Primer

Current Approaches to the Study of Movement Control

Alla Katsnelson

Almost every sensation we experience or decision we make results in movement. Actions like reaching for a glass of water, shifting a car's transmission from first to second gear, or petting a dog are generally accomplished without much difficulty or reflection. But in order to pet that dog, the brain must take into account an enormous array of information, including the starting position and velocity of the arm, the force required in the fingers to stroke rather than annoy, and the dog's position in space, in order to signal the stimulation of muscle and angling of joints for the necessary movement.

The brain must therefore integrate sensory information from several sources—vision, touch, and even the internal sensors on muscles and joints—to generate an appropriate movement. To understand how these elements of motor cognition interact to produce coherent motor behaviour, research is conducted at several levels. Psychophysical studies of simple movement tasks define the range of possible motor behaviours and adaptations (Figure 1). Electrophysiological recordings from neurons in the sensorimotor system can resolve signals present in the brain during particular motor behaviours. And more recently, computational models are being used to simulate simple movement tasks and compare the outcomes with real behaviours and real neural elements, thereby testing ideas of how brain signals are processed to achieve sophisticated motor control.

One mechanism responsible for controlling numerous biological processes is feedback. Broadly speaking, feedback mechanisms use the outcome of a biological process to continually adjust and fine-tune that process, whether it be gene transcription through operons, hormone production within the body, or the act of reaching for a target. While feedback mechanisms are certainly a factor of motor control—sensory feedback, for example, allows you to judge whether you have stroked your dog—feedback cannot be the primary biological mechanism for control of an ongoing movement, simply because it takes too long. The time delay for visual feedback on an arm movement is estimated to be 150–250 ms, but the brain has the capability to execute movements within as little as 150 ms (Kawato 1999).

Instead, researchers have proposed the existence of internal models as a key mechanism for regulating motor control. Simply put, an internal model is a learned script in the central nervous system that takes into account the dynamical properties of the body to predict the consequences of a motor command (Davidson and Wolpert 2003). From the fact that one brain commands the body through a lifetime of massive changes in size and density, it is immediately obvious that the basis for predictions engendered by internal models must be constantly modified with experience. Distinct internal models are thought to act as predictors for distinct parameters of a motor act—for example, one internal model might represent hand velocity and another might represent position in space. In this sense, internal models have been referred to as "motor primitives" or "building blocks" (Wolpert et al. 2001) that might interact to generate specific coordinated movements.

Internal models themselves are of two types (Figure 2). Forward internal models predict sensory consequences of a planned motor event, and inverse internal models calculate how a movement should be controlled to achieve the desired consequence to essentially transform the desired

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Figure 1. A Psychophysics Experiment on the Control of Reaching Movements
The subject is instructed to make arm movements while holding a manipulandum, which can exert forces on his arm during the movement. The ability to adapt to such forces can give insight into the neural organization underlying movement. (Photograph courtesy of Reza Shadmehr.)

Primers provide a concise introduction into an important aspect of biology that is of broad and current interest.

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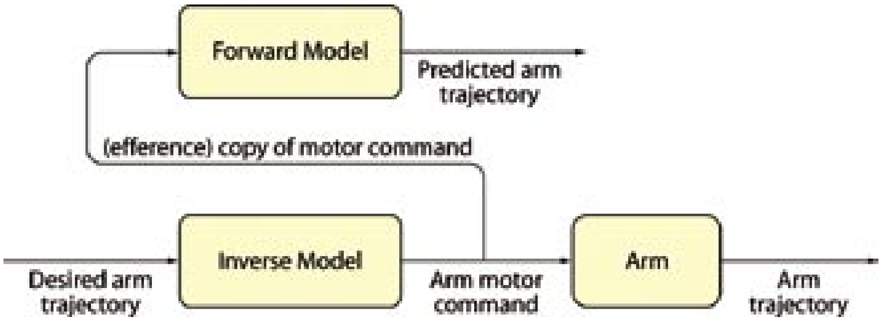

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Figure 2. Internal Models in the Control of Movement
The brain is hypothesized to use forward models and inverse models to control movement. Both models are subject to change based on errors that are computed by comparing predicted and actual trajectories. (Flowchart adapted from Kawato [1999].)

movement into a motor command based on this calculation. In a review synthesizing a full-scale concept of how multiple internal models might interact with each other, Wolpert et al. (1998) described a complex modularity between different parameters and a computational mechanism that could account for the dynamic interaction between the different modules.

