The brain has a body: adaptive behavior emerges from interactions of nervous system, body and environment

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Studies of mechanisms of adaptive behavior generally focus on neurons and circuits. But adaptive behavior also depends on interactions among the nervous system, body and environment: sensory preprocessing and motor post-processing filter inputs to and outputs from the nervous system; co-evolution and co-development of nervous system and periphery create matching and complementarity between them; body structure creates constraints and opportunities for neural control; and continuous feedback between nervous system, body and environment are essential for normal behavior. This broader view of adaptive behavior has been a major underpinning of ecological psychology and has influenced behavior-based robotics. Computational neuroethology, which jointly models neural control and periphery of animals, is a promising methodology for understanding adaptive behavior.

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THE NERVOUS SYSTEM is often regarded as a central processing unit that uses environmental inputs and its internal state to plan future actions, and then generates motor commands to execute its plans (Fig. 1A). This view implies that an understanding of adaptive behavior requires a primary focus on the nervous system. By adaptive behavior, we mean behavior that enhances the survival and reproduction of an animal. Using reduced preparations that can generate output patterns similar to those seen *in vivo*, it has been possible to understand the biophysical and molecular biological properties of nerve cells within the context of neural circuits, and determine the neural architectures underlying a variety of different adaptive behaviors[1–3]. Despite these remarkable successes, recent results suggest that adaptive behavior can best be understood within the context of the biomechanics of the body, the structure of an organism's environment, and the continuous feedback between the nervous system, the body and the environment.

Processing of inputs to and outputs from the nervous system

The body processes inputs to and outputs from the nervous system (Fig. 1B). An example of sensory preprocessing is the ability of the body to filter and amplify specific auditory inputs. For example, the ears of crickets are located in the tibiae of their front legs. The tympanum of the ear is interconnected via hollow tubes (acoustic trachea) to the acoustic spiracle on the thorax, as well as to the acoustic spiracle and the tympanum of the ear on the contralateral side. A recent study has shown that amplitude and phase changes in sound transmitted from the contralateral thoracic spiracle, which is most sensitive to the frequency of the cricket calling song (that is, between 4 and 5 kHz), combine with the amplitude and phase changes from the ipsilateral thoracic spiracle to yield robust directional information for sounds originating in front of the animal[4]. Moreover, perforations of the septum of the transverse trachea connecting the two sides of the body degrade the ability of crickets to walk directly to an artificial calling song, or to distinguish the direction of a song[5,6].

Extra-tympanic structures throughout the body play an important role in the hearing of vertebrates. In frogs, sound conduction through the mouth, lateral body wall, lungs and the whole body affect the directionality of tympanic membrane vibrations and responses of the auditory nerve[7]. Although 45% of auditory nerve fibers have spiking responses that are highly positively correlated with eardrum velocity, 55% do not, and these fibers may be more responsive to extratympanic pathways[8]. In general, animals that must discriminate sounds whose wavelength is small relative to their body size take advantage of measurements of pressure differences, utilizing whole body structures to provide additional phase and amplitude information[9].

The body also post-processes outputs from the nervous system (Fig. 1B). Muscle acts as a low pass filter of motor neuronal outputs, that is, it filters out the high frequency components of the neural outputs[10]. Moreover, the tendons connecting muscle to bones create a musculotendon actuator whose filtering properties in response to neural outputs or changes in length are greatly affected by the different degrees of stiffness or compliance of the tendon, as well as by the level of activation of the muscle[11]. In addition, the mechanical advantage of a muscle and the response of the whole body to the contraction of any particular muscle are a complex function of the geometric relationships and positions of other muscles and joints, and the prior history of activation of that muscle[12]. Thus, motor neuronal output is transformed significantly by the properties of the body. These data

