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Visual cortical networks: of mice and men

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The visual cortical network consists of a number of specialized areas that are connected in a highly structured way. Understanding the function of this network is a milestone goal of visual neuroscience. This goal is pursued at different levels of description, including large-scale neuroanatomical as well as molecular and cellular perspectives. As a consequence, visual cortical networks are studied with a diverse set of methods across the order of mammalian species, ranging from the human all the way down to the mouse. Remarkable progress has been made at both ends of the spectrum. On the basis of work in humans, the last decade has seen ongoing refinements of the intricate functional organization of the cortical visual network. Neuroimaging studies have opened up the possibility to map individual visual areas, characterize their function and, search for an overarching organizational principle. Meanwhile, the mouse has become a valuable model system for early visual processing. A number of studies have demonstrated that basic response properties observed in higher-order mammals are also present in the mouse, making it possible to apply genetic tools to study visual network function. Here, we discuss the progress in these two fields side-by-side. We summarize new findings that have shaped our current understanding of the human cortical network. In addition, we review recent work that has laid the foundation for a mouse model of visual cortical processing. Although their brains are different, the visual cortical networks of mice and men share structural and functional principles.

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The visual cortical network in humans

Human visual neuroscience has seen major advancements during the past decade through the development of advanced neuroimaging techniques in combination with an experimental leap toward studying natural vision. Going beyond the classical stimulus-response mapping, new paradigms and analysis techniques — incorporating methods from computational neuroscience — allow the investigation of active vision: vision that is more than meets the eyes. Recent studies have not only led to a deeper understanding of the functional organization of the human visual network, but also revealed that vision is an active process already at the level of the primary visual cortex (V1).

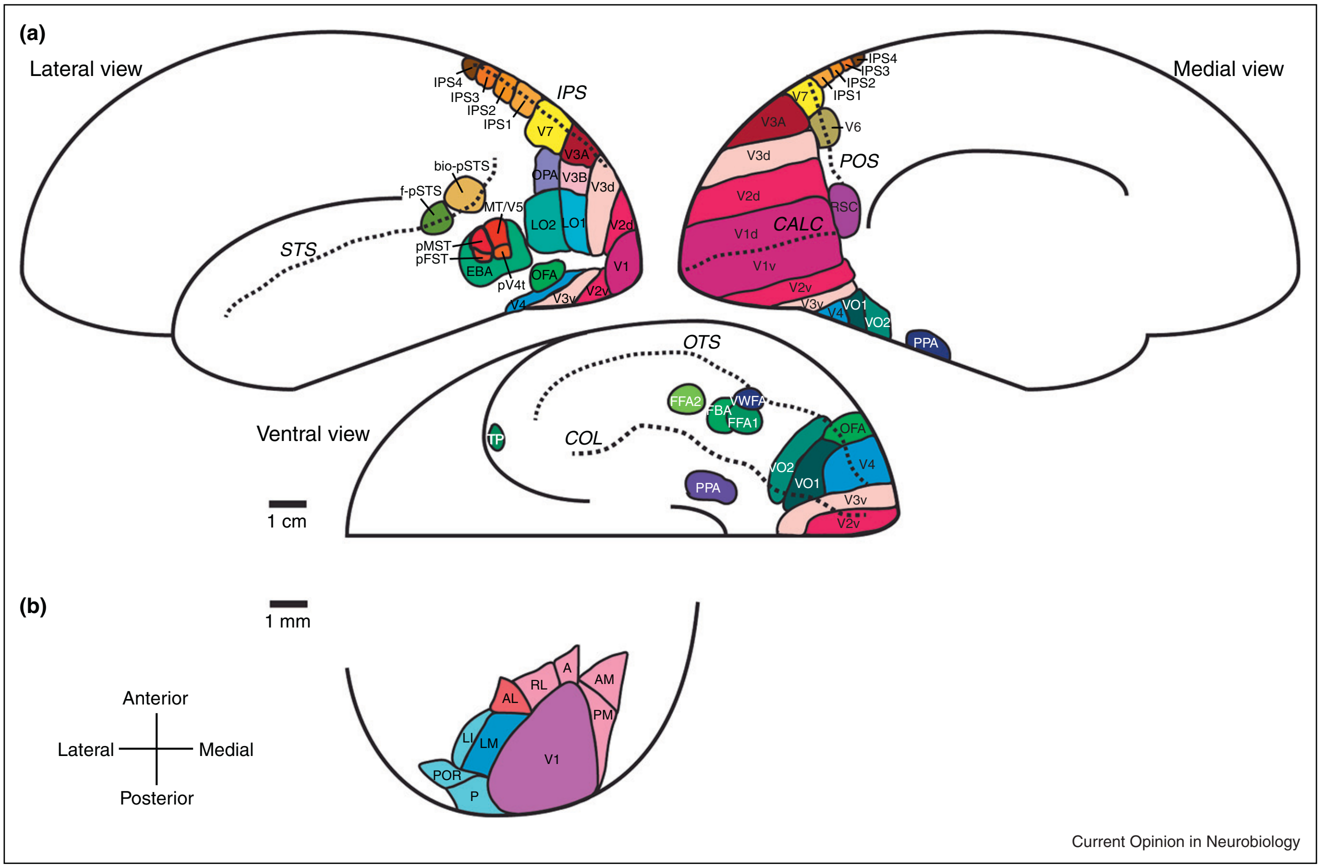
Functional organization of the human visual system

