

# Twitching in Sensorimotor Development from Sleeping Rats to Robots Minireview

Mark S. Blumberg,<sup>1</sup> Hugo Gravato Marques,<sup>2,3</sup> and Fumiya Iida<sup>3</sup>

It is still not known how the ‘rudimentary’ movements of fetuses and infants are transformed into the coordinated, flexible and adaptive movements of adults. In addressing this important issue, we consider a behavior that has been perennially viewed as a functionless by-product of a dreaming brain: the jerky limb movements called myoclonic twitches. Recent work has identified the neural mechanisms that produce twitching as well as those that convey sensory feedback from twitching limbs to the spinal cord and brain. In turn, these mechanistic insights have helped inspire new ideas about the functional roles that twitching might play in the self-organization of spinal and supraspinal sensorimotor circuits. Striking support for these ideas is coming from the field of developmental robotics: when twitches are mimicked in robot models of the musculoskeletal system, the basic neural circuitry undergoes self-organization. Mutually inspired biological and synthetic approaches promise not only to produce better robots, but also to solve fundamental problems concerning the developmental origins of sensorimotor maps in the spinal cord and brain.

## Introduction

Bodies and limbs come in many shapes and sizes. They change across early development and across the lifespan. They can be typically or atypically formed [1]. And yet despite this incredible diversity, animals develop similar capacities for coordinated neural control of the muscles that move each joint within each limb. Whether we are observing a human infant reaching for a toy, an elephant using its trunk to paint with a brush, or a two-legged dog walking upright, it is apparent that all animals learn to use the body they have in functional and flexible ways. But how does this functionality and flexibility arise?

Some believe that complex behaviors are built from ‘motor primitives’: endowed units of behavior, hardwired in the spinal cord, that arise fully formed without the need for experience [2]. However, demonstrations of motor learning in *fetal* rats [3] and prolonged plasticity in the spinal reflexes of human infants [4] have long revealed the limitations of such concepts. Also, developmental psychologists [5–7] and developmental roboticists [8,9] have emphasized how infants *discover* through self-generated movement how their bodies work, and how they change over time. Not surprisingly, this process of discovery has been presumed to occur when infants are awake and engaging in such *intentional* movements as reaching, crawling and walking. In addition, awake infants exhibit a variety of *spontaneous* movements,

including “kicking, rocking, scratching, waving, bouncing, banging, and swaying” ([10] p. 130), which may form the foundation for the later-emerging intentional movements. But movements are not restricted to periods of waking, a fact whose significance looms larger when we consider the predominance of sleep, especially active (or REM) sleep, during the perinatal period in both humans and other mammals [11,12]. For example, human newborns sleep for 16 hours each day, 50% of which is active sleep [11].

Here we argue for consideration of another class of movements — also spontaneous but occurring during active sleep — comprising brief, discrete and jerky movements of the limbs. Traditionally, these *myoclonic twitches* have been dismissed as mere flotsam of the dreaming brain [13]. Indeed, to the naked eye, twitches seem to have no discernible purpose. But when we look deeper, we see that twitching is a distinct form of movement that seems well suited to contribute to the development of the sensorimotor system. Specifically, and in contrast to wake movements, twitches are discrete movements produced against a background of muscle atonia, thereby making it easier for the nervous system to track the relationship between the motor signal that triggers a twitch and the sensory feedback signal arising from that twitch. In other words, twitching is a particular kind of spontaneous motor activity that, like spontaneous activity elsewhere in the nervous system [14,15], may contribute in a variety of ways to activity-dependent developmental processes, including processes affecting bone formation, neuromuscular development, and somatotopic organization [16,17].

## Self-organizing the Sensorimotor System: A Metaphor

Early in mammalian fetal development, pools of motoneurons in the spinal cord begin to establish connections with skeletal muscles in the limbs. Initially, these connections are imprecise and somewhat haphazard, but by adulthood, precise mapping relationships have emerged [18]. How are these precise relationships between spinal cord and muscle established, refined and maintained? And how does the developing animal integrate this foundational sensorimotor loop within the web of additional sensorimotor loops that span the brainstem and forebrain [19]?

