Sensory systems
Editorial overview
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David Fitzpatrick's main focus is on the primary visual pathway. His laboratory uses anatomical and physiological methods to work out how this sophisticated pathway extracts and interprets the myriad of visual clues that ultimately give rise to visual perception.

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Linda Buck is a Howard Hughes Medical Institute Investigator, whose focus is the exploration of the mechanisms underlying smell, taste, and pheromone sensing in mammals. She aims to understand how the nervous system translates thousands of different chemical structures into diverse perceptions and behavioral responses.

Abbreviations

V1	primary visual cortex
VR1	vanilloid receptor 1

Introduction

Sensory systems are the doors to perception and a logical starting point for exploring basic mechanisms of brain function. With advances in technology, different aspects of sensory systems have been targeted for investigation. The past hundred years has witnessed the development of a variety of different approaches that have been used to study the senses, including psychophysics, anatomy, electrophysiology, biochemistry, molecular biology, and more recently, genetics, imaging, and computational methods. Each of these approaches has contributed fresh insights into the workings of the brain and, in turn, provided an enriched understanding of the complexity of sensory systems and thus an expanded substrate for subsequent investigations, conceptualizations, and innovative applications of technology.

The past several years are no exception and, as the reviews in this issue attest, diverse experimental approaches continue to be the hallmark of research into mechanisms of sensation. We begin at the periphery, with advances in the understanding of molecules used to detect sensory stimuli and new insights into the coding of sensory information in sense organs. Between the sense organs and cortical centers, where signals are thought to be ultimately translated into conscious perceptions, lie structures through which sensory signals transit and are transformed. The processing of signals at these sites is the next focus in the series of articles presented here. At higher levels of the nervous system, the understanding of sensory systems becomes increasingly challenging, with queries into the functions of neocortical circuitry, the strategies used to encode different features of sensory stimuli, and the roles played by divergent streams of sensory inputs. Studies of these questions are reviewed in the final section of this issue.

The transformation of sensory stimuli into neural signals

Recent studies have provided a wealth of new information about how signals are transduced in peripheral sense organs, where our issue starts. Cermakian and Sassone-Corsi (pp 359–365) discuss the discovery of a subset of retinal ganglion cells in the eye that express a novel photopigment and are dedicated to signaling the central circadian clock mechanism. They also review one of the most surprising findings of the past few years: the presence of clocks in peripheral tissues. As a prime example of how new tools can yield advances in biological understanding, Montmayeur and Matsunami (pp 366–371) describe the identification of bitter and sweet taste receptors using bioinformatic approaches and discuss what the expression of these receptors in taste buds has revealed about the encoding of gustatory stimuli.

A landmark discovery five years ago was the identification of the vanilloid receptor 1 (VR1), the detector for painful stimuli on nociceptor neurons that transmit pain signals to the spinal cord. Di Marzo, Blumberg and Szallasi (pp 372–379) describe recent work on endogenous ligands for VR1 and mechanisms that alter VR1 ligand sensitivity. Both these topics are of keen interest for the development of pharmaceutical agents for treating pain syndromes. Despite intensive efforts to identify the auditory transduction channel of cochlear hair cells in the ear, this key molecule is persistently elusive. Strassmaier and Gillespie (pp 380–386) review the characteristic features of this channel and discuss potential candidates currently under consideration.

Sensory transformations en route to cortex

In each sensory system, signals generated in peripheral sense organs are relayed through one or more intermediate structures before reaching cortical areas. Although the benefit of this design is a matter of speculation, it is abundantly clear in at least some sensory systems that sensory signals undergo transformations at these intermediate way stations. These transformations provide information important to an understanding of how sensory signals are deconvoluted and then presumably combined in some manner in the neocortex to yield different perceptions.

