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EDITORIAL

Neurophysiology and computational neuroscience

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Issues 3–4 of the 200th volume of *Experimental Brain Research* are devoted to neurophysiology and computational neuroscience. Neurophysiology has remained a major focus of *Experimental Brain Research* since the founding of the journal in 1966 by an editorial board that included Sir John Eccles. Issue 3 continues this long tradition by including two reviews and five original articles that use or consider neurophysiological approaches to provide insights into sensory processing and sensorimotor integration by the nervous system.

Issue 3 begins with a review by Green and Angelaki regarding the processing of sensory inputs by the vestibular system. The vestibular system is vital for motor control and spatial motion perception. Over the years, studies of the vestibular system have served as an excellent model framework for investigating the basic strategies by which sensory signals are transformed into central representations that give rise to behavior. For this reason, *Experimental Brain Research* has published over 1,000 manuscripts related to the vestibular system. In the review by Green and Angelaki, the authors describe recent advances in identifying the neural correlates for a number of fundamental computations and transformations of vestibular signals implemented by brainstem–cerebellar circuits. These include the sensorimotor transformations for reflex generation, the neural computations for inertial motion estimation, the distinction between active and passive head movements, as well as the integration of vestibular and proprioceptive information for body motion estimation. The authors emphasize why the study of these problems has revealed important organizational principles (e.g., the concept of "internal models", multisensory integration, reafference, reference frame transformations) that are generally relevant for all sensorimotor systems. Although explicit neural correlates for such computations (e.g., internal models) have often been difficult to identify in other systems (e.g., limb control circuits), this review emphasizes the significant advances made in so doing in the vestibular system. As a result, studies of this system continue to have great potential to yield new insights into common neural processing strategies relevant for both reflexive and goal-directed, voluntary movement as well as perception.

A second review by Rizzolatti and Fabbri-Destro on the mirror neurone system begins with a short historical account of the important role of *Experimental Brain Research* in publishing much of the early animal work on mirror neurons at the end of the 1980s and early 1990s. Professor Rizzolatti recalls that in those days, *Nature* failed to recognize the importance of the work and declined publication. He was in good company: the same journal had earlier rejected the Nobel prize-winning work of Otto Krebs on the citric acid cycle. The bulk of the review focuses on the rapidly expanding literature on the mirror neurone system in humans which has been made possible by advances in neuroimaging, transcranial brain stimulation and clever behavioral experiments. These have led to an explosion of interest that had never been anticipated in the early days. Indeed, the relevance of the mirror neuron system to cognition

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and a possible role of the "broken mirror" in explaining some aspects of autism is a fascinating extension of basic neurophysiology into complex human behaviors.

The first research report in issue 3 by Park et al. considers the effects of changes in core body temperature on the discharge properties of vestibular-nerve afferents in mice. The findings showed that both resting firing rate and sensitivity to head velocity of vestibular afferents were markedly reduced at low compared to high core body temperatures (31 vs. 36°C). The response properties of irregular afferents showed the greatest dependence on temperature with a threefold reduction in sensitivity to head velocity at the low versus high temperature. These findings suggest that changes in core body temperature (which varies considerably in accordance with the time of day and physical activity of the animal) could have a profound influence on the transduction of head movements.

The following paper by Middleton et al. considers processing of sensory information by the somatosensory system. High-frequency electrical stimulation is being increasingly applied in the treatment of numerous clinical disorders, yet little is known about how it affects the propagation of sensory information to the cortex. Using the whisker-related somatosensory system of rats, the authors found that an interaction between subcortical electrical stimulation and sensory stimulus-evoked afferent signals sets the cortex in an adapted state of responsiveness. This type of stimulation may find application in the treatment of sensory disorders where input cortical layers exhibit abnormally elevated levels of activity.

The following three papers lie at the boundary between neurophysiology and cognitive neuroscience and reflect the strong representation of this area of research in *Experimental Brain Research* at the present time. Hannah et al. take up the mirror neuron story with a behavioral experiment in which they ask whether watching a hand manipulate an invisible object increases the ability of subjects to subsequently recognize objects that typically involve that action. It does, scoring yet another victory for mirror neurons in influencing complex human behaviors, and illustrates the important interactions between systems involved in object recognition and object-directed action.

The report from Sciutti et al. again addresses questions about the interaction of motor control systems with perception. When we make a voluntary movement, efference copy of the motor command is thought to generate an expectation of sensory input that can be used to update internal models of motor control. The question is whether this expected sensory input is used to improve our haptic perception of objects. In the experiments, subjects compared the curvature of two virtual objects produced by a robotic manipulandum. In some trials they moved along the curvature themselves, hence generating an expectation of sensory feedback, whereas in others they were moved passively by the robot. There was no difference in the discrimination in the two sets, suggesting that the haptic perceptual system relies primarily on afferent tactile and proprioceptive inputs.

The paper from Wing et al. also tackles the question of combining information from multiple sensory sources. In this case, it is tapping a finger in time to auditory and/or proprioceptive cues. The work is framed in the context of maximum likelihood estimate (MLE) models in which information from two sources is combined according to the reliability of their signals. Examination of the variability of the tapping rate as well as the time of the tap with respect to the sensory cue shows that when subjects are provided with a combination of auditory and proprioceptive cues, then they are combined in the expected fashion. However, when the variability of the auditory cue is increased, then rather than weighting more importance to the proprioceptive cue, subjects persist in relying more strongly on information from the auditory modality.

The computational field is represented by two reviews and two original papers. In their review, Morris, Schmidt, and Bergman examine the problem of how the brain chooses optimally between alternative actions. Selection of action, in principle, should take into account both the expected rewards of the action and its costs. Availability of dopamine in the cortico-striatal network generally increases with expected reward, but there is also a sub-population of neurons that increase activity when there is increased expectation of costs (i.e. punishment). The authors propose that this latter group produces a smaller increase in dopamine levels than the more common group associated with positive rewards. In this way dopamine concentration becomes a crucial parameter for plasticity rules at cortico-striatal synapses. This would account for recent work showing that dopamine-dependent changes in synaptic plasticity are important in reward-related learning whereas during aversion learning, the levels of dopamine released only allow dopamine-independent forms of synaptic plasticity to occur.

Sensory feedback plays a fundamental role in control of a limb's stability. Generally, the main sensory contribution has been assumed to be via spindle afferents which report changes in muscle length. In their research paper, Mugge et al. suggest that force feedback from Golgi tendon organ afferents plays a significant role in maintaining stability.

The research paper by Wachter et al., returns to the role of the striatum in motor skill learning. Injection of protein synthesis inhibitors is well known to prevent learning-related changes in synaptic plasticity in hippocampus and cortex, but this has never been examined in the striatum. They find, reassuringly, that early injection of protein synthesis inhibitors into striatum disrupted skill learning. However, the same injections on days 10 and 1, at a stage when learning had reached a behavioral plateau, produced no changes in performance.

Finally, Giszter et al., review the evidence for modularity in the motor system, with particular reference to the body of work on motor primitives (in their terms, the simplest possible modules of behavior) in the spinal cord. They apply a Jacksonian approach and argue that these modules and primitives are in significant part already organized at birth, but are then overlaid by more complex control systems. It is the presence of these underlying modules of behavior that may not only explain why we can have exquisite human motor performance, but also explain why, in conditions like low back pain, we can sometimes have massively debilitating interference in motor control after relatively minor degenerative changes or trauma.