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Introduction to the Special Issue on Multimodality of Early Sensory Processing: Early Visual Maps Flexibly Encode Multimodal Space

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As living organisms, we have the capability to explore our environments through different senses, each making use of specialized organs and returning unique information. This is relayed to a set of cortical areas, each of which appears to be specialized for processing information from a single sense — hence the definition of 'unisensory' areas. Many models assume that primary unisensory cortices passively reproduce information from each sensory organ; these then project to associative areas, which actively combine multisensory signals with each other and with cognitive stances. By the same token, the textbook view holds that sensory cortices undergo plastic changes only within a limited 'critical period'; their function and architecture should remain stable and unchangeable thereafter. This model has led to many fundamental discoveries on the architecture of the sensory systems (e.g., oriented receptive fields, binocularity, topographic maps, to name just the best known). However, a growing body of evidence calls for a review of this conceptual scheme. Based on single-cell recordings from non-human primates, fMRI in humans, psychophysics, and sensory deprivation studies, early sensory areas are losing their status of fixed readouts of receptor activity; they are turning into functional nodes in a network of brain areas that flexibly adapts to the statistics of the input and the behavioral goals. This special issue in *Multisensory Research*

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aims to cover three such lines of evidence: suggesting that (1) the flexibility of spatial representations, (2) adult plasticity and (3) multimodality, are not properties of associative areas alone, but may depend on the primary visual cortex V1.

1. Flexible Spatial Vision

Size constancy, or knowing that an elephant is always larger than a mouse even if their retinal images may be matched in size, is a fundamental visual ability. The key to perceptual constancy is the ability to dissociate the representations sub-serving perception from the proximal stimulus, e.g., the retinal image; this implies integrating retinal information with extra-retinal (contextual, motor, cognitive) cues. Sperandio and Chouinard (in this special issue) review strong evidence for this multimodal integration to occur as early as in V1, affecting the basic receptive field properties of a large fraction of neurons. Neuroimaging studies have repeatedly shown that V1, far from being a mirror of the retinal image, provides a representation of space that is close to what we perceive — more often than not, the location and size of fMRI activations in V1 match the perceived location and size of objects, not the proximal stimulus. Is this flexibility of spatial maps an intrinsic process of V1? Or does it depend on feedback from higher levels? This remains an open question, which is directly addressed in Schwarzkopf's review in this issue. Starting from the intriguing finding of a correlation between susceptibility to size illusions and individual's V1 surface area, his review offers suggestions for exploiting a range of experimental approaches to disentangle the contributions of V1 and other cortical areas in mediating spatial perception.

2. Adult Plasticity

If the layout of V1 activity can change depending on perceptual demands, then retinotopic maps cannot be rigidly determined by the anatomy of retino-thalamic pathways; they must retain a level of flexibility. How does this adult flexibility compare to the plasticity that the cortex displays during the critical period? To address this issue, Haak, Morland and Engel (this issue) juxtapose the effects of sensory deprivation in the adult *vs.* developing brain, highlighting the relative stability of the adult brain when deprived of oriented input (long-term orientation adaptation) or suffering a local loss of vision (retinal scotoma). The claim is that plastic changes can occur, possibly even in early sensory areas like V1, but they are generally not maintained as a stable feature of the system. This may reflect the cost-benefit trade off between reallocating resources to optimize sensory processing and the 'coding catastrophe' that may result when information is passed along to higher areas. Biasing this trade off in favor of plasticity is the aim of many rehabilitative approaches for ameliorating visual deficits. One possibility is that a residual plasticity potential is more prominent in areas where the sensory deprivation (and the necessary neural reorganization) is less dramatic — for example, in the 'transition areas' bordering the retinal scotomata. This hypothesis has guided the work on a large cohort of patients with heterogeneous deficits, led by the group of Bernhard Sabel, reviewed in this issue by Turco, Albamonte, Ricci, Fortini and Mariamore. Keeping in mind the varied outcome of these rehabilitative attempts, and more generally the potential for plastic reorganization of the adult cortex, is important, especially as sight-restoration technology marches on at a rapid pace.

3. Multimodality

Of course, while the adult plasticity potential is somewhat debated and generally small, dramatic reorganization of sensory areas results from early and congenital deprivations. Part of this reorganization involves the rerouting of preserved sensory inputs to deprived primary cortical areas, e.g., auditory input to V1 or visual input to A1. Considering these results, one may come to a profoundly new characterization of primary cortices. Rather than being identified by their dominant input, they may instead be better defined by their function: V1 as a spatial map, A1 as a temporal map. These maps are usually populated with visual/auditory signals, but their potential may also be fulfilled with information from other modalities. To what extent is this strategy part of the regular functioning of adult brains with intact sensory experience? Azevedo, Ortiz-Rios, Li, Logothetis and Keliris address this point in this issue, starting from a description of the interactions between visual and auditory signals in the spatial domain and noting how these may imply early and immediate integration of audio-visual information, which may be instantiated in V1. This leads to the more general issue of whether the integration of multisensory cues occurs at an early level of processing or at a later, cognitive stage. Besides investigating this question at a neurophysiological level, two behavioral approaches have established their utility over the past decades. Each is instantiated in the two original research papers in this special issue. Ho, Orchard-Mills and Alais adopt one such classic approach, which entails testing for spatial specificity of multisensory interactions — specifically temporal recalibrations. The rationale is that, if the integration is due to centralized cognitive processes, then it should generalize across spatial positions; spatial specificity, on the other hand, speaks against a cognitive-level hypothesis. The other traditional approach focuses on mandatory interferences across sensory modalities whereby strict modularity predicts little cross-sensory interference. This approach, forms the basis for Wahn and König's work. Both these experimental efforts lead to the suggestion that the ability to combine cues from different sources pervades all levels of sensory processing, both early and late.

4. Conclusions

Starting from the consideration of three very different problems, flexible spatial vision, adult plasticity and multisensory processing, the papers in this special issue converge on a similar solution: that multimodal, flexible integration of sensory information may not be found only at high-level, associative stages of sensory processing. At the same time, the special issue highlights the importance of acknowledging the limits of low-level flexibility, as cortical reorganization and sensory rehabilitation may in some cases have only partial or no success. By combining the evaluation of bold new ideas with critical reviews of the literature, the papers in this special issue provide a strong impulse towards establishing a new theoretical framework for multisensory processing and its plasticity.

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