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Review

Imaging retinotopic maps in the human brain

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ABSTRACT

A quarter-century ago visual neuroscientists had little information about the number and organization of retinotopic maps in human visual cortex. The advent of functional magnetic resonance imaging (MRI), a non-invasive, spatially-resolved technique for measuring brain activity, provided a wealth of data about human retinotopic maps. Just as there are differences amongst non-human primate maps, the human maps have their own unique properties. Many human maps can be measured reliably in individual subjects during experimental sessions lasting less than an hour. The efficiency of the measurements and the relatively large amplitude of functional MRI signals in visual cortex make it possible to develop quantitative models of functional responses within specific maps in individual subjects. During this last quarter-century, there has also been significant progress in measuring properties of the human brain at a range of length and time scales, including white matter pathways, macroscopic properties of gray and white matter, and cellular and molecular tissue properties. We hope the next 25 years will see a great deal of work that aims to integrate these data by modeling the network of visual signals. We do not know what such theories will look like, but the characterization of human retinotopic maps from the last 25 years is likely to be an important part of future ideas about visual computations.

1. Introduction

Light absorption is a fundamental but insufficient competence for a visual system. Most organisms that absorb light have no sight: To see requires encoding the spatial structure of the image. In human the image spatial structure is preserved by many different optical and neural systems. The cornea and lens, and then the photoreceptor sampling mosaic, maintain the spatial arrangement of the image. The image spatial structure is further preserved by image processing within the retina; specifically, the receptive field centers of the retinal output neurons (ganglion cells) form an orderly mosaic that samples the visual field. While the spatial map is not fully preserved in a cross-section of the axons within the optic nerve (Fitzgibbon & Taylor, 1996; Horton, Greenwood, & Hubel, 1979), the map is resurrected in the pattern of connections formed by axonal projections in the lateral geniculate nucleus.

It has been more than a century since Henschen (1893), Inouye (1909), Holmes and Lister (1916) and Holmes (1918) discovered that the spatial arrangement of the image is maintained in primary visual cortex (V1): stimuli adjacent in the visual field are represented in adjacent positions in visual cortex. More surprising than the existence of a single V1 map was the subsequent discovery that many species have multiple retinotopic maps in visual cortex (Allman & Kaas, 1971; Cowey, 1964; Gattass et al., 2005; Hubel & Wiesel, 1965; Talbot, 1940, 1942; Talbot & Marshall, 1941; Thompson, Woolsey, & Talbot, 1950; Tusa, Palmer, & Rosenquist, 1978; Zeki, 1969b, 1971, 1976), including animals like mice with very poor visual acuity (Wang & Burkhalter, 2007). The value of arranging neurons into multiple retinotopic maps, so that each location in the visual field is represented many times in cortex, calls for an explanation (Barlow, 1986). Perhaps the need to combine information from nearby locations in the image remains important to many cortical functions (stereo, motion and color), it is sometimes argued that certain types of efficiencies, such as minimal wiring costs, arise from using short axonal connections that reflect the computational objectives (Chklovskii & Koulakov, 2004).

While image spatial relationships are preserved in many regions of cortex, they are not absolutely preserved. There are important deviations (discontinuities) from retinotopy which may result from compromises between the multiple objectives of visual computations. For example, in primate the visual field is divided along the midline so that each hemisphere receives a spatial map of only half of each retina. Why the representation of the retina should have such a discontinuity in the primate cortex, but not other species (e.g., mouse) or even in all individuals of the same species (e.g., albinos (Guillery et al., 1984; Hoffmann, Tolhurst, Moore, & Morland, 2003; Huang & Guillery, 1985; Morland, Baseler, Hoffmann, Sharpe, & Wandell, 2001)) is an interesting question. Perhaps in primate the importance of binocular vision,

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coupled with limitations in axon guidance mechanisms, makes it necessary to divide the human V1 map into two parts in order to achieve binocular integration.

We summarize advances in understanding the number, organization and functional responses of visual field maps (also called retinotopic maps) in the human brain. We have been asked to emphasize discoveries made over the last 25 years, and we can report that during this period the advances were extraordinary. There are excellent reviews that emphasize the longer history (Glickstein & Whitteridge, 1987; Zeki, 1993) as well as reviews that focus on more recent developments (Silver & Kastner, 2009; Tootell, Dale, Sereno, & Malach, 1996; Tootell, Tsao, & Vanduffel, 2003; Wandell, Brewer, & Dougherty, 2005; Wandell, Dumoulin, & Brewer, 2007). Following our discussion of the past, we speculate on what may be in store for the next 25 years.

2. Cortical visual field maps

Progress in magnetic resonance imaging (MRI) technologies enabled measurements of the human brain that were beyond any expectations of the scientists working in 1985. These measurement technologies have been supported by new experimental methods and software tools that clarify the arrangement and properties of retinotopic maps in healthy human observers.

