Chapter 8

Functional Neuroanatomy of the Human Visual System: A Review of Functional MRI Studies

8

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Core Messages

- This chapter reviews work on the method of functional magnetic resonance imaging (fMRI), which has been used to describe the structural and functional anatomy of the human visual system.
- Exploitation of the endogenous paramagnetic contrast agent deoxyhemoglobin has yielded functional maps of:
  - lateral geniculate nucleus of the thalamus
  - the columnar organization of primary visual cortex
  - multiple representations of the visual hemifields in the ventral and dorsal visual pathways
  - the interface between the visual system and cortical networks underlying the control of oculomotor behavior, visual working memory, and higher visual cognition.
- In a significant advance beyond the traditional localistic "one region, one type of processing" paradigm, new methods, such as dynamic causal modeling and discriminant analysis, seek to determine temporal relationships among the fMRI time series of multiple brain regions.
- Applying these new methods, neuroscientists can discern how spatially distributed brain regions interact via feedforward and feedback signals sent within neural circuits.
- fMRI promises to contribute more to our understanding of the complex neural circuits that subserve visual perception and visuospatial cognition.

8.1 Introduction

Our visual system is one of the great success stories of evolution. Together with the other sensory systems, its purpose is to provide information about the world so that we can operate within a changing environment to fulfill our goals. The representations that our visual system creates of events and objects within a 3D scene are so accurate and produced so quickly, that most of us operate under the false impression that we perceive the world in a veridical way. Perceived qualities such as redness or brightness do not exist in the world; they are creations of our brain. Of course they generally correspond to properties of energy in the environment, such as spectral composition or luminance, but percepts are not the same as what they represent. This is made obvious by the fact that there is no visible light impinging on the cortex; there are only neurons communicating in

total darkness. Moreover, cortical neurons do not respond directly to light at all. They only respond to their particular set of dendritic inputs. The culmination of multiple stages of neuronal processing within the dark space of our skull is our visual experience of an external world. How the highly ambiguous pattern of light that is detected at the retina is transformed into visual consciousness remains one of the greatest unsolved problems of science.

In some cases, which we tend to dismiss as mere visual illusions, the visual system makes mistakes. It tells us that a color, shape, motion, or light is present when we know that it is not. Visual illusions testify to the fact that even ordinary visual experiences are constructions of the brain. They occur as a consequence of the way the visual system processes its input. In general, these processing steps lead to veridical information about real-world objects. But in cases where they do not, we can learn something about the steps that the visual systems invokes in creating visual representations. For example, when you see a light jumping back and forth on the top of an ambulance, you know that there is no real motion. You perceive these sequences of lights as motion, even though you know that there is no physical movement present, a phenomenon known as apparent motion. From this mistake we can infer how motion percepts in general are constructed. What we have learned from such instances is that the visual system has prior assumptions concerning the mapping between sensory input and the structure of the world. Indeed, the visual system must have these "priors" because visual input is often ambiguous. For example, countless 3D objects could lead to any given pattern of 2D retinal images. To create veridical 3D representations within a fraction of a second, the visual system must solve this inverse mapping problem on the basis of information processing procedures that also make use of extraretinal signals. The visual system must construct object representations that can only be inferred on the basis of the input. How the visual system accomplishes this is partially understood, but much remains to be explained. Many of the most basic issues remain unexplained, including, for example, the neural code used by neurons to communicate among themselves, and the neural basis of consciousness.

