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.

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. 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. 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.

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. 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. 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.

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. 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. 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.

Thus, motor neuronal output is transformed significantly by the properties of the body. These data...
The nervous system (NS) is embedded within a body, which in turn is embedded within the environment. This feedback may fundamentally alter the behavior of the nervous system itself. Many sensory inputs are extensively pre-processed by the body itself, and outputs of motor neurons are transformed by muscle and the biomechanical properties of the body. The matching and complementarity between their properties occurs in animals such as insects or frogs, whose larval and adult bodies differ. Since sensory and motor cortical maps are plastic, even in the adult, coordinated changes in motor control and peripheral structures occur in animals such as insects or frogs, whose larval and adult bodies differ. Since the nervous system and periphery are 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. Another example of coordinated evolution is provided by the feeding behavior of the leop- ard frog Rana pipiens, which uses a mode of feeding common to all primitive anurans for large prey, handling 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.

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. Coordinated changes in motor control and peripheral structures occur in animals such as insects or frogs, whose larval and adult bodies differ. Since sensory and motor cortical maps are plastic, even in the adult, and the morphology of the body changes throughout the life span, 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. 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.

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. Hard skeletal elements impose other...
constraints: for example, activation of postural muscles must minimize shear stresses on bone19. Structures composed entirely of muscle, such as tentacles, tongues or trunks (muscular hydrostats) have an extraordinarily large number of degrees of freedom20, but changes in the mechanical advantage of their constituent muscles greatly affect the forces and movements they can generate20.

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 freedom21. The musculoskeletal properties of the human body restrict the feasible accelerations that can restore posture in response to a perturbation, and this 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 stiffnesses27. 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 control20.

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 P11 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 development14. 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 the success in reaching their goals15.

In adults, proprioceptive feedback plays a fundamental role in the generation of normal patterns of postural activity16. Thelen and his colleagues demonstrated that phasic feedback from stretch receptors was essential for maintaining the frequency and duration of normal flying movements in the locust16. 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 activity10. 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 clawing movements when activated with fictive clawing motor patterns observed in isolated nervous systems, but does generate movements when activated by clawing motor patterns observed in intact leeches, which only occur when sensory feedback is present17. Third, sensory 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 model20. 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 continuous 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, 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 machines41, and, in particular, Ashby’s view of the brain as a dynamical system that generates appropriate behavior44, 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 organism55–58. Ecological psychology has long emphasized such a dynamical perspective on perception and action, and the importance of organism/environment mutuality55–58. Allman and Kien have emphasized that the sensory and biomechanical contexts in which neurons operate occur, as well as the contexts created by the activity within and between different neural networks, are crucial for the flexibility and richness of behavior59. 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 cognition60.

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 interact41. 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’41. In our own work on biologically-inspired robotics, done in collaboration with Roger Quinn and Roy Rittmann, 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 mechanical dynamics70. Mathematical tools of dynamic systems analysis have been applied to understanding some of these simpler models42.

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 neuroethology60,61. 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 then assess the importance of changes in a motor program. To do this, one can construct more abstract models motivated by theoretical questions. The advantages 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 insects62–64, nematode worms65, hoverflies66, frogs67, and more abstract “agents” capable of locomotion, chemotaxis, learning and visually guided behaviors68–70. A coupled model of an oscillator and a pendulum limb demonstrated that motor behavior emerges from interactions between neural and physical dynamics68. Mathematical tools of dynamic systems analysis have been applied to understanding some of these simpler models68.

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 robots71–73, robot crickets that can respond to mating calls74, and robots guided by insect-like compound eyes75.

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.

Selected references

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Fletcher, Frith and Rugg1 gave an insightful episodic memory retrieval the fact that encoding and retrieval oper-
ations... 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 - 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 damaged loci are usually not confined to the hemisphere in memory retrieval, with the retrieval of episodic memories being disturbed by the damage to one hemisphere (but see

Letters to the Editor

The functional neuroanatomy of episodic memory retrieval

Fletcher, Frith and Rugg gave an insightful description of the rela-
tionships between brain structures and episodic memory processing, as currently discussed. 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 the prefrontal cortex to episodic memory, and the fact that encoding and retrieval oper-
ations... 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 - 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 Karp et al. and Markowitsch et al., several cases have been collected in the past years that all point to a differential involvement of the two hemispheres in memory retrieval, with the retrieval of episodic memories being disturbed by the damage to one hemisphere (but see...