The three columns in Fig. 1 offer a visual impression of the advances in brain imaging technology. In the mid-80s magnetic resonance imaging was in its infancy, and functional magnetic resonance imaging based on the blood oxygen signal had not yet been invented. The only method for imaging brain activity in healthy humans was positron emission tomography (PET) (Fox, Miezin, Allman, Van Essen, & Raichle, 1987; Fox et al., 1986). These PET images (Fig. 1, left column) were among the first images of activity in V1 of healthy human subjects, and they also offered a glimpse of extrastriate activity. The PET data were sufficient to confirm some of the inferences about maps from neurology and electrocorticography in surgical patients (Brindley & Lewin, 1968; Dobelle & Mladejovsky, 1974; Dobelle, Turkel, Henderson, & Evans, 1979).

The images make clear that there are significant limitations to these PET measurements. First, the signal-to-noise is low so that the authors combined data from six different subjects. Combining data across subjects is not desirable because the V1 size and stereotaxic border positions vary greatly between subjects (Dumoulin et al., 2003; Stensaas, Eddington, & Dobelle, 1974). The V1 size differences are not predicted by overall brain size and thus the size variance is not easily normalized away (Dougherty et al., 2003). Second, these PET measurements had coarse spatial resolution – a point spread function of 18 mm (full-width at half the maximum amplitude). Perhaps because of this limitation, the authors could not improve on the map of human V1 proposed by Holmes and Lister (1916; Holmes, 1918, 1944) which differed from V1 maps in other primates. Moreover, limitations in the data made it appear that primary visual cortex 'failed to extend onto the lateral surface of the occipital lobe', contrary to what is now routinely observed in functional imaging measurements. Third, there was limited ability to identify extrastriate maps from the extrastriate responses.

While these PET measurements were a very important step forward, many open questions remained. Summarizing the state of our knowledge of human visual cortex, Sereno and Allman (1991) wrote:

> The only human visual area whose borders are surely known is V1. Recent advances in anatomical techniques for monitoring activity (e.g., positron emission tomography, Miezin et al., 1987) are beginning to change this. Fixed-tissue injections suggest that human visual areas V1 and V2 are organized quite similarly to those of other primates (Burkhalter & Bernardo, 1989). Also, there is a heavily myelinated, ellipsoidal region located in a dorsolateral occipital sulcus (Fig. 7.5) that may correspond to human visual area MT.

2.1. Anatomical MRI

Horton and Hoyt (1991b) combined the spatial resolution of anatomical MRI with neurological investigations of cortical damage, making two important advances. First, reporting on subjects with focal lesions in occipital cortex, they were able to correct some inaccuracies in Holmes and Lister's visual field map, showing that the map failed to allocate enough cortical territory to the central visual field. This measurement brought the human map into better agreement with estimates from closely related non-human primates.

In a second paper, Horton and Hoyt (1991a) used anatomical MRI to draw conclusions about two human extrastriate maps, V2 and V3. They analyzed images from two subjects with quadrantanopia, a homonymous field defect with a sharp edge on the horizontal meridian. Prior to this analysis, the cause of a sharp loss of vision at the horizontal meridian was uncertain. Holmes (1918) suggested that optic radiation fibers carrying signals from the upper and lower visual fields were separated, perhaps by the ventricle (Monbrun, 1919), a sharp quadrantic field defect could be explained by a lesion to one of the two parts of the optic radiation. Using anatomical MRI, Horton and Hoyt could see lesions located in extrastriate cortex at locations that appeared to correspond to V2 and V3 gray matter, rather than in the optic radiation. They acknowledged that in human there was uncertainty about the locations of these maps, writing: "Little is known about the organization of extrastriate visual areas in the human brain. Therefore, to construct our proposal we must draw upon data from experimental work in monkeys. Our argument hinges upon the topographic arrangement of the first three cortical visual areas: V1, V2 and V3." They concluded that the quadrantanopia was explained by cortical lesions to V2/V3; in turn, they used their analysis of quadrantanopia to support the hypothesis that human V2 and V3 surround V1, as they do in non-human primates (see below).

Anatomical measurements continue to be important, although these developments have been somewhat overshadowed by the ability to make functional measurements. Among the advances in anatomical measures we can list better identification of different brain tissues, including gray matter and white matter; analyses of the geometry of cortical folding patterns; measurements of cortical thickness; and the assessment of integrity of different types of tissues (Deoni, Rutt, Arun, Pierpaoli, & Jones, 2008; Fischl & Dale, 2000; Meyers et al., 2009; Nordahl et al., 2007; Sowell et al., 2004). These measures have been applied to understanding developmental disorders or disease conditions, notably blindness (Noppeney, Friston, Ashburner, Frackowiak, & Price, 2005; Park et al., 2009; Shimony et al., 2006). There also have been significant developments in both MR acquisition and analysis methods – particularly those based on diffusion-weighted and spectroscopic imaging. In the final section of this article we return to describe some of these methods, and how they are applied to understanding human visual field maps (Edden, Muthukumaraswamy, Freeman, & Singh, 2009; Kim et al., 2006; Muthukumaraswamy, Edden, Jones, Swettenham, & Singh, 2009).

2.2. Functional MRI

The development of fMRI was rooted in the systematic study of MR contrast mechanisms carried out by S. Ogawa and his collaborators. In a series of studies using animal models, Ogawa and