Functional magnetic resonance imaging (fMRI) offers a means by which neuroscientists can determine how the brain constructs visual perception. Visual information can evoke or modify neural activity in a majority of cortical areas. Loss of any single function of the visual system can impair a patient's ability to efficiently interact with the environment. Thus, our motivation to achieve a scientifically grounded understanding of how the brain realizes visual perception and visual consciousness is correspondingly high. This chapter reviews our current state of knowledge about the systems-level functional anatomy of the human visual system. The emphasis will be placed on the results of fMRI as a noninvasive imaging technique that combines structural information (gray/white matter, fiber tracts) with functional activity (blood-oxygen-level dependent, BOLD) with a spatial resolution of 1 mm (or better) and a temporal resolution of under 1 s. Sparing excessive methodological detail, the techniques used to make retinotopic maps of the human visual cortex and the resultant normalized atlases will be described. Taking advantage of the functional specificity of higher visual areas, topographical representations of image features such as color, form, and motion (speed and direction), among other aspects, will be discussed. Stereopsis, the ability to detect disparity in fused binocular images, is detected by neurons with binocular receptive fields. Functional MRI has revealed neural correlates of disparity detection and clarified its role in the perception of motion-in-depth of looming stimuli. Finally we consider recent work on the interface between the visual system and systems involved in the preparation of oculomotor action. In this context, the neural control of saccadic eye movements has been investigated with fMRI and the functional connectivity between the frontal and parietal eye fields and areas in the visual cortex are now better understood. The analysis of such "micro-behavior" opens a window into the functioning of the human brain with respect to higher cognitive functions such as visual working memory and consciousness.

8.2 Imaging the Lateral Geniculate Nucleus

With the increase of magnetic field strength from 1.5 to 4 Tesla and greater, it has now become possible to map subcortical structures. The human lateral geniculate nucleus (LGN) is estimated to have a volume that varies from 91 mm^3 to 157 mm^3 (Andrews et al. 1997). Using high-field fMRI, Kastner et al. (2004) and Schneider et al. (2004) mapped the human LGN using hemifield checkerboard stimuli. They showed that the amplitude of the BOLD response in LGN depends on the attentional state of the observer, suggesting a functional role for the massive cortico-thalamic feedback projections to the LGN that have been observed anatomically. That is to say, cortico-thalamic projections modify the thalamic input received by the cortex via neural mechanisms that subserve selective attention.

Sylvester et al. (2005) acquired BOLD responses from the LGN and V1 while subjects performed saccades in both an illuminated Ganzfeld and in the dark. Interestingly, saccades in the full-field light condition led to a suppression of activity in the LGN and V1, whereas saccades in the dark led to an increase in activity. Their findings suggest that signals from oculomotor centers have a suppressive effect on on-going activity in V1 and the LGN, in line with recent work from our laboratory (Vallines and Greenlee 2006; see below). Saccades in the dark led to an increase in activation in both V1 and LGN, suggesting an excitatory signal in the absence of visual stimulation (Sylvester et al. 2005). These findings and others suggest that the LGN is not a mere relay station between the retina and the cortex, but rather plays an active role in shaping the retinal information that arrives in V1 and other regions in the brain.

8.3 Functional Maps of the Visual Field

Regions in the primate visual cortex are said to be retinotopically organized when neighboring locations within a visual quadrant are mapped onto neighboring portions of cortex (Horton and Hoyt 1991; van Essen et al. 1998; van Essen 2004). Each visual neuron has a receptive field that responds to stimuli falling within a well-defined region of this retinotopic space. Figure 8.1 depicts a schematic illustration of human visual area 1 (V1) and its corresponding retinotopic map of visual space taken from Horton and Hoyt (1991). Neighboring neurons in the cortical sheet exhibit receptive fields that overlap in visual space. Assuming steady fixation, the human visual cortex can be sequentially stimulated using flickering checkerboard wedge or ring stimuli (Engel et al. 1994; Sereno et al. 1995; Dale et al. 1999; Tootell et al. 1995; Brewer et al. 2002) thereby evoking a traveling wave of activation over the cortical surface. To take advantage of computational algorithms such as fast Fourier transform (FFT), this traveling wave of activity can be reduced to a temporal frequency distribution with a maximal amplitude at the stimulation (rotational) frequency (Warnking et al. 2002). The phase of this FFT component thus provides a reliable index of the spatial location of the peak of activity during the stimulation cycle, after correcting for the time lag of the hemodynamic response. Using these methods, accurate and reproducible maps of the human visual cortex have been produced in which the borders between V1, V2 and higher retinotopic areas are revealed by the so-called mirror sign (a reversal of the phase sequence from vertical to horizontal meridian, or the other way round). Examples of retinotopy are shown in Fig. 8.2.

