Sensory and motor systems
Editorial overview
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Introduction

Virtually all sensation occurs in the context of some motor behavior. For example, we generally handle an object in order to feel its shape and texture, and knowledge of our movements is critical to interpreting these somatosensory signals. Similarly, visual signals must be interpreted with reference to the current position of the head and eyes. Auditory signals must also be interpreted with reference to the position of the head and ears. Even smelling and tasting involve a motor component: olfactory and gustatory information is generally acquired through active sniffs and chews.

Conversely, virtually all motor behaviors are influenced by sensory signals. This is obvious for actions which are triggered by a sensory stimulus. But even for an action which is triggered by an internal cue, effective motor planning requires accurate information about the state of the body. The position and velocity of body parts, and the external forces acting on the body, are all important variables in planning and executing an effective motor action.

For these reasons, sensory and motor neuroscience are deeply entwined. In tribute to this idea, we have chosen to devote this issue to articles that examine the integration of sensing and movement. In the past, it was not possible to devote a Current Opinion issue to this topic, for the simple reason that Sensory Systems and Motor Systems were two separate issues of the journal. This year, however, the editors of the journal — Cori Bargmann and Edvard Moser — decided to combine these two topics, and invited us to serve as guest editors. We saw this as an opportunity to emphasize the connections between sensory and motor neuroscience by organizing this entire issue around the theme of sensorimotor integration.

Contextual modulation of neural circuits: an overview

Sensory modulation of motor behavior, and behavioral modulation of sensory signals, are essentially two specific examples of the same general phenomenon. Namely, neural circuits do not operate in the same way at all times. Rather, the operation of a neural circuit is generally in a constant state of flux. For this reason, the relationship between the environment and the organism's behavioral choices is constantly changing.

This fundamental principle is clearly stated in the review by Palmer and Kristan. This review tackles an ambitiously broad subject: how context modulates behavioral choice. Drawing on examples ranging from leeches and locusts to mice and monkeys, these authors make the point that contextual modulation is pervasive at every level of the nervous system.

Invertebrate models

Some of the oldest and still most revealing of experimental preparations for studying sensorimotor integration are those that focus on organisms having relatively few neurons. In these organisms, sensorimotor circuits are often composed of only tens or hundreds of neurons. Many of these neurons are uniquely identifiable across individuals, and thus their function in the circuit can be unambiguously linked to their connectivity and their intrinsic properties.

Several reviews in this issue highlight the power of invertebrates for studying sensorimotor integration. Huston and Jayaraman provide a general overview of sensorimotor integration in insects. Srinivasan discusses a more specific example of insect sensorimotor integration: the visual control of navigation. This review illustrates how studies of sensorimotor integration can have direct applications to the design of robots. Finally, Blitz and Nussbaum describe how sensory signals regulate the selection of motor programs in the crustacean stomatogastric ganglion.

Behavioral modulation of vision and visual modulation of behavior

Humans are visual creatures, and so it is natural for us to turn to vision for examples of sensorimotor integration. The eyes and the head are highly mobile, and this means the visual system is always in motion. Indeed, the primate eye makes a rapid leap (called a saccade) once every several hundred milliseconds. A consequence of saccadic eye movement is that the visual scene is blurred for the duration of the eye movement. If the visual system did not account for this, we might confuse the motion of objects in the world with the motion of our eye. As it happens, the visual system deftly solves this problem by inhibiting visual signals for the duration of the saccade. The review by Ibbotson and Krekelberg surveys recent progress in understanding this rather mysterious trick that each of us performs effortlessly several times each second.

The review by Maimon takes a somewhat broader perspective on the behavioral modulation of visual signals. Maimon draws an explicit parallel between studies in monkeys and studies in fruit flies describing how visual signals are modified by behavioral state. This review proposes that research in fruit flies could shed light on the fundamental processes and mechanisms underlying complex phenomena in primates.

The function of visual processing is ultimately to guide behavior, and this can require rapidly integrating visual signals into the planning and execution of movements. The review by Davare et al. describes how the primate brain integrates visual and somatosensory information to guide reaching movements of the hand and arm. A striking finding from this literature is that visual signals can cause grasping movements to be updated very rapidly, within 100–150 ms, which places strong constraints on

what features of visually evoked neural activity are guiding this process.

Motor learning in rodents

Many sensorimotor integration tasks, particularly in vertebrates, involve a substantial amount of learning. Two of the reviews in this issue discuss the phenomenon of motor learning with a particular focus on rodent model systems. Some of the excitement associated with this field reflects the fact that the mouse genetics offers powerful tools for genetic perturbations of neural activity.

In his review, Olveczky argues that rodents have distinctive virtues as compared with two other classical animal models for motor learning, namely monkeys and songbirds. This review also argues that rodent motor learning suffers from too great a diversity of learning paradigms, and proposes a way forward for the field that emphasizes a shared group of core paradigms.

Costa also focuses on rodent motor learning, but emphasizes conceptual rather than practical issues. The viewpoint of this review is a 'selectionist' one: it emphasizes the role of the organism's internal state in initially generating a variety of motor behaviors, and argues that the role of the environment is to select among many such behaviors, and to refine these behaviors so that they are increasingly precise and useful. This review also discusses recent progress in understanding the roles of cortico-basal ganglia circuits in rodent motor learning.