Let us simplify the problem and consider a switchboard (see [Figure 1](#)) in which each switch (motoneurons) is connected in unknown ways to an array of light bulbs (muscles). To determine how the switches control the lights, the solution is straightforward: throw each switch in succession and keep track of the lights that turn on. If a brightly lit room makes it harder to see which bulbs are lighting up, dimming the room lights will help. Once a map of the connections linking switches and lights is established, the switchboard can be used to turn on the lights in any desired sequence or pattern. Moreover, additional switchboards can be added to produce more complex patterns with the throw of a single switch. Returning to the sleeping infant, we see how myoclonic twitching, like the successive throwing of each switch, comprises discrete events that give rise to discrete sensory responses. By producing twitches against a background of muscle atonia, analogous to dimming the room lights, their signal-to-noise ratio is enhanced. In contrast, if several

<sup>1</sup>Departments of Psychology and Biology, The University of Iowa, Iowa City, Iowa 52242, USA. <sup>2</sup>AI Lab, Institute for Neuroinformatics, University of Zurich 8050, Switzerland. <sup>3</sup>BIRL, Department of Mechanical and Process Engineering, ETH, Zurich 8092, Switzerland. E-mail: [mark-blumberg@uiowa.edu](mailto:mark-blumberg@uiowa.edu) (M.S.B.), [hgmarques@googlemail.com](mailto:hgmarques@googlemail.com) (H.G.M.)

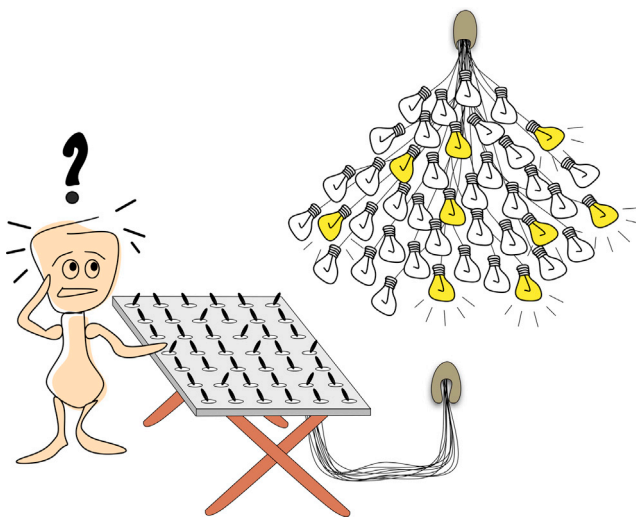


Figure 1. A metaphor for understanding how discrete twitches can help self-organize the sensorimotor system.

Faced with a bank of unlabeled switches (left) and a cluster of light bulbs (right), it is not possible to know *a priori* how to control the lights. A similar problem is faced by the developing sensorimotor system. To achieve a functional map between each switch (motoneurons) and tally the lights (muscles) that turn on. Developing animals may use discrete twitches during active sleep to establish, refine, maintain, and repair sensorimotor circuits at multiple levels of the nervous system.

switches are thrown at once in a brightly lit room — analogous to high-amplitude, coordinated limb movements during wakefulness — the resulting sensory information would be more ambiguous and thus more difficult to resolve in a developing sensorimotor system.

In addition to establishing and refining connections and topographies, twitching may play functional roles later in development and throughout the lifespan. After all, once these maps are established, they must be continually recalibrated as bodies grow and change in size and shape; and when disease or accident strikes, the maps must be repaired. At present we cannot explain this capacity to develop, recalibrate, and repair sensorimotor maps at multiple levels of the neuraxis, but twitching provides one credible mechanism. The fact that twitching occurs during sleep is also consistent with contemporary views of sleep as a period of heightened neural plasticity and consolidation of memories [20], including motor memories [21].

### Sleep-related Twitching in Perinatal Rats

Human infants spend a disproportionate amount of time in active sleep. This fact inspired the *ontogenetic hypothesis*, which posited a direct link between active sleep and brain development [11]. Like humans, rat pups also spend a disproportionate amount of time in active sleep [12,22]. Based on this and other similarities, we can look to pups to test basic hypotheses about the structure and functions of sleep. Although newborn rats are the focus of the discussion here, however, it should be stressed that sleep-related twitching emerges from the earliest movements of mammalian fetuses [23] and is a prominent and ubiquitous feature of early postnatal mammalian life, especially in altricial species (such as cats) but also in precocial ones (such as guinea pigs) [12].

When a rat pup is awake, it may move around, lift its head, suckle, yawn, kick and stretch. If muscle activity is recorded while the pup performs these acts, it will reveal a high baseline level of muscle tone along with bursts of muscle activity, especially in those muscles that control the particular movements. Even when behaviorally quiescent, a pup may exhibit heightened muscle tone. But as a pup falls asleep and the limbs and head noticeably relax, muscle tone decreases. Then, suddenly, a flurry of limb jerks ensues accompanied by sharp spikes of muscle activity. To the naked eye, this flurry of activity appears random and uncoordinated. The combined presence of muscle twitches against a background of muscle atonia is a hallmark of active sleep (Figure 2A). Also, in rat pups, twitching appears to be controlled by neural systems located within the spinal cord and brainstem, but not the forebrain [22].