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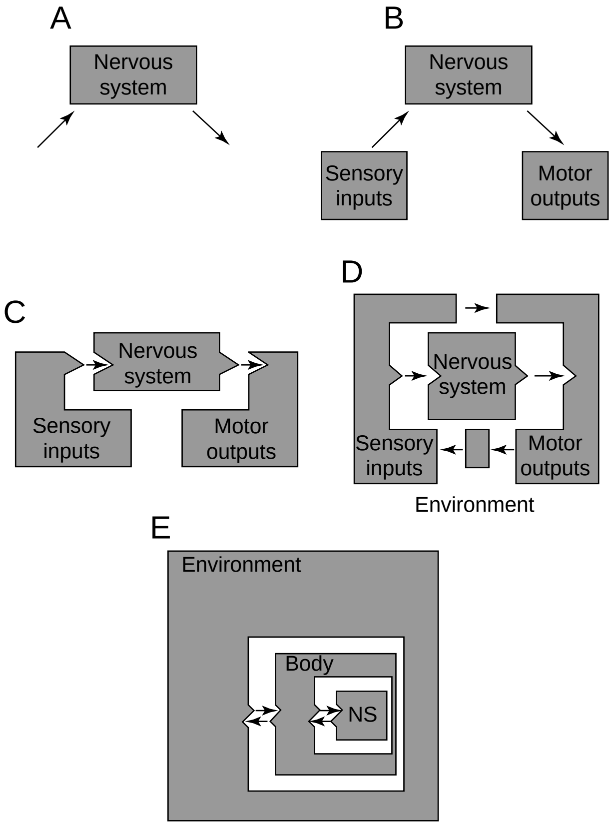

Fig. 1. ***Changing understanding of the interactions between the nervous system, the body, and the environment.*** **(A)** *Much work on the neural basis of behavior has focused primarily on the function of the nervous system, assuming that its role in the generation of adaptive behavior is central.* **(B)** *Many sensory inputs are extensively preprocessed by the body itself, and outputs of motor neurons are transformed by muscle and the biomechanical properties of the body.* **(C)** *The co-evolution and co-development of the nervous system and the body lead to extensive matching and complementarity between them, which create both constraints and opportunities for neural control. The matching and complementarity between the nervous system, its sensory inputs and its motor outputs is indicated by the projecting triangular regions.* **(D)** *The nervous system's function is affected by feedback, some of which is generated by its own motor outputs, and some of which comes from the environment. This feedback may fundamentally alter the behavior of the nervous system itself.* **(E)** *A broader viewpoint of adaptive behavior (based on Ref. 42). The nervous system (NS) is embedded within a body, which in turn is embedded within the environment. The nervous system, the body, and the environment are each rich, complicated, highly structured dynamical systems, which are coupled to one another, and adaptive behavior emerges from the interactions of all three systems.*

strongly suggest that one cannot simply 'peel away' the body to understand the nervous system's role in adaptive behavior.

Co-evolution and co-development lead to matching of neural and peripheral properties

Since the nervous system and periphery have co-evolved, and develop together during the life of an animal, there is extensive matching between their properties (Fig. 1C). Changes in behavior over evolutionary time are associated with coordinated changes in both the periphery and the nervous system. For example, computed tomography of the bony semicircular canals subserving the vestibular system indicates that hominid fossils have larger anterior and posterior canal sizes, and smaller lateral canal sizes, than those of great apes. Since the anterior and posterior canals are oriented vertically, they are likely to be particularly sensitive to vertical movements essential for maintaining balance during bipedal locomotion, suggesting that the change to bipedal locomotion was coordinated with a change in the sensory apparatus for balance[13]. Another example of coordinated evolution is provided by the feeding behavior of the leopard frog *Rana pipiens*, which uses a mode of feeding common to all primitive anurans for large prey, lunging at the prey and ingesting it using jaw prehension. In contrast, tongue prehension is used for small prey. Lesions of the hypoglossus nerve abolish the mouth opening in response to small prey, but do not affect mouth opening in response to large prey. These results suggest that distinct neural circuitry using tactile sensory feedback has evolved for the new tongue-based mechanism of small prey capture[14].

Changes in behavior during development are also associated with coordinated changes in both the periphery and the nervous system. Hamburger's classic studies of the effects of adding or removing limb buds in chicks demonstrated that the number of motor neurons was matched to the size of the periphery[15]. Coordinated changes in motor control and peripheral structures occur in animals such as insects or frogs, whose larval and adult bodies differ[16,17]. Since sensory and motor cortical maps are plastic, even in the adult[18–20], and the morphology of the body changes throughout the life span[21], it is likely that changes in the periphery are coordinated with changes in the nervous system to maintain the match between them.