8.4 Striate and Extrastriate Visual Areas in Human Visual Cortex (V1, V2, V3)

There are now several reports on the retinotopic organization of primary visual cortex in humans (Engel et al. 1994; Sereno et al. 1995, Tootell et al. 1995; Dale et al. 1999; reviewed in Wandell et al. 2005), most of which rely on the phase-angle method. A step-by-step description of this methodology has been given by Warnking and colleagues (2002). The group of David van Essen has taken information from several studies with different methodologies to produce average maps of the human cortex. This group has also made this software and database available to the com-

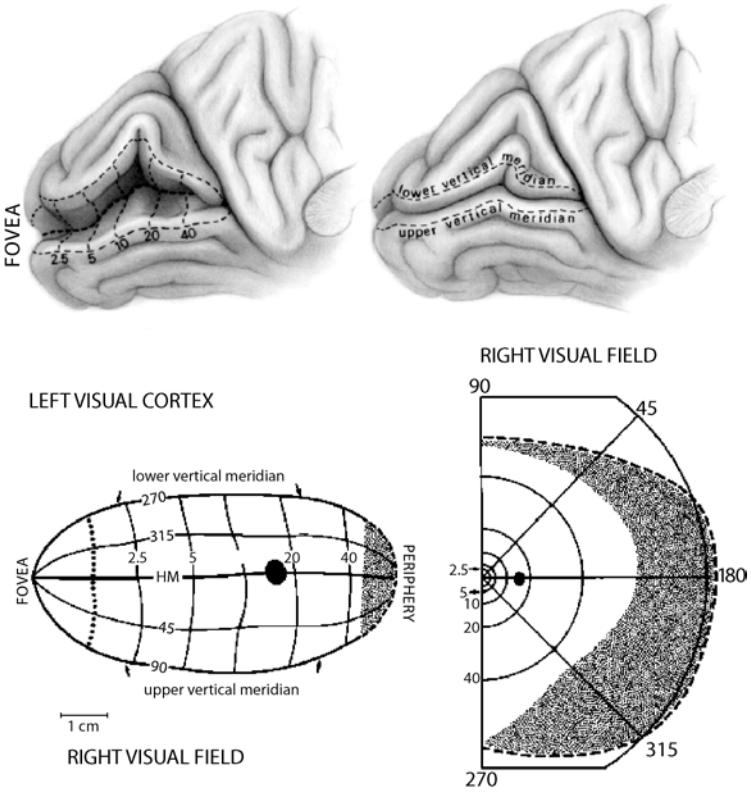

Fig. 8.1. Schematic illustration of the retinotopic organization of the primary visual cortex in the human brain. The *upper panels* depict the medial view of the left hemisphere with approximate isoeccentric radii marked on the surface of the calcarine sulcus. Note that the central 2.5° of visual angle around the foveal representation of the right visual field (*lower panel*) activates a much larger region of visual cortex than an equivalently sized portion of the peripheral visual field. This anisotropic mapping is known as cortical magnification and reflects the relative importance given to the central visual field in cortical processing. The *black spot* in the *lower panel* represents the location and extent of the blind spot (*lower right panel*) and its monocular representation on the cortical surface (adapted from Horton and Hoyt 1991, with permission)

munity (http://brainmap.wustl.edu/caret/). Individual differences in the border location, size and shape of human V1 and V2 have been presented recently (Schira et al. 2007). These data suggest significant differences among individuals, in line with the variations noted in post-mortem specimens (Andrews et al. 1997).

An example of retinotopic maps obtained from two subjects is shown in Fig. 8.2 (Tse et al. 2005). As is evident in these maps, considerable variability exists between the size and border locations of the primary and extrastriate visual areas across subjects.