All skeletal muscles examined thus far twitch during active sleep. This includes the skeletal muscles that control the limbs, head, and tail. Rapid eye movements (REMs) are produced by twitches of the eye muscles [24]; even rat pup whiskers twitch [25]. Over just one 15-minute period, a single muscle can exhibit hundreds of twitches, which translates into hundreds of thousands of twitches across the body each day. Clearly, sleep is not an absence of behavior. But is this behavior, as it appears to the naked eye, random and uncoordinated?

In fact, twitching is a highly structured motor behavior. Using high-speed videography and three-dimensional motion tracking (Figures 2B–D), we investigated the spatiotemporal organization of twitching at individual forelimb joints in newborn rats. Figure 2D depicts twitching at three time-scales in an eight-day-old rat; the shoulder, elbow and wrist of the right and left forelimbs exhibit a complex spatiotemporal structure comprising bouts within bouts. Detailed analysis of these bouts reveals synergistic joint movements within and between limbs. For example, when the right shoulder twitches toward the body (adducts) there is a high likelihood that, within 100 ms, the right elbow will flex, the right wrist will extend, and the opposite shoulder will adduct. We also routinely see the complementary synergy of shoulder abduction with elbow extension and wrist flexion. In other words, there is nothing random or uncoordinated about twitches: They are as organized as the more familiar wake movements, even as they are strikingly and profoundly different from them.

Although assessments of limb biomechanics during twitching reveal rich spatiotemporal structure in postnatal rats, spontaneous motor activity, including twitching, begins as early as embryonic day (E) 17 [26,27]. The within-limb kinematics of these prenatal movements are not known, but between-limb movements are clearly organized into bouts and, as late as E20, they rely largely on spinal mechanisms for at least some aspects of their temporal structure [26]. Over development, brainstem mechanisms are increasingly important for producing twitches and for coordinating their expression with other components of sleep, including muscle atonia, but it seems likely that spinal mechanisms continue to contribute to some aspects of twitching at least through the early postnatal period [22,28,29]. Even in adults, the neural mechanisms of atonia and twitching have yet to be fully understood. However, recent work in rats [30] shows that muscle atonia in trigeminal motoneurons results from concurrent inhibition by GABA<sub>A</sub>, GABA<sub>B</sub>, and glycine; in contrast, twitches are triggered by glutamatergic inputs

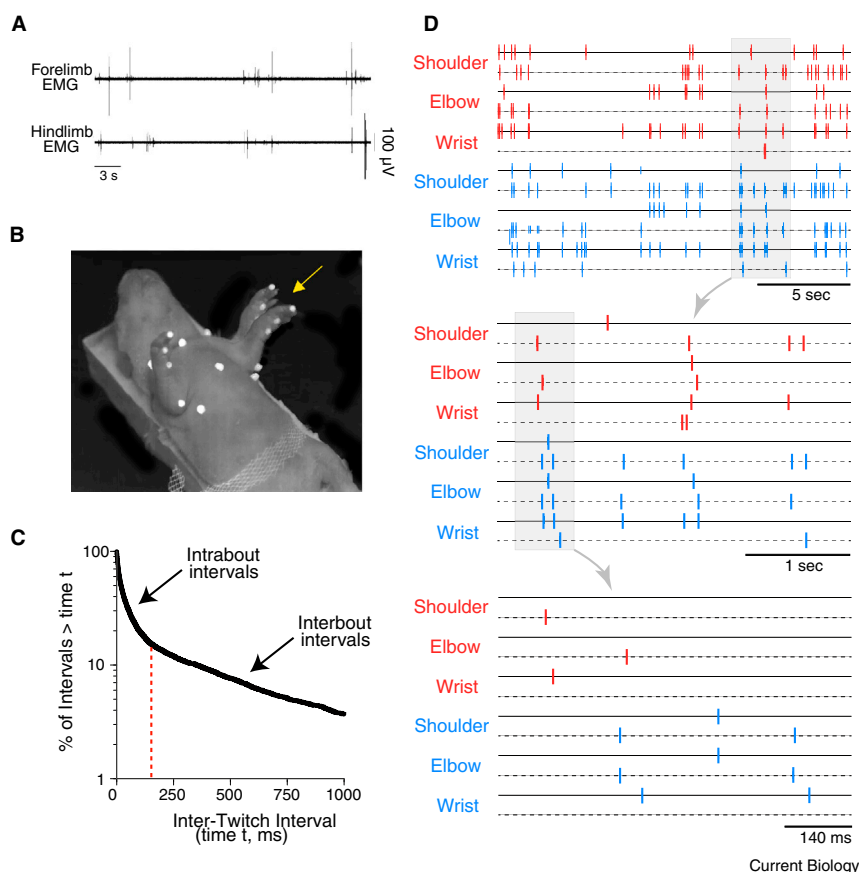


Figure 2. Spatiotemporal organization of twitching.