Evidence for the match between neural control and the periphery is striking in adult animals. There is matching between the properties of motor neurons and the muscles that they innervate[22]. Studies of muscles that are used for cyclic, rhythmic movements such as flight suggest that the timing and duration of neural inputs to them are designed to maximize their work and power output[23,24]. Studies of an identified muscle in the marine mollusk *Aplysia* indicate that there is matching between the neural control and force/frequency properties of the muscle (S-Y. Yu, P. Crago and H. Chiel, unpublished observations; Ref. 25). A rostrocaudal gradient of mechanical advantage in the parasternal intercostal muscles of the dog is matched by a rostrocaudal gradient of electrical activation[26,27].

Constraints and opportunities imposed by the periphery

The close matching between the nervous system and the periphery creates both constraints and opportunities for the nervous system. The nervous system cannot process information that is not transduced by the periphery, nor can it command movements that are physically impossible for that periphery. At the same time, properties of the periphery may simplify complex neural processing and control problems (Fig. 1C).

The body plan of an animal affects the kinds of movements that it can generate. Animals with worm-like bodies (hydrostatic skeletons) can easily penetrate tortuous spaces, but cannot easily exert the point forces that are readily generated by animals whose periphery consists of hard skeletal elements and musculature[28]. Hard skeletal elements impose other constraints: for example, activation of postural muscles must minimize shear stresses on bone[29]. Structures composed entirely of muscle, such as tentacles, tongues or trunks (muscular hydrostats) have an extraordinarily large number of degrees of freedom[30], but changes in the mechanical advantage of their constituent muscles greatly affect the forces and movements they can generate[31].

Properties of the periphery also offer significant simplifications for neural control. For example, when an octopus uses a tentacle to reach for an object, it generates a propagating bend that moves within a single plane and has a tangential velocity (a velocity in the direction of movement) that is stereotyped. Controlling this bend may simplify the control problem of moving a muscular hydrostatic structure with many degrees of freedom[32]. The musculoskeletal properties of the human body restrict the feasible accelerations that can restore posture in response to a perturbation that causes the body to sway. These restrictions provide a rationale for understanding the rotations around the ankle or hip that are experimentally observed[33]. Using a mass–spring model to represent running animals clarifies the absorption and release of energy by the musculoskeletal system, and provides a unified perspective for understanding animals with different numbers of legs and different body masses, locomoting at different speeds and over terrains of different stiffnesses[34]. The relative stiffness of muscles around a joint create an equilibrium point to which a limb will return after perturbation, and this may be exploited by spinal cord networks to simplify control[35].

Continuous feedback from the body and the environment

The most important evidence suggesting that the nervous system cannot be the exclusive focus for understanding adaptive behavior is that it continuously receives and responds to feedback both from the movements that it induces in its own periphery and from the surrounding environment (Fig. 1D).

Feedback plays vital roles in normal developmental processes. In rats, locomotion takes on its adult form after postnatal day 15 (P15). Immobilizing one leg from P1 to P13 does not prevent the development of a normal locomotor pattern 1–2 weeks after the leg is freed from restriction; but it does cause a persistent deficit in the duration and timing of electromyogram (EMG) to leg muscles of the restricted side, suggesting that feedback from movement contributes to normal neural development[36]. Thelen and associates have obtained data suggesting that the development of reaching movements in infants is related to the ability of the infants to adjust for the dynamics of the reaching movements that they spontaneously generate (that is, fast or slow, weak or strong movements) by feedback from their success in reaching their goals[37].

In adult animals, proprioceptive feedback plays a fundamental role in the generation of normal patterns of motor activity. Pearson and his colleagues demonstrated that phasic feedback from stretch receptors was essential for maintaining the frequency and duration of normal flying movements in the locust[38]. These results led Pearson to suggest that there was no such thing as a pure central pattern generator, since all pattern generators need sensory feedback to generate biologically useful patterns of activity[39]. Recent results from the leech have provided further evidence for the fundamental role of sensory feedback in normal pattern generation. First, the frequency of firing of swim interneurons is too low in reduced preparations to provide functional outputs, but in the presence of normal sensory feedback, the neurons fire at an effective rate. Second, a realistic model of the leech body does not generate effective crawling movements when activated with fictive crawling motor patterns observed in isolated nervous systems, but does generate effective movements when activated by crawling motor patterns observed in intact leeches, which only occur when sensory feedback is present[40]. In the absence of feedback from an animal's own movements, the nervous system may not generate meaningful activity patterns for behavior.