8.5 Receptive Field Size as a Function of Retinal Eccentricity

Following a similar line of reasoning as that used in phase-encoded flatmaps, the average receptive field size can be estimated as a function of retinal eccentricity (Kastner et al. 2001; Smith et al. 2001). Instead of identifying the phase of the response, the "duty cycle" of the "on" compared to the "off" periods of the response time course provides an estimate of the average receptive field size: large receptive fields would be associ-

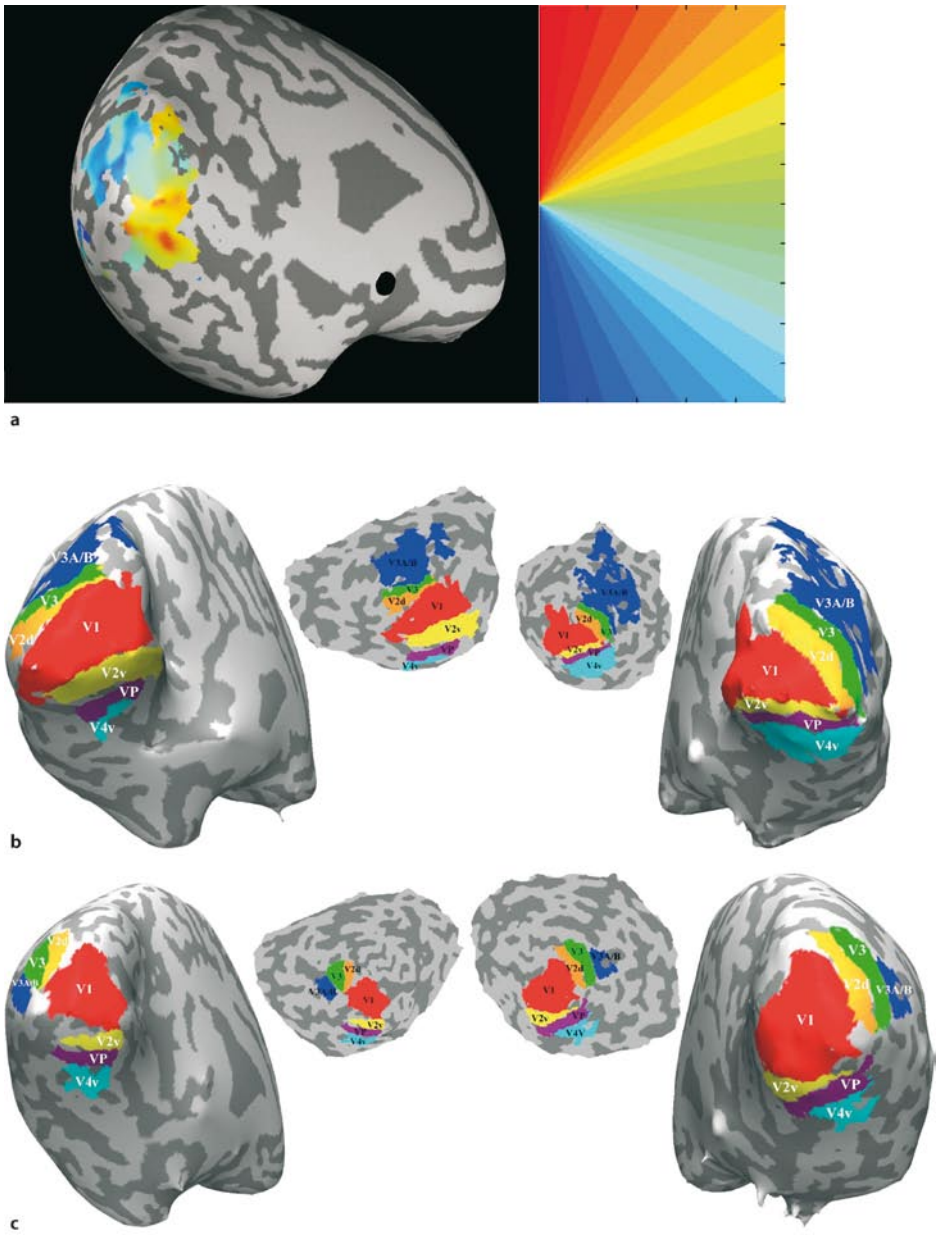

Fig. 8.2a–c. Retinotopic mappings projected upon inflated cortical meshes and flattened meshes of the occipital cortex. **a** The areas of cortex responsive to particular regions of the contralateral visual field are indicated by the corresponding color code. Of particular importance is the determination of the boundaries between visual areas corresponding to the lower vertical meridian (*blue* present at the V1/V2d and V3/V3A border), upper vertical meridian (red present at the V1/V2v and VP/V4v border), and horizontal meridian (*greenish cyan* present at the V2d/V3 and V2v/VP border). Note that V3 is also commonly named V3d, and VP is commonly named V3v, representing the dorsal and ventral parts of V3. **b** The segmented retinotopic areas from one subject on inflated left and right hemispheres as well as corresponding occipital flatmaps. **c** The same for a different subject. While topological relationships among areas remain generally constant across brains, the particular shape and extent of areas vary a great deal from brain to brain

ated with a longer "on" period (i.e., with a larger duty cycle) than small receptive fields (Smith et al. 2001). In these experiments, an expanding or contracting ring stimulus was used. The duty cycle of the best-fitting square wave response function is illustrated in Fig. 8.3c–e for each voxel as a color ranging from dark green to bright yellow. The relative size of receptive fields determined using this method, as well as the way receptive field sizes increase with retinal eccentricity, closely resembles the pattern found in nonhuman primates using single-unit recording techniques (see Fig. 8.3; adapted from Smith et al. 2001).

8.6 Alternative Methods of Retinotopic Mapping

The phase-encoding method assumes linearity of responses within the cortex. Alternative approaches have employed M-sequences (Hansen et al. 2004; Vanni et al. 2005) to compare the localized responses to individual pixels within the random-dot stimulus sequence. For the most part, the findings from these studies are consistent with the results of earlier studies and thus suggest that the area borders are reasonably robust and do not depend on the exact method used.