(A) Representative segment of electromyographic (EMG) activity during active sleep in a five-day-old rat, recorded from forelimb and hindlimb muscles. Numerous twitches against a background of atonia are clearly visible. Adapted from [34]. (B) Time-lapse photograph, compiled from two high-speed video frames, of a supine eight-day-old rat exhibiting a discrete twitch of the left elbow (arrow). The white dots are used for motion tracking of joint movements. (C) Log-survivor plot of inter-twitch intervals for eight-day-old rats across shoulder, elbow, and wrist joints in the two forelimbs (pooled over >5000 intervals). The red dashed line indicates the approximate inflection point separating intervals occurring within and between bouts of twitching at this timescale. (D) Spatiotemporal organization of twitching in an eight-day-old rat at three timescales. Each tick mark indicates the occurrence of a twitch in the right (red) or left (blue) forelimb at the shoulder, elbow, or wrist, as determined using high-speed video and motion tracking. For each joint, two movements are depicted: adduction and abduction for the shoulder and flexion and extension for the elbow and wrist (denoted by solid and dashed lines for each joint). Non-random distribution of twitching is evident at each timescale, especially at the two smaller timescales in which the bout-within-bout structure of twitching is most apparent.

Current Biology

onto motoneurons coupled with phasic glycinergic inhibition [31]. In addition, transgenic mice with disrupted glycinergic and GABAergic functioning exhibit a variety of abnormal motor behaviors during sleep that are reminiscent of those observed in REM Sleep Behavior Disorder [32].

Although there is a clear abundance of twitching in neonates, it does not necessarily follow that twitching contributes to brain development. Given the general consensus that sleep is a period of diminished sensory experience, it seemed unlikely that any sensory feedback from twitches could affect brain activity. But beginning ten years ago with the discovery that twitches trigger so-called spindle bursts (brief oscillatory events) in the somatosensory cortex of newborn rats [33], it became clear that the sensory experience of the sleeping infant is not as impoverished as it once seemed. As is now known, sleep-related twitches trigger neural activity throughout the neuraxis in infant rats as well as humans [25,34–38]. Sensory feedback from twitching in rat pups has also been implicated in the self-organization of the spinally mediated withdrawal reflex [39]. Thus, in a surprising twist, twitching—similar to retinal waves in the developing visual system [40]—has emerged as a primary driver of neural activity in early development. Moreover, based on the sheer volume of twitching and twitch-triggered neural activity, twitches seem likely to participate in the development of sensorimotor maps at multiple levels of the neuraxis.

#### ‘Sleeping Robots’ and the Self-organization of Spinal and Supraspinal Circuitry

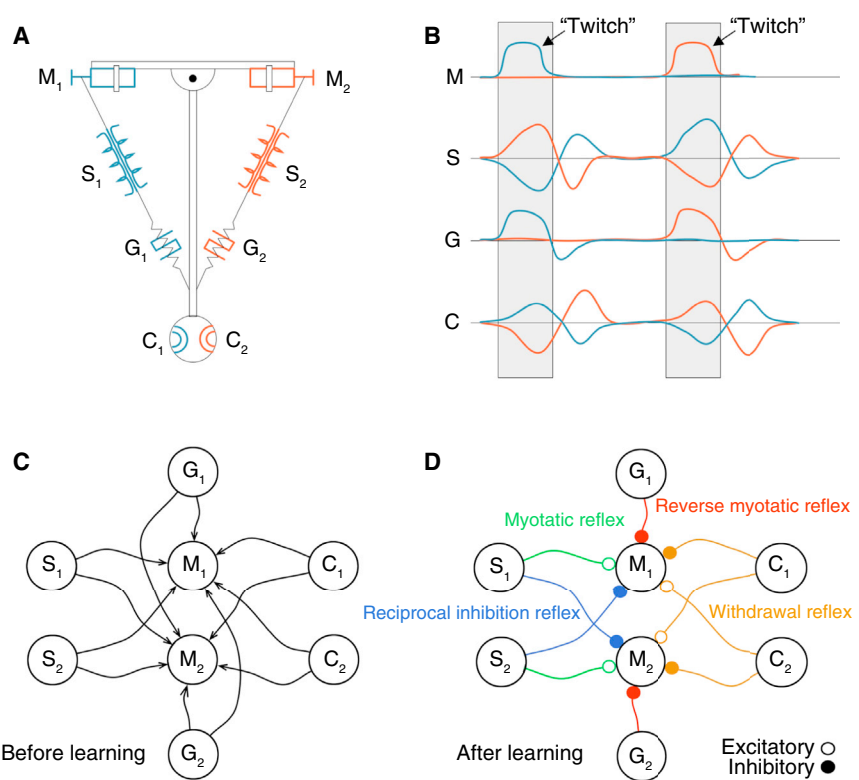
In recent years, the steep challenge of building robots that behave in flexible and adaptive ways has led roboticists to