Feedback from the environment, and the dynamical properties of the environment itself, also play a vital role in the generation of adaptive behavior. A detailed biomechanical model of the lamprey indicated that the hydrodynamics of water was essential for generating normal traveling waves of contraction along the body of the animal. If this hydrodynamics was not present, the model generated inappropriate whole body contractions. Removing a lamprey from water and inducing it to swim generated the same inappropriate movements predicted by the model[41]. Thus, the embedding of an animal's body in an environment is crucial for the behavior that it generates.

A broader viewpoint and its implications

These observations can be summarized using two contrasting musical metaphors. The nervous system is often seen as the conductor of the body, choosing the program for the players and directing exactly how they play. The results reviewed above suggest a different metaphor: the nervous system is one of a group of players engaged in jazz improvization, and the final result emerges from the continued give and take between them. In other words, adaptive behavior is the result of the continuous interaction between the nervous system, the body and the environment, each of which have rich, complicated, highly structured dynamics. The role of the nervous system is not so much to direct or to program behavior as to shape it and evoke the appropriate patterns of dynamics from the entire coupled system (see Fig. 1E; Ref. 42). As a consequence, one cannot assign credit for adaptive behavior to any one piece of this coupled system.

There are several important implications of this broader viewpoint. New behaviors might emerge that are properties only of the coupled system. For example, as a predator and prey interact, their unfolding behavior depends both on their own actions and the changing behavior of the other animal. Furthermore, each system cannot control all aspects of the behavior of the system to which it is coupled. Rather, each system's response depends on its own internal state as well as the perturbations it receives from the other system. Instead of asking 'What is the neural basis of adaptive behavior?', one should ask 'What are the contributions of all components of the coupled system and their interactions to adaptive behavior?'

Versions of this viewpoint have been previously articulated by others. The view of behavior espoused by cybernetics, the theoretical study of control in animals and machines[43], and, in particular, Ashby's view of the brain as a dynamical system that generates appropriate behavior[44], is consonant with this viewpoint. Maturana and Varela's views on the nature of biological organization and its consequences for adaptive behavior also emphasize the ongoing interactions between the organism and the environment as essential for maintaining the self-organizing integrity of the organism[45,46]. Ecological psychology has long emphasized such a dynamical perspective on perception and action, and the importance of organism/environment mutuality[47–50]. Altman and Kien have emphasized that the sensory and biomechanical contexts in which neural activity occurs, as well as the contexts created by the activity within and between different neural networks, are crucial for the flexibility and richness of behavior[51,52]. Within cognitive science, there is a growing awareness that one must take into account the embeddedness of the brain in the body and world to understand aspects of cognition[53].

Recent work in the field of autonomous robotics has emphasized that intelligent behavior is an emergent property of an agent embedded in an environment with which it must continuously interact[54]. Raibert and Hodgins, who have built robots that hop, run, and jump, have made this argument: 'Many researchers in neural motor control think of the nervous system as a source of commands that are issued to the body as "direct orders". We believe that the mechanical system has a mind of its own, governed by the physical structure and the laws of physics. Rather than issuing commands, the nervous system can only make "suggestions" which are reconciled with the physics of the system and the task'[55]. In our own work on biologically-inspired robotics, done in collaboration with Roger Quinn and Roy Ritzmann, we have demonstrated that incorporating biomechanical properties similar to those of insects into hexapod robots can simplify their control, allowing them to traverse irregular terrain and making them robust to lesions[56,57].

Adopting this broader viewpoint poses difficulties for an experimentalist: it is already a daunting task to understand the neurons and neural circuits in isolation; taking into account the periphery and the environment only makes a hard problem even harder. To cope with the challenges of this broader viewpoint, we and others have begun to utilize a promising methodology termed computational neuroethology[58,59].