In the olfactory bulb, the first intermediate in the olfactory system, signals from a thousand different types of peripheral odor receptors are segregated at stereotyped locations. Korsching (pp 387–392) discusses imaging studies that probe the roles of spatial and temporal coding in this structure as well as new evidence for another, different stereotyped map in the olfactory cortex, the next olfactory relay. Christensen and Hildebrand (pp 393–399) focus on a related question, the processing and coding of olfactory versus pheromone signals in the antennal lobe, the insect equivalent of the olfactory bulb. Although the role of signal timing in most sensory systems is still uncertain, it is of the utmost importance in the auditory system. Trussell (pp 400–404) discusses how giant synapses ensure temporal fidelity in auditory brainstem nuclei. He also reviews recent studies suggesting that these synapses may actually be under the control of a variety of neuromodulators. In the visual system, a significant degree of signal processing occurs in the peripheral sense organ, the retina. New findings, described by Vaney and Taylor (pp 405–410), reveal how a specific class of retinal ganglion cells becomes imbued with direction selectivity by the appropriate weighting of excitatory and inhibitory inputs from a subset of retinal interneurons, the starburst amacrine cells.

Cortical processing

In most sensory systems, information from the periphery travels through the thalamus before reaching the neocortex. Although heavily outnumbered by inputs from intracortical sources, the thalamocortical synapse plays a critical role in the introduction of sensory information to cortical circuits. Usrey (pp 411–417) reviews recent evidence for millisecond precision in spike timing at this synapse, and its significance for regulating the efficacy of information transfer.

Beyond the thalamocortical synapse lies the baffling and daunting complexity of the neocortex. Even in the best-studied sensory system, the visual system, we are still far from understanding the synaptic interactions between identified populations of neurons that shape the response properties unique to the cortex. Martin (pp 418–425) discusses the progress now being made in this arena by combining different approaches, including functional imaging, anatomical and physiological measures of connectivity, and computational methods. Shapley and Hawken (pp 426–432) review recent evidence suggesting that a substantial amount of information about color boundaries is represented in the responses of primary visual cortex (V1) neurons that have received relatively little attention. These V1 neurons respond to both color and luminance boundaries by selectively integrating feedforward inputs from color-opponent in the lateral geniculate nucleus of the thalamus. Read, Winer and Schreiner (pp 433–440) consider whether the functional rules that have emerged from studies of visual cortex are applicable to auditory cortex. They identify common themes in the organization of these cortical areas (parallel processing streams, modular organization with specificity in connections) as well as patterns of connectivity that are unique to auditory cortex.

Although most of the experimental work on cortical circuits has focused on explaining the receptive field properties of individual neurons, even simple sensory stimuli evoke a complex distributed pattern of activity whose spatial and temporal properties are thought to encode the attributes of the stimulus. Petersen, Panzeri and Diamond (pp 441–447) review recent efforts to probe the nature of population coding in somatosensory cortex, efforts that emphasize the importance of both spatially localized activity and precise spike timing. It appears that timing is also likely to be critical in taste. Katz, Nicolelis and Simon (pp 448–454) describe recent work on the dynamics of distributed coding in the gustatory system. They discuss how different types of information are evident at different epochs of time in the response of neurons in gustatory cortex, and how these time-varying responses may emerge from interactions between neurons in the same and spatially separate gustatory and somatosensory regions. At the other end of the experimental spectrum are studies of the human brain by functional smagnetic resonance imaging and positron emission tomography. Recent imaging studies, reviewed by Savic (pp 455–461), are generating surprising findings in the olfactory system, including the discovery that pleasant versus unpleasant odors stimulate different brain regions and that putative human pheromones generate sexually dimorphic responses.

Conclusion

In all too short a time, this volume will take its place on the library shelf or the web page directory serving as little more than a snapshot of the ever-changing stream of techniques and theories that continue to shape our analysis of sensory processes. Although it is impossible to predict the twists and turns that the field will take, there is ample cause to be optimistic that progress in understanding how we sense will continue to be fuelled by the creative application of new technologies to fundamental issues in transduction, transformation and cortical processing that have been discussed here.