appreciate that even the most sophisticated software, when coupled with static hardware, will not suffice. This challenge has encouraged the pursuit of control strategies that are more general and adaptive, and more biologically inspired [41], than those traditionally used. The emerging field of *developmental robotics* is the outcome of this pursuit [9,42,43]. Developmental robotics looks to developmental biology for guiding principles that offer insights into how artificial systems might acquire appropriate control strategies in an autonomous and incremental way. Furthermore, the field is guided by the notion that robots acquire critical information about their mechanical structure through self-generated movements and the resulting sensorimotor feedback. The expectation is that a robot equipped with this basic general bodily knowledge could subsequently exploit that knowledge to learn a variety of motor tasks, including reaching and walking.

So, can twitching, as a special form of self-generated movement, contribute to a robot’s knowledge about its body and how it works? As a first step toward addressing this question, computer simulations of limbs and associated neural circuitry were created [44,45]. More recently, these simulations have migrated to an actual robotic platform, with similar results. In both the simulations and robots, the general approach was the same: to mimic the production of, and sensory feedback from, ‘twitches’ and assess the possibility of transforming initially undifferentiated neural circuits into differentiated circuits comprising functional sensorimotor connectivity. These circuits take the shape of a fully connected perceptron, in which the connections mediating sensor and motor signals are self-organized using

Figure 3. ‘Twitches’ self-organize spinal reflexes in a robotic limb.

(A) Robot platform consisting of a rigid pendulum actuated by a pair of antagonistically arranged artificial muscles (M1, M2). Sensory feedback is provided by sensors analogous to muscle spindles (S1, S2), Golgi tendon organs (G1, G2), and cutaneous receptors (C1, C2). (B) Temporal relations among the three sensory components (S, G, and C) of the robot limb upon ‘twitching’ of muscles M1 (blue) and M2 (orange). The twitch periods are marked by gray rectangles. (C) Neural connectivity of the sensory and motor components before the ‘twitch’ learning regimen. The network is instantiated as a fully connected perceptron. (D) Self-organized reflex connectivity of the sensory and motor components after the ‘twitch’ learning regimen. Excitatory (unfilled circles) and inhibitory (filled circles) connections are also shown.



an anti-Hebbian learning rule [46]. Our experiments with these robots show how initially unstructured patterns of ‘twitching’ can contribute to the self-organized differentiation of the most basic spinal circuits — circuits that are routinely considered primitive, hardwired, and innate.

The methodology used for these simulations is based on that used to investigate the self-organization of the limb withdrawal reflex in infant rats [39]. In addition to the withdrawal reflex, other spinal reflexes were examined including the myotatic reflex (which counteracts the stretching of a limb muscle), the reciprocal inhibition reflex (which prevents competition by antagonist muscles around a single joint), and the reverse myotatic reflex (which helps to prevent excessive forces at joints). The robot platform used in these experiments is shown in Figure 3A. It consists of a rigid rod (analogous to a bone) that moves as a pendulum about a single axis. The rod is actuated using a pair of antagonistically arranged artificial muscles (M1 and M2). The artificial muscles consist of an electric motor in series with a spring element [47]. The platform has sensors that are meant to mirror those projecting to the mammalian spinal cord: length sensors provide information analogous to muscle spindles (S), force sensors provide information analogous to Golgi tendon organs (G), and tactile sensors provide information analogous to cutaneous tactile receptors (C). The pendulum is immersed in water so as to simulate the uterine environment as well as to make possible tactile feedback from muscle contractions.

Within this artificial system, ‘twitches’ are generated that, like their *in vivo* counterparts in rats, entail discrete activation of muscles followed by their resulting discrete sensory feedback. During the initial training stage, ‘twitches’ are delivered to the robotic muscles in an alternating temporal sequence. This process is meant to mimic the conditions of active sleep. Critically, to provide a convincing demonstration of the power of the developmental robotic approach, it is important that, at least initially, the ‘twitches’ have no inherent spatiotemporal structure that might bias the results.

With each twitch, the resulting movements of the pendulum trigger distinct patterns of feedback in the sensory channels (Figure 3B). Across this training period, all possible pairs of sensor and motor signals are correlated using an anti-Hebbian learning rule [44]. The correlation between each sensor–motor pair defines the weight of the connection. Remarkably, from an initially undifferentiated network in which every sensor element is connected indiscriminately to every motor element (Figure 3C), highly structured reflex circuitry, analogous to that found in the mammalian spinal cord, is obtained (Figure 3D). Given that the sensor information induced by a single ‘twitch’ is highly stereotypical, the final reflex circuitry is stable and can be achieved reliably. Also, alterations or disruptions to the ‘twitches’ or their sensory feedback result in different mapping relationships between sensors and muscles [44].