Computational neuroethology involves creating joint models of the relevant parts of an animal's nervous system, body and environment. This requires experimental investigation not only of neural circuitry, but also of the relevant aspects of an animal's biomechanics and ecological niche, and then construction of models that incorporate these components. Using these models, one can study the contributions of the components to adaptive behavior, and the new phenomena that may emerge from their interactions. Adopting this methodology has consequences for experimental neuroscience. For example, assessing the importance of changes in a motor program can only be done by 'playing it' through the body, or a model of the body, and observing the behavioral consequences. This approach is distinctive from that of computational neuroscience[60], in that biomechanics and ecology are on an equal footing with neural activity, and the primary focus is relating neural activity to behavior.

Three broad approaches can be distinguished within computational neuroethology, each of which has benefits and drawbacks. First, one can construct biologically realistic models motivated by experimental questions. Drawbacks of these models are the extensive experimental work required to set the model parameters, and the complexity of the models, which are difficult to analyze theoretically. The advantage is that one can make quantitative, experimentally testable predictions. Examples of this approach are realistic models of neural control and biomechanics of reptilian tongue-lapping[31], leech crawling[61] and lamprey swimming[41,62].

Second, one can construct more abstract models motivated by theoretical questions. Drawbacks of these models are that they may not make quantitative, experimentally testable predictions. The advantages are that they highlight key features of a problem, can determine what is or is not essential, have few parameters to set and are tractable to theoretical analysis. Examples of this approach are the creation of simplified models of insects[58,63], nematode worms[64], hoverflies[65], frogs[66], and more abstract 'agents' capable of locomotion, chemotaxis, learning and visually guided behaviors[67–69]. A coupled model of an oscillator and a pendular limb demonstrated that motor behavior emerges from interactions between neural and physical dynamics[70]. Mathematical tools of dynamic systems analysis have been applied to understanding some of these simpler models[42].

Third, one can create physical models by building devices that exhibit properties of the system under study. Drawbacks of this approach are that building an actual device can be difficult, slow, and expensive, and it may fail to work for reasons that have nothing to do with one's understanding of the biological system. There are great advantages for engineering, since it would be a major advance to create robots with the flexibility and adaptiveness of animals. There are also scientific advantages. Building an 'animal' provides a unique perspective on how it works. What aspects of biomechanics, neural control, or environment are important for a behavior, and which can be safely ignored? What are possible solutions that generate equivalent results? Will one's ideas about how a system works actually succeed in interaction with the real world? Examples of this approach are insect-like hexapod robots[57,71–73], robot crickets that can respond to mating calls[74], and robots guided by insect-like compound eyes[75].

In summary, several lines of converging experimental evidence suggest a broader viewpoint in which the roles of the brain, body and environment are fully appreciated. The emerging methodology of computational neuroethology, in which joint models of neural circuitry, biomechanics and environment can be studied, provides an effective means to progress.

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LETTERS TO THE EDITOR

The functional neuroanatomy of episodic memory retrieval

Fletcher, Frith and Rugg[1] gave an insightful and clearly written description of the relationships between brain structures and episodic memory processing, as currently discovered. They based their sketch on studies that have used dynamical imaging methods, particularly positron emission tomography (PET), and emphasized that both the 'extent of the contribution of prefrontal cortex to episodic memory, and the fact that encoding and retrieval operations…are differentially lateralized, were unexpected on the basis of evidence from lesion studies' (Summary).

While I would underline as well that the contribution of the prefrontal cortex to episodic memory processing was – with a few exceptions[2] – less apparent from the results of lesion studies, there exist since the 1990s a number of reports on patients with focal brain damage lending support to the lateralized processing of episodic memory (retrieval). Starting with the papers of Kapur *et al.*[3] and Markowitsch *et al.*[4,5], several cases have been collected in the past years[6–8] that all point to a differential involvement of the two hemispheres in memory retrieval, with the retrieval of episodic memories being disturbed after principally right-hemispheric damage.

As was discussed in a theoretical contribution on the possible brain loci involved in episodic memory retrieval[8], the difference between the results of studies based on functional imaging and those based on brain-damaged patients is that the damaged loci are usually not confined exclusively to one hemisphere (but see