Behavioural Relevance of Internal Models

While internal models for motor planning were initially conceived as theoretical constructs to deconstruct the cognitive processes' underlying movement, psychophysics-based research conducted over the last decade has made much progress in substantiating the existence of internal models in human subjects as well as nonhuman primates and also in defining how these models function for different parameters of a movement task. In a well-designed psychophysical study, hypothetical neurophysiological processes are tested by evaluating subjects' responses to experimentally controlled stimuli and comparing the results to theoretical predictions. Advances in robotics have refined the ability to control the experimental environment.

In an early experiment on the existence of internal models, subjects were asked to perform reaching movements while holding a robotic handle that could exert unexpected forces during the movement. They at first made errors in the task, but with practice learned the correct movement trajectories that took the learned forces into account. When the forces were no longer applied, subjects again made errors, the trajectories of which were mirror images of the errors initially produced when the forces were first applied (Shadmehr and Mussa-Ivaldi 1994). The symmetry of these errors, as well as the observation that subjects were consistently able to generalize training experience to movement outside the area in which they were trained, suggested that subjects generated an internal model of hand trajectory to deal with the applied forces and that with experience this model became more refined for the task.

Experiments such as this one, which examine how broadly learning of specific motor tasks is generalized outside the training conditions, provide a key paradigm for investigating the functional organization of internal models. Generalization experiments are designed to tease out different components of a motor task (e.g., arm velocity and direction) and involve analysis of the systematic errors made when new forces are imposed on trained tasks.

Kawato (1999) explains that theoretically, if generalization is perfect, then a subject who has learned a motor task under specific conditions (e.g., a force field) can go on to perform it perfectly in a different context (e.g., without the force field), adapting the parameters (e.g., velocity) appropriately without any further training. Such a model would be something of a monster, because it would have to be able to simultaneously analyze all of the contributions to a motor task. On the other hand, if motor learning is not generalized at all beyond the trained task, then any changes in context would bring subjects back to square-one error levels. This scenario would be reflective of an internal model that was essentially a look-up table, requiring rote memorization of specific conditions related to specific outcomes. Instead of either of these extremes, studies have consistently shown an intermediate degree of generalization, with changes in context disrupting the task but not setting performance to zero (see Imamizu et al. 1995; Conditt et al. 1997; Kawato 1999). This imperfect generalization supports a modularly organized structure of internal models, like that proposed by Wolpert et al. (1998), described above.

To date, internal models encoding several distinct parameters of motor control in the arm have been hypothesized based on generalization experiments. A few examples include hand velocity (described above; Thoroughman and Shadmehr 2000), inertial anisotropy (the relationship between hand acceleration and arm inertia; Flanagan and Lolley 2001), and load force (a measure of the relationship between movement and hand grip; Flanagan and Wing 1997). Importantly, generalization experiments can also reveal that parameters, such as timing information, are *not* represented as internal models (Conditt and Mussa-Ivaldi 1999).

An elegant experiment conducted in space on the Neurolab space shuttle mission suggested the existence of an internal model relating to gravity by examining the timing of a simple catching task (McIntyre et al. 2001). During space flight (at zero gravity) as well as before and after (at normal Earth gravity), experimenters measured limb stiffness and muscle activation in the bicep (two components of catching) while astronauts caught a ball dropped from above at different initial speeds. Although the astronauts could see that the ball was not accelerating as it would on Earth, subjects tended to start catching movements too early in zero gravity, reflecting a partial generalization of the effects of gravity.

In this month's issue of *PLoS Biology*, Hwang et al. (2003) address an apparent contradiction among results of motor-learning experiments. Internal models of both acceleration and velocity show broad generalization in space. This would imply that we do not form an internal model of position. However, the finding that human subjects can readily adapt to position-dependent force fields shows that position must be encoded. To resolve this issue, the authors examined adaptation to forces that were dependent on both position and velocity of the limb. The results suggest that both position and velocity are encoded in a multiplicative fashion (via a gain field). The most parsimonious way to view this finding is that neural elements actually encode a direction signal that is modulated by position; such a conclusion is strongly supported by the results of neural recording experiments in motor cortex.

Practical Implications

Understanding the control of movement is not just an abstract exercise. As another paper in this month's issue of *PLoS Biology* shows, signals extracted from the brain can be used directly to control artificial prosthetic devices, which in principle could be adapted to help people with permanent paralysis interact with their environment. Carmena et al. (2003) recorded multiple signals from the cortex of monkeys trained to perform reaching and grasping tasks. These signals, in turn, were used to control a robotic arm to perform the same tasks, and soon the animals were able to directly control the artificial device apparently by simply thinking about the movement. The investigators recorded signals from many brain areas and used several types of empirically derived procedures to extract the necessary signals from the neural-recording data. They demonstrated that multiple cortical areas contain information about hand position, velocity, and other relevant signals, albeit to different degrees. They further showed data suggesting that the brain may adapt to incorporate an internal model of the artificial manipulandum. As more research fills in the gaps in our understanding of the cortical control of movement, it is possible that even more sophisticated control of such artificial devices could be practically achieved.