There are many important ways that robots can help test specific hypotheses concerning the functions of twitching, particularly where such tests might be difficult to perform *in vivo*. We have emphasized the spatiotemporal organization of twitches and muscle atonia as two potentially important ‘design’ features of this system. Thus far, as already described, the patterning of robot ‘twitches’ has been very simple: only single ‘twitches’ with relatively long inter-twitch intervals — and no bout structure — have been used. From what we know about twitching in rat pups, however, it will be possible to ‘play’ actual twitch patterns to robots and assess the functional costs and benefits of such patterns. Such an analysis may gain additional relevance as the robot model is elaborated further to include more than one limb and multiple levels of sensorimotor loops; within that context, the possible functional value of the

'bout-within-bout' spatiotemporal organization of twitching (Figure 2D) for the development of sensorimotor maps may reveal itself.

Similarly, we can use robots to assess the functional value of muscle atonia, also something that would be very difficult to test in animals. For any given set of twitch parameters that produce differentiated neural circuits in robots, we can modulate the background muscle tone against which the twitches are occurring and assess the consequences of the increased tone for sensory feedback and circuit differentiation. Also, we could go further to assess the relative value of 'twitch' and 'wake' movements — with and without muscle atonia — for neural circuit differentiation, an approach that has the potential to reveal the critical differences between the states of sleep and wake for the development of sensorimotor systems.

In the initial model of the sensorimotor system [45], the neural source of 'twitching' was conceptualized exclusively as an output device, impervious to the sensory consequences of twitching. However, experiments in fetal and neonatal rats suggest that patterns of twitching may become more complex with age, reflecting the addition of new neural elements and also the modification of existing neural elements [26,28,29]. In other words, twitches may be both a product of the nervous system and a source of feedback to the sensorimotor system that modifies the future expression of limb movements, including twitches. It will be important to determine *in vivo* whether twitching modulates its own expression, but it is also an issue that can be explored within the robot platform by modifying the neural elements that produce 'twitching'.

## Conclusions

Developmental psychologists have highlighted how human infants autonomously create their own development [5–7]. Among the more striking observations within this tradition is the finding that human infants accumulate thousands of steps each day — and hundreds of falls — on their path to skilled walking [7]. This immense 'practice regimen', exhibited during waking, is mirrored by the equally immense 'practice regimen' in the form of twitching, exhibited during sleep. As a pup probes each of its limbs through twitching, biomechanical information about the limb is relayed to the spinal cord and brain, including information about the number of joints, the number of muscles controlling each joint, and the active and passive limb movements that result from individual muscle activation. It is through this process of self-discovery that a young animal learns how each of its limbs is structured, how it works, and how it changes with age. We believe that it is also through this process that peripheral limbs and muscles are topographically mapped and integrated within the hierarchically nested sensorimotor loops that span the neuraxis.

It is generally acknowledged that robotics and biology have great potential for cross-fertilization [48], and some roboticists are looking specifically to developmental biology and developmental psychology for clues to flexible and adaptive behavior [9,41]. Experiments in developmental robotics have already revealed how increasingly complex movements "can be discovered and acquired by the neural-body dynamics without pre-defined coordinated control circuits" ([49] p. 589). This interdisciplinary approach inspired the prediction that a robotic limb probed with discrete 'twitches' would exhibit self-organization of functional neural

circuits. As we have seen, this prediction was borne out quickly and powerfully. Now, building on this initial success and looking to the future, we envision many additional rounds of theory construction and hypothesis testing with the mutual aim of building better robots and better models of sensorimotor development.

## Acknowledgments

This work was supported by grants from the National Institutes of Health (HD63071, MH66424) to M.S.B., the EU's FP7, Cognitive Systems, Interaction, Robotics Grants (207212, 288219) to H.G.M., and the Swiss National Science Foundation NCCR Robotics Grant to F.I. We thank Cassandra Coleman and Ashlynn Gerth for their contributions to the data presented in Figure 2 and Mathias Weyland for his contributions to the data presented in Figure 3. We also thank Karen Adolph, Asif Ghazanfar, Greta Sokoloff, and Alex Tiriac for helpful comments on an earlier draft of this paper.