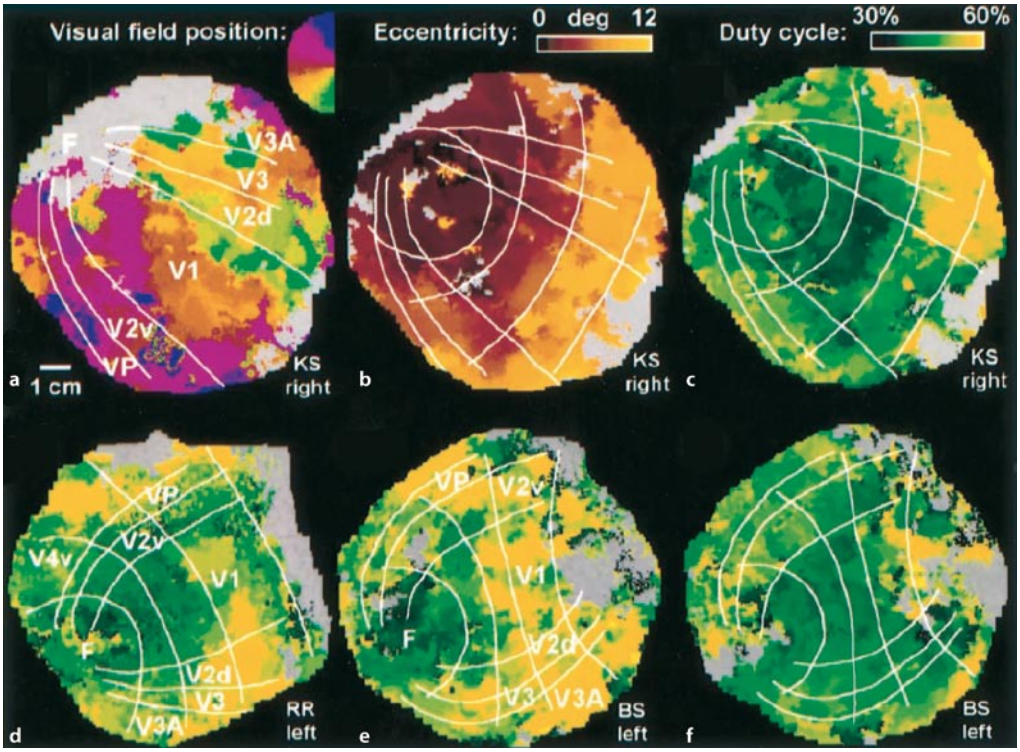

Fig. 8.3a–f. Activation flat maps of human cortex depict the retinotopic organization of the primary visual cortex in the human brain (**a**). **b** The encoding of eccentric position with the contralateral visual hemifield demonstrates the preponderance of the foveal representation on the surface of the visual cortex. **c–e** The colour maps present the results from three subjects with respect to the relative "on" and "off" components of the cyclic response to the flicking ring stimulus, whereas **f** presents the findings when the wedge stimulus was used (adapted from Smith et al. 2001, with permission). Area VP is also commonly known as V3v, and V3 as V3d

Summary for the Clinician

- Using high-field fMRI, responses in the human LGN have been mapped using checkerboard stimuli. The BOLD response in LGN depends on the attentional state of the observer, suggesting a functional role for cortico-thalamic feedback projections.
- The retinotopic organization of the human visual cortex can be determined using fMRI and flickering checkerboard wedge or ring stimuli. Sequential stimulation of sections of the visual field provides information concerning the borders between V1 and V2, V2 and V3 and higher visual areas.
- Based on phase-encoded flatmaps, the average receptive field size can be estimated as a function of retinal eccentricity.

8.7 Columnar Structures within Human V1

Thalamic input into layer 4cα of primary visual cortex is characterized by alternating columns of left and right eye input with a period length of about 1 mm (Hubel and Wiesel 1968), which have been referred to as ocular dominance columns (ODC). Optical imaging techniques relying either on intrinsic (oxyhemoglobin and deoxyhemoglobin; Malonek et al. 1997) or extrinsic (voltage-sensitive dyes; Blasdel and Salama 1986; reviewed in Grinvald and Hildesheim 2004) signals have supported the existence of ocular dominance columns in primate V1 and support the idea of a neurovascular coupling between intrinsic (blood oxygenation) and extrinsic (voltage-sensitive) optical signals. Functional MRI studies of the pattern of ocular dominance have compared the relative magnitude of the BOLD response in human V1 during alternating (i.e., left, right, dark) ocular stimulation. Using high-field (4 T) MRI, Menon and Goodyear (Menon and Goodyear 1999; Goodyear and Menon 2001) were first able to track the pattern of ODC in human V1. In a carefully conducted study with 4-T field strength and a surface coil positioned over the occipital cortex, Cheng et al. (2001) reported a pattern of BOLD responses that correspond to an ODC width of 1.1 mm. The applied imaging technique allowed for an in-plane voxel size of 0.47 mm, which is necessary to resolve the human ODC. The test-retest reliability of the technique conducted in the same subjects within the same recording session or over a time span of 3 months indicates that this method is highly reliable (Fig. 8.4b).

Binocular interactions have also been demonstrated with fMRI. Using 1.5-T field strength, Buchert et al. (2002) demonstrated that simultaneous binocular stimulation led to a reduced BOLD response compared to sequential alternating eye stimulation. This pattern of responses was only evident in the central visual field representation of V1 in persons with normal binocular vision and suggests the existence of inhibitory binocular interaction in human visual cortex.