Conclusions

A major goal in cognitive research, of course, is to directly demonstrate hypothesized mechanisms of cognitive processes in the cellular structure and organization of the brain. Internal models are powerful concepts for understanding how the nervous system breaks down motor tasks. Psychophysical experiments such as those described above can provide a theoretical framework from which to approach neurophysiological investigation, but comparisons of neuronal firing properties, both in the cerebellum and the cortex, with mathematical properties of computational models can bring these models closer to a physiological reality. ■

References

Carmena JM, Lebedev MA, Crist RE, O'Doherty JE, Santucci DM, et al. (2003) Learning to control a brain–machine interface for reaching and grasping by primates. PLoS Biol 1: DOI: 10.1371/journal.pbio.0000042.

Conditt MA, Mussa-Ivaldi FA (1999) Central representation of time during motor learning. Proc Natl Acad Sci U S A 96: 11625–11630.

Conditt MA, Gandolpho F, Mussa-Ivaldi FA (1997) The motor system does not learn dynamics of the arm by rote memorization of past experience. J Neurophysiol 78: 554–560.

Davidson PR, Wolpert DM (2003) Motor learning and prediction in a variable environment. Curr Opin Neurobiol 13: 232–237.

Flanagan JR, Lolley S (2001) The inertial anisotropy of the arm is accurately predicted during movement planning. J Neurosci 21: 1361–1369.

Flanagan JR, Wing AM (1997) The role of internal models in motion planning and control: Evidence from grip force adjustments during movements of hand-held loads. J Neurosci 17: 1519–1528.

Hwang EJ, Donchin O, Smith MA, Shadmehr R (2003) A gain-field encoding of limb position and velocity in the internal model of arm dynamics. PLoS Biol 1: DOI: 10.1371/journal.pbio.0000025.

Imamizu H, Uno Y, Kawato M (1995) Internal representation of motor apparatus: Implications from generalization in visuomotor learning. J Exp Psychol Hum Percept Perform 21: 1174–1198.

Kawato M (1999) Internal models for motor control and trajectory planning. Curr Opin Neurobiol 9: 718–727.

McIntyre J, Zago M, Berthoz A, Lacquaniti F (2001) Does the brain model Newton's laws? Nat Neurosci 4: 693–694.

Shadmehr R, Mussa-Ivaldi FA (1994) Adaptive representation of dynamics during learning of a motor task. J Neurosci 14: 3208–3224.

Thoroughman KA, Shadmehr R (2000) Learning of action through adaptive combination of motor primitives. Nature 407: 742–747.

Wolpert DM, Miall RC, Kawato M (1998) Internal models in the cerebellum. Trends Cogn Sci 2: 338–347.

Wolpert DM, Ghahramani Z, Flanagan JR (2001) Perspectives and problems in motor learning. Trends Cogn Sci 5: 487–494.

Community Page

Biodiversity Conservation Demands Open Access

Gustavo Fonseca and Philippa J. Benson

Over the past 25 years, conservation biology has become a credible scientific discipline—and in the process has brought a steady supply of disturbing facts to light. We now know that the natural habitat around the world has been and continues to be threatened and destroyed at alarming rates, with more than 60% of terrestrial plant species now finding safe harbor on less than 1.4% of the Earth's landmass. The Atlantic Forest region of South America (Figure 1), for example, has been cut to less than 7% of its original range, and more than 110 species

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Figure 1. Paraguay Atlantic Forest
The lush forested ecosystems of the Atlantic Forest, such as shown here in Paraguay, have been cut to less than 7% of their original extent, eliminating the habitat for thousands of plant and animal species. (Photograph by Russell Mittermeier.)

still living within the remaining area are threatened with extinction. Since the 1600s, over 250 species of birds, mammals, reptiles, and amphibians worldwide have become extinct as a result of human activities. In the past four years alone, 121 species have been added to the 11,167 already known to be threatened with extinction (i.e., those currently on the Red List of Threatened Species issued by the Species Survival Commission of the World Conservation Union [IUCN]).

At the same time, the conservation status of hundreds of thousands of described terrestrial, aquatic, and marine species remains unknown. To develop effective conservation actions, scientists must continue to uncover basic information, such as how much continuous landscape many species need to survive, and researchers also need to understand the complex dynamics among disease factors, climate change, and human activities that may further threaten species' survival. The tension between what we know and what we need to know to develop effective responses to the growing threats to biodiversity is driving a growing army of researchers in academia, government institutions, and nongovernmental organizations (NGOs) to learn how to read and respond to the pulse of the planet more accurately.