## References

1. Blumberg, M.S. (2009). *Freaks of Nature: What Anomalies Tell Us about Development and Evolution* (New York: Oxford University Press).
2. Dominici, N., Ivanenko, Y.P., Cappellini, G., d'Avella, A., Mondì, V., Cicchese, M., Fabiano, A., Silei, T., Di Paolo, A., Giannini, C., et al. (2011). Locomotor primitives in newborn babies and their development. *Science* 334, 997–999.
3. Robinson, S., Kleven, G., and Johnson, S. (2005). Learning to move before birth. In *Prenatal Development of Postnatal Functions*, B. Hopkins and S.P. Johnson, eds. (Westport, CT: Praeger), pp. 131–175.
4. Myklebust, B.M., and Gottlieb, G.L. (1993). Development of the stretch reflex in the newborn: reciprocal excitation and reflex irradiation. *Child. Dev.* 64, 1036–1045.
5. Gibson, E.J. (1988). Exploratory behavior in the development of perceiving, acting, and the acquiring of knowledge. *Annu. Rev. Psych.* 39, 1–41.
6. Thelen, E., Ulrich, B., Jensen, J., Woollacott, M., and Shumway-Look, A. (2000). Motor development as foundation and future of developmental psychology. *Int. J. Behav. Dev.* 24, 385–397.
7. Adolph, K.E., Cole, W.G., Komati, M.M., Garciaguirre, J.S., Badaly, D.D., Lingeman, J.M., Chan, G.L.Y., and Sotsky, R.B. (2012). How do you learn to walk? Thousands of steps and dozens of falls per day. *Psych. Sci.* 23, 1387–1394.
8. Pfeifer, R., and Bongard, J. (2007). *How the Body Shapes the Way We Think* (Cambridge: MIT Press).
9. Lungarella, M., Metta, G., Pfeifer, R., and Sandini, G. (2003). Developmental robotics: a survey. *Connect. Sci.* 15, 151–190.
10. Thelen, E., and Fisher, D.M. (1983). From spontaneous to instrumental behavior: Kinematic analysis of movement changes during very early learning. *Child. Dev.* 54, 129–140.
11. Roffwarg, H.P., Muzio, J.N., and Dement, W.C. (1966). Ontogenetic development of the human sleep-dream cycle. *Science* 152, 604–619.
12. Jouvet-Mounier, D., Astic, L., and Lacote, D. (1970). Ontogenesis of the states of sleep in rat, cat, and guinea pig during the first postnatal month. *Dev. Psychobiol.* 2, 216–239.
13. Blumberg, M.S. (2010). Beyond dreams: Do sleep-related movements contribute to brain development? *Front. Neurol.* 1, 140.
14. O'Donovan, M.J. (1999). The origin of spontaneous activity in developing networks of the vertebrate nervous system. *Curr. Opin. Neurobiol.* 9, 94–104.
15. Wong, R. (1999). Retinal waves and visual system development. *Annu. Rev. Neurosci.* 22, 29–47.
16. Purves, D. (1994). *Neural Activity and the Growth of the Brain* (Cambridge: Cambridge University Press).
17. Müller, G. (2003). Embryonic motility: environmental influences and evolutionary innovation. *Evol. Dev.* 5, 56–60.
18. Purves, D., and Lichtman, J. (1980). Elimination of synapses in the developing nervous system. *Science* 210, 153–157.
19. Ahissar, E., and Kleinfeld, D. (2003). Closed-loop neuronal computations: focus on vibrissa somatosensation in rat. *Cereb. Cortex* 13, 53–62.
20. Diekelmann, S., and Born, J. (2010). The memory function of sleep. *Nat. Rev. Neurosci.* 11, 114–126.
21. Korman, M., Doyon, J., Doljansky, J., Carrier, J., Dagan, Y., and Karni, A. (2007). Daytime sleep condenses the time course of motor memory consolidation. *Nat. Neurosci.* 10, 1206–1213.
22. Blumberg, M.S., and Seelke, A.M.H. (2010). The form and function of infant sleep: From muscle to neocortex. In *The Oxford Handbook of Developmental Behavioral Neuroscience*, M.S. Blumberg, J.H. Freeman, and S.R. Robinson, eds. (New York: Oxford University Press), pp. 391–423.
23. Corner, M. (1977). Sleep and the beginnings of behavior in the animal kingdom – Studies of ultradian motility cycles in early life. *Prog. Neurobiol.* 8, 279–295.