8.8 Orientation Specificity of BOLD Responses in Visual Cortex

A hallmark of visual cortical function is the orientation columns in primary visual cortex (Hubel and Wiesel 1968). Optical imaging techniques have revealed a "pinwheel" organization, such that all possible stimulus orientations are represented systemically within columnar structures (Blasdel and Salama 1986). Kamitani and Tong (2005) presented fMRI evidence that linear discriminate analysis can be applied to the temporal response patterns of a selected population of individual voxels to predict which of two orientations the observer is currently attending. This method has been applied to predict the perceptual outcome of binocular rivalry, where orthogonal orientations are presented simultaneously to each eye (Haynes and Rees 2006; see below). Using 4-T high-field imaging, Sun and colleagues (2006) have recently described orientational selectivity in individual voxels in V1. The continuous change in orientation preference corresponds well with the orientation specific-

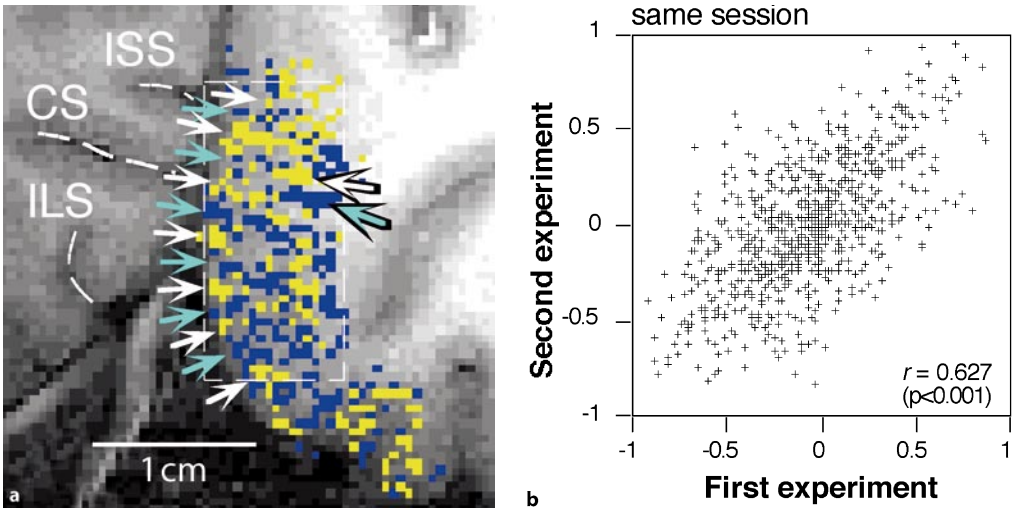

Fig. 8.4a,b. Ocular dominance columns in human primary visual cortex (**a**) and scatter plots of the results (ocular dominance index: –1 corresponding to right eye dominance, 1 to left eye dominance) from the same subject measured twice during the same session (**b**) indicating the relatively high test-retest reliability of the method (r=0.627). The blue and yellow colors indicate the extent to which the individual voxel was activated better by stimulation from the right or from the left eye, respectively (adapted from Cheng et al. 2001, with permission). (CS Calcarine sulcus, ILS intralingual sulcus, ISS inferior sagittal sulcus)

ity in macaque V1. Using adaptation techniques, Boynton and Finney (2003) mapped changes in BOLD responses in V1, V2, V3 as well as V4, and compared them to psychophysical changes in sensitivity. The findings indicate that the BOLD response is reduced by adaptation in areas V3 and V4 (similar to psychophysical sensitivity) but not in V1 and V2. Using spectrally broadband checkerboard stimuli with longer periods of adaptation and re-adaptation, Gardner et al. (2005) reported equally sized shifts in the contrast response functions in V1, V2, V3 and V4, and these shifts corresponded well with earlier psychophysical findings (Greenlee and Heitger 1988).

8.9 Visual Maps of Higher Visual Function: V4

Responses to luminance and color stimuli have been compared in the human homolog of V4 in ventral occipital cortex (Engel et al. 1997; Zeki and Bartels 1999; Bartels and Zeki 2000). Tootell and colleagues suggested the existence of a further visual area involved in the processing of chromatic stimulus information, which they termed V8 (Hadjikhani et al. 1998; Tootell and Hadjikhani 2001). Wandell and colleagues described a hemifield representation in the ventral occipital cortex and this region responded selectively to chromatic information (Wade et al. 2002; Wade and Wandell 2002). The existence of V8 as an independent visual area with a hemifield representation remains unclear.