At the Center for Applied Biodiversity Science (CABS) at Conservation International, we focus on monitoring, understanding, and protecting the Earth's biodiversity hotspots, areas where endemic species are both highly concentrated and highly threatened (see www.biodiversityhotspots.org). Our approach is complemented by a focus on a few other major areas, also biodiversity rich, but that are still mostly intact—the High Biodiversity Wilderness Areas—in particular, the large tropical rainforest blocks of Amazonia, the Congo region of Central Africa, and the island of Papua New Guinea. Unless we take care of emerging threats to these areas, they will become the hotspots of the future. Our biodiversity conservation research must also consider a multitude of other factors, addressing not only the biological parameters, but also the social, cultural, and economic realities of these regions.

Although free and open access to the progress of scientific thought is vital for the advancement of many disciplines, it is particularly necessary for conservation science. This is true not only because resources for high-cost items such as scientific publications are limited in many of the countries with the most complex and urgent conservation problems, but also because effective conservation solutions must draw ingredients from a wide range of disciplines. Many efforts to foster access to conservation-related information are now being developed, some anchored in models of traditional print publishing and others focused on developing Web-based resources such as online journals, electronic forums, and literature archives. We at CABS are taking an active role in many of these kinds of endeavors (Figure 2).

The imperative of open access to conservation is perhaps best illustrated by the Tropical Ecology, Assessment, and Monitoring (TEAM) Initiative, set up as part of CABS in 2002 with support from a grant from the Gordon and Betty Moore Foundation. TEAM is a growing network of international field stations that use novel standardized research protocols to monitor biodiversity in the world's biologically richest and most endangered regions. The Initiative was created with the aim of accurately tracking large-scale changes in tropical forest ecosystems, in part to gather information that will allow scientists to distinguish the effects of human disturbance from the natural ebb and flow of biological processes. Armed with this up-to-date information, conservation planners will be able to design conservation actions that address the most urgent and real conservation needs more effectively. TEAM researchers, who will eventually include scientists in a network of 50 tropical forest field stations, will add data to a centralized location where it will be analyzed and distributed. By making data and analyses freely available, the Initiative will build an open resource fully stocked with quality information that is comparable across multiple sites, allowing the assessment and monitoring of key indicators of

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the health of tropical ecosystems, with the potential for benchmarking the effectiveness of different conservation strategies. In addition, by making TEAM analyses publicly available, the Initiative will create a forum in which researchers from widely disparate disciplines can learn from each other's disciplinary languages and practices and can invent ways of bringing together their skills and knowledge (see www.teaminitiative.org).

CABS is also designing other mechanisms to provide the open-access cross-searchable information necessary to achieving conservation goals. For example, we've designed a Web-based conservation Knowledge Management System (KMS) (http://cabs.conservation.org/cabskms) that allows users to search, organize, and share data and other resources, including publications. We are also supporting SALVIAS (Synthesis and Analysis of Local Vegetation Inventories across Scales), a project led by researchers at the University of Arizona in Tucson, and by the recently created Andes and Amazon Biodiversity Information Network, designed to assemble, maintain, and disseminate a global database from diverse heterogeneous sources, uniting information on local plant abundance, biomass, productivity, and diversity. CABS has also been helping the United States Geological Survey develop a large collaborative network among academic institutions, NGOs, and for-profit companies, to meet the mission of the National Biological Information Infrastructure (www.nbii.gov). This includes the Towards Best Practices (TBP) eForum, a large searchable database of biological data, information, and scientific literature that combines a free archive with an open electronic forum for dissemination and discussion of tested conservation practices (www.nbii.gov/datainfo/bestpractices).

These examples of models of sharing scientific information, together with a multitude of others that are now emerging, are based on a diverse set of economic incentives and schemes, most of which are still under evaluation. Which models are successful and sustainable will depend on changes in technology, in the culture of science and scientists, and in the marketplace. Perhaps the community of conservation scientists will lead the charge to push the boundaries of scientific publishing models. Although this community is diverse and dispersed, the rewards associated with finding and using reliable information as quickly as possible are increasing dramatically. Precious conservation dollars can be saved or put to more effective and rapid use by avoiding duplication of efforts through the wide and free dissemination of relevant information and by fostering the collaboration among researchers, policy-makers, and funders. These goals should no longer be allowed to fall hostage to the existing constraints imposed by the profit-driven publishing marketplace or by old-fashioned practices of handling scientific data. ■

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Figure 2. Conservation Priority Setting Workshop
In partnership with scientists and institutions around the world, CABS researchers are increasingly making use of open-access databases, species lists, and other types of biological information to identify global and regional priorities, to address upcoming threats, and to monitor the results of conservation interventions. (Photograph by Carly Vynne.)