Functional magnetic resonance imaging (fMRI) has greatly advanced our knowledge of the human cortical visual network revealing its intricate functional organization: from the first retinotopic mapping of V1 [1] to the understanding that there are at least 17 retinotopic maps per hemisphere [2], from the first description of a motion-selective region [3,4] to the discovery of several other highly selective visual regions, for example, for faces, places, bodies, and word forms [5]. We now know at least 30 visual cortical regions per hemisphere (Figure 1a), and major research efforts aim at a deeper understanding of each of these regions' structure and function.

Beyond focusing on individual regions, researchers have long sought to uncover general organizational principles of the human visual network. The division into ventral and dorsal streams [6,7] is undoubtedly the most influential as well as the most challenged notion [8,9]. Very recently, complementary schemes have been proposed for the ventral visual cortex, in which two super-regional organizational principles were described: a center-periphery organization that goes beyond retinotopic mapping [10,11], and a mirror-symmetric arrangement of object-selective areas [12]. A third organizational principle was recently discovered: real-world size. Presenting small (e.g. strawberry) and big (e.g. piano) objects at the same retinal size revealed a medial (big objects) to lateral (small objects) gradient of object representations depending on their real-world size [13•].

Recent theoretical and experimental studies have identified maps or gradients as core elements of functional organization [14,15]. Maps are defined as 'clusterings of neurons with similar functional properties that are characterized by a gradual progression of preferred stimulus values across the cortical sheet' [14]. By a combination of maps, functional regions (such as the ones selective for faces) might arise. First evidence supporting this

Figure 1



(a) Schematic illustration of the human visual cortical network consisting of at least 30 brain regions devoted to visual processing. Dotted lines mark major sulci: STS, superior temporal sulcus; IPS, intraparietal sulcus; POS, parietal occipital sulcus; CALC, calcarine sulcus; OTS, occipital temporal sulcus; COS, collateral sulcus. Abbreviation of visual areas: bio, biological motion-sensitive area; FFA1 and FFA2, fusiform face area 1 and 2; FBA, fusiform body area; f-pSTS, face-selective area in posterior STS; LO1 and LO2, lateral occipital areas 1 and 2; MT/V5, middle temporal; OFA, occipital face area; OPA, occipital place area; pMST, posterior medial superior temporal area; pFST, posterior fundus of the superior temporal area; PPA, parahippocampal place area; pV4t, posterior V4 transitional zone; RSC, retrosplenial cortex; TP, temporal pole; VO1 and VO2, ventral occipital areas 1 and 2; VWFA, visual word form area. **(b)** Schematic illustration of the mouse visual cortical network in the posterior half of the left cerebral cortex, shown as a flatmap (adapted from Wang and Burkhalter [36] and Niell [37]). Abbreviation of visual areas: A, anterior; AL, anterolateral; AM, anteromedial; LI, laterointermediate; LM, lateromedial; P, posterior; PM, posteromedial; POR, postrhinal; RL, rostrolateral.

hypothesis came from a study revealing two super-regional clusters corresponding to animate and inanimate objects in human ventral visual cortex [15]. A very recent exciting study lends further support to the existence of functional maps in human visual cortex: Computational modeling of neuroimaging data obtained during natural viewing uncovered a semantic space spreading across most of visual (and even non-visual cortex) [16••]. The semantic space consists of gradients, whose main axes refer to, for example, dynamic versus static or social versus non-social dimensions. The discovery of such an overarching organizational principle is consistent with previously found category-selective regions, and opens up a fresh and unifying look into the overall functional organization of the visual system. To which extent the newly discovered semantic maps are based on visual or conceptual features of object classes remains to be investigated — for sure, this finding will inspire many follow-up studies searching for other types of maps.

In the future, an even more complete picture of the human visual network could be obtained by the combination of methods, in particular by fusing functional measures with anatomical information, for example, obtained through ultra-high-field imaging [17], diffusion tensor imaging [18], or cytoarchitectonical analyses [19].

Active vision in human V1

Besides transforming our view on the functional organization of the human visual network, neuroimaging also had a major impact on how we think about visual processing today: as an active process starting in V1.