. https://doi.org/10.1126/science.abp8852.

149. Senzai, Y., and Scanziani, M. (2024). The brain simulates actions and their consequences during REM sleep. Preprint at bioRxiv, https://doi.org/10.1101/2024.08.13.607810.

150. Young, B.K., Mindlin, G.B., Arneodo, E., and Goller, F. (2017). Adult zebra finches rehearse highly variable song patterns during sleep. PeerJ *5*, e4052. https://doi.org/10.7717/peerj.4052.

151. Fainstein, F., Goller, F., and Mindlin, G.B. (2025). Song-like activation of syringeal and respiratory muscles during sleep in canaries. J. Comp. Physiol. A *211*, 135–148. https://doi.org/10.1007/s00359-024-01720-7.

152. Kolasinski, J., Makin, T.R., Logan, J.P., Jbabdi, S., Clare, S., Stagg, C.J., and Johansen-Berg, H. (2016). Perceptually relevant remapping of human somatotopy in 24 hours. eLife *5*, e17280. https://doi.org/10.7554/elife.17280.

153. Carmel, J.B., Kimura, H., and Martin, J.H. (2014). Electrical stimulation of motor cortex in the uninjured hemisphere after chronic unilateral injury promotes recovery of skilled locomotion through ipsilateral control. J Neurosci. *34*, 462–466. https://doi.org/10.1523/jneurosci.3315-13.2014.

154. Carmel, J.B., and Martin, J.H. (2014). Motor cortex electrical stimulation augments sprouting of the corticospinal tract and promotes recovery of motor function. Front. Integr. Neurosci. *8*, 51. https://doi.org/10.3389/fnint.2014.00051.

155. Martin, E., Roberts, M., Grigoras, I.F., Wright, O., Nandi, T., Rieger, S.W., Campbell, J., den Boer, T., Cox, B.T., Stagg, C.J., *et al*. (2025). Ultrasound system for precise neuromodulation of human deep brain circuits. Nat. Commun. *16*, 8024. https://doi.org/10.1038/s41467-025-63020-1.

156. Elias, G.J.B., Loh, A., Gwun, D., Pancholi, A., Boutet, A., Neudorfer, C., Germann, J., Namasivayam, A., Gramer, R., Paff, M., *et al*. (2020). Deep brain stimulation of the brainstem. Brain *144*, 712–723. https://doi.org/10.1093/brain/awaa374.

157. Christiansen, T.G., Sokoloff, G., Long, H.C., Kopp, O.K., Karr, L.K., and Blumberg, M.S. (2026). Does twitch-spindle coupling differ between N2 and N3 sleep in 6-month-olds? Sleep, https://doi.org/10.1093/sleep/zsaf410.

158. Sokoloff, G., Christiansen, T.G., Long, H.C., Karr, L.K., Kopp, O.K., Kriz, D.N., Sanderson, A.C., Liu, W., Johnson, I.K., Coulter, B.J., *et al*. (2026). Twitching in sleeping premature infants provides a sensitive behavioral assay of early motor control. Preprint at bioRxiv, https://doi.org/10.64898/2026.01.15.699697.

159. Sauleau, P., Lapouble, E., Val-Laillet, D., and Malbert, C.-H. (2009). The pig model in brain imaging and neurosurgery. Animal *3*, 1138–1151. https://doi.org/10.1017/s1751731109004649.

160. Wells, K.M., Kelley, K., Baumel, M., Vieira, W.A., and McCusker, C.D. (2021). Neural control of growth and size in the axolotl limb regenerate. eLife *10*, e68584. https://doi.org/10.7554/elife.68584.

161. Libourel, P.A., and Herrel, A. (2016). Sleep in amphibians and reptiles: A review and a preliminary analysis of evolutionary patterns. Biol. Rev. *91*, 833–866. https://doi.org/10.1111/brv.12197.