Neural circuits for filtering self-induced stimuli

Sensory signals are triggered by both external events in the environment and an organism's own actions. Organisms generally must distinguish self-generated signals from external events. Solving this problem is an essential part of sensorimotor integration.

Self-movement creates ripples in the vestibular, proprioceptive, and visual systems. All these signals are integrated to create an accurate representation of self-movement. Moreover, the brain learns the relationship between motor commands and the multisensory representation of self-movement to produce an internal model, which is then used to produce a reliable prediction of how self-movement 'feels'. Cullen reviews what is known about this phenomenon in primates, and in particular, how the brain discriminates expected (active) self-movement from unexpected (passive) self-movement.

Internal models of self-movement have been proposed to reside at least partly in the cerebellum. Bastian reviews the evidence for this idea, along with evidence for an alternative hypothesis — namely, that the cerebellum's main role is to act as an internal 'clock' that controls the pace of self-movement. This review focuses on studies in humans, and highlights the relevance of sensorimotor

integration studies for understanding human neurological disorders.

How are internal models actually implemented, at the level of cells and synapses? The answer to this question is perhaps best illustrated by the electrosensory lobe of weakly electric fish. These fish generate electric fields which are perturbed by nearby objects, allowing the fish to sense these objects using its electrosensory neurons. The electrosensory lobe filters out electrosensory signals that are due to the fish's own movements. The review by Requarth and Sawtell describes recent progress in understanding the cellular and circuit mechanisms underlying these filters. Importantly, when the relationship between electrosensory signals and self-movement changes, the properties of these filters are also changed, due to plasticity in the electrosensory lobe.

Strikingly, the functional architecture of the cerebellar cortex has a strong family resemblance to that of the fish electrosensory lobe. Carey describes this architecture and discusses recent studies of synaptic plasticity in the cerebellum. This review also points out that not all cerebellar physiologists agree on where the major locus of cerebellar plasticity resides. In particular, the synapses downstream from the cerebellar cortex are also sites of plasticity, and this has been proposed to play a key role in fine-tuning the vestibulo-ocular reflex.

Medina also focuses on the cellular mechanisms of cerebellar motor control and motor learning. Specifically, this review focuses on the role of Purkinje cells, which form the sole output of the cerebellar cortex. Medina critically examines the question of what Purkinje cell spike trains actually encode, and concludes that Purkinje cells contribute to a wide range of processes — generating a motor command, serving as a 'teaching signal', and predicting errors — at different time points during the process of sensorimotor control and learning.

Noise and uncertainty

Sensorimotor integration is complicated by the fact that sensory cues are often not sufficient to completely specify the state of the world. Moreover, neural signals are always contaminated by noise, which may arise in sensory circuits and/or motor circuits. The presence of ambiguity and noise suggests that the best strategy for solving a sensorimotor task should take account of these sources of uncertainty.

Osborne highlights the importance of neural noise in the coordination of eye movements. This review argues that noise in sensory circuits, not motor circuits, is what limits the precision of eye movements. This in turn suggests that motor control strategies are adapted to minimize motor noise, and this helps account for some features of eye movement kinematics.

The reviews by Wolpert and by Krakauer and Mazzoni link these ideas to the framework of Bayesian statistical inference. The Bayesian view proposes that the brain contains a representation not only of the relevant variables needed to execute a movement (e.g. visual signals, proprioceptive signals, etc.) but also a representation of the uncertainty associated with each of these variables. These reviews describe recent evidence that sensorimotor control strategies do take account of this sort of uncertainty. A major challenge for this field is to understand how uncertainty is actually represented in the brain at the level of spike train ensembles.

Neuroethological perspectives

Many neurobiological studies use laboratory environments where sensory stimuli are precisely controlled and behavior can be precisely measured. By contrast, the field of neuroethology takes a different approach: these studies take their inspiration from natural animal behavior, and try to recreate sensorimotor integration tasks that the animal has evolved to perform very accurately. Indeed, these studies tend to deliberately choose animals that display amazing virtuosity in a specialized sensorimotor behavior.

One of these virtuosi is the echolocating bat. These bats use acoustic echoes to probe their environment while simultaneously executing spectacular aerobatic maneuvers and hunting for prey. Moss *et al.* describe how bats modulate their acoustic emissions depending on the nature of their environment, the distance and angle between their body and their prey, and even the presence of other bats — all to improve their prey capture performance.

Another virtuoso is the barn owl, which hunts small rodents by flying low over open ground, often in dim light or darkness. In this situation, an owl must make a rapid decision about where to strike, despite often having poor visual cues and competing auditory cues. Mysore and Knudsen describe how neural circuits in the midbrain guide target selection in this sort of task. Specific neurons in one region of the barn owl midbrain show abrupt 'switch-like' responses as the relative strengths of competing stimuli are varied, and recent studies have shed light on the mechanistic basis of this phenomenon and its implications for target selection.

Summary

The field of neuroscience still has a relatively primitive understanding of how sensory and motor signals are combined. Nevertheless, this problem is clearly a central one. We are struck by the enormous diversity and creativity of the experimental approaches that have been brought to bear on this question, as exemplified by the reviews in this issue. We would argue that future progress is likely to depend on continuing this diversity of approaches — but also on trying to increasingly synthesize these results in order to extract fundamental principles.