24. Seelke, A.M.H., Karlsson, K.Æ., Gall, A., and Blumberg, M.S. (2005). Extraocular muscle activity, rapid eye movements and the development of active and quiet sleep. *Eur. J. Neurosci.* 22, 911–920.
25. Tiriác, 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.
26. Robinson, S.R., Blumberg, M.S., Lane, M.S., and Kreber, L.S. (2000). Spontaneous motor activity in fetal and infant rats is organized into discrete multilimb bouts. *Behav. Neurosci.* 114, 328–336.
27. Narayanan, C., Fox, M., and Hamburger, V. (1971). Prenatal development of spontaneous and evoked activity in the rat (*Rattus norvegicus*). *Behaviour* 40, 100–134.
28. Blumberg, M.S., and Lucas, D. (1994). Dual mechanisms of twitching during sleep in neonatal rats. *Behav. Neurosci.* 108, 1196–1202.
29. 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.
30. Brooks, P.L., and Peever, J.H. (2012). Identification of the transmitter and receptor mechanisms responsible for REM sleep paralysis. *J. Neurosci.* 32, 9785–9795.
31. Brooks, P.L., and Peever, J.H. (2008). Glycinergic and GABA(A)-mediated inhibition of somatic motoneurons does not mediate rapid eye movement sleep motor atonia. *J. Neurosci.* 28, 3535–3545.
32. Brooks, P.L., and Peever, J.H. (2011). Impaired GABA and glycine transmission triggers cardinal features of rapid eye movement sleep behavior disorder in mice. *J. Neurosci.* 31, 7111–7121.
33. Khazipov, R., Sirota, A., Leinekugel, X., Holmes, G.L., Ben-Ari, Y., and Buzsáki, G. (2004). Early motor activity drives spindle bursts in the developing somatosensory cortex. *Nature* 432, 758–761.
34. Mohns, E.J., and Blumberg, M.S. (2010). Neocortical activation of the hippocampus during sleep in newborn rats. *J. Neurosci.* 30, 3438–3449.
35. Mohns, E.J., and Blumberg, M.S. (2008). Synchronous bursts of neuronal activity in the developing hippocampus: Modulation by active sleep and association with emerging gamma and theta rhythms. *J. Neurosci.* 28, 10134–10144.
36. Milh, M., Kaminska, A., Huon, C., Lapillonne, A., Ben-Ari, Y., and Khazipov, R. (2007). Rapid cortical oscillations and early motor activity in premature human neonate. *Cereb. Cortex* 17, 1582–1594.
37. Marcano-Reik, A.J., Prasad, T., Weiner, J.A., and Blumberg, M.S. (2010). An abrupt developmental shift in callosal modulation of sleep-related spindle bursts coincides with the emergence of excitatory-inhibitory balance and a reduction of somatosensory cortical plasticity. *Behav. Neurosci.* 124, 600.
38. McVea, D.A., Mohajerani, M.H., and Murphy, T.H. (2012). Voltage-sensitive dye imaging reveals dynamic spatiotemporal properties of cortical activity after spontaneous muscle twitches in the newborn rat. *J. Neurosci.* 32, 10982–10994.
39. Petersson, P., Waldenström, A., Fähræus, C., and Schouenborg, J. (2003). Spontaneous muscle twitches during sleep guide spinal self-organization. *Nature* 424, 72–75.
40. Ackman, J.B., Burbridge, T.J., and Crair, M.C. (2012). Retinal waves coordinate patterned activity throughout the developing visual system. *Nature* 490, 219–225.
41. Pfeifer, R., Lungarella, M., and Iida, F. (2007). Self-organization, embodiment, and biologically inspired robotics. *Science* 318, 1088–1093.
42. Asada, M., MacDorman, K.F., Ishiguro, H., and Kuniyoshi, Y. (2001). Cognitive developmental robotics as a new paradigm for the design of humanoid robots. *Robot. Auton. Syst.* 37, 185–193.
43. Weng, J., McClelland, J., Pentland, A., Sporns, O., Stockman, I., Sur, M., and Thelen, E. (2001). Autonomous mental development by robots and animals. *Science* 291, 599–600.
44. Marques, H.G., Imtiaz, F., Iida, F., and Pfeifer, R. (2013). Self-organization of reflexive behavior from spontaneous motor activity. *Biol. Cybern.* 107, 25–37.
45. Marques, H., Völk, K., König, S., and Iida, F. (2012). Self-organization of spinal reflexes involving homonymous, antagonist and synergistic interactions. *From Anim. Animat.*, 269–278.
46. Földiák, P. (1990). Forming sparse representations by local anti-Hebbian learning. *Biol. Cybern.* 64, 165–170.
47. Holland, O., and Knight, R. (2006). The anthropomimetic principle. In *Proceedings of the AISB06 Symposium on Biologically Inspired Robotics*, J. Burn and M. Wilson, eds.
48. Webb, B. (2009). Animals versus animats: Or why not model the real iguana? *Adapt. Behav.* 17, 269–286.
49. Kuniyoshi, Y., and Sangawa, S. (2006). Early motor development from partially ordered neural-body dynamics: experiments with a cortico-spinal-musculo-skeletal model. *Biol. Cybern.* 95, 589–605.