8.10 Visual Maps of Higher Visual Function: V3A, V3B and KO

The identification of area V3A has been debated in the literature. There is a general agreement that V3A has a contralateral hemifield representation. However, there is evidence for a second retinotopic area (V3B) lateral to V3A that shares the same foveal representation (Smith et al. 1998; Press et al. 2001). It has been argued that V3B is

actually the same as the "kinetic occipital" area (KO; Smith et al. 1998; Zeki et al. 2003), which is an area particularly responsive to motion-defined borders (Dupont et al. 1997; Van Oostende et al. 1997; Grossman et al. 2000; Kononen et al. 2003). However, it is important to note that the conclusion that V3B and KO are in fact the same was made without employing retinotopic criteria, but rather on the basis of the similarity between normalized Talairach coordinates. Because of individual differences, this conclusion should be regarded with caution. An alternative segmentation of the areas has been put forth, in which all the cortex lateral to V3A has been grouped into a common topographically defined "V4d topology" (Malach et al. 1995; Sereno et al. 1995; Tootell et al. 1995, 1996, 1997, 1998a, 1998b; Hadjikhani et al. 1998; Tsao et al. 2003). V4d is anatomically rather than functionally defined, and encompasses both V3B and KO. It is therefore still a matter of debate whether V3B is distinct from V3A, and whether V3B, if it exists, is the same as KO.

8.11 Segmenting Extrastriate Areas and MT+ into Functional Subregions

Many studies have indicated that the human homolog of the primate region middle temporal area (MT, also referred to as V5) lies in the ascending part of the inferior temporal gyrus in BA 37 (Dumoulin et al. 2000). In one of the first fMRI studies of the human visual cortex, Tootell et al. (1995) showed how MT responded selectively to the contrast of moving stimuli, showing a saturating response for low contrast levels of around 4% (Tootell et al. 1995). In a further study, Tootell et al. (1997) reported that V3a, a region in extrastriate cortex, responds selectively to moving stimuli. Smith et al. (1998) investigated the response of early visual areas to first- order (luminance modulated) and second-order (contrast-modulated) motion stimuli. They suggested the existence of a novel area, V3b, as one with a retinotopic map of the contralateral visual field and a high sensitivity to second-order motion, and related it to the so-called kinetic occipital area (KO, see above). By comparing responses to combinations of sine wave gratings, Heeger et al. (1999) suggested the existence of motion opponency in area MT. Here the responses to sine wave gratings drifting in one direction were higher than those for counterphase flickering gratings, suggesting inhibition from neurons tuned to opposite directions. Singh et al. (2000) also reported that MT+ (V5) responded well to low spatial and high temporal frequencies of drifting gratings. In that study, MT+ responded better to drifting gratings and showed a low-pass spatial and band-pass temporal tuning of the response.

Huk et al. (2002) were the first to suggest that Human middle superior temporal area (MST) could be delineated from MT by comparing responses to contralateral and ipsilateral visual stimulation. Using a similar design, we recently replicated these findings in a small group of subjects (Rutschmann and Greenlee, unpublished results). The findings are shown in Fig. 8.5 and suggest that MST exhibits an ipsilateral field representation that is not evident in MT, or in earlier visual areas V1 and V2.

Summary for the Clinician

- Functional MRI studies of the pattern of ocular dominance have compared the relative magnitude of the BOLD response in human V1 during alternating (i.e., left, right, dark) ocular stimulation.
- The reported pattern of BOLD response corresponds to an ODC width of 1.1 mm. The reliability of these results, measured over a time span of 3 months, indicates that this method is reliable.
- Responses to luminance and color stimuli have been compared in the human homolog of V4 in ventral occipital cortex.
- There is a general agreement that V3A has a contralateral hemifield representation. Some studies point to a second retinotopic area (V3B) lateral to V3A that shares the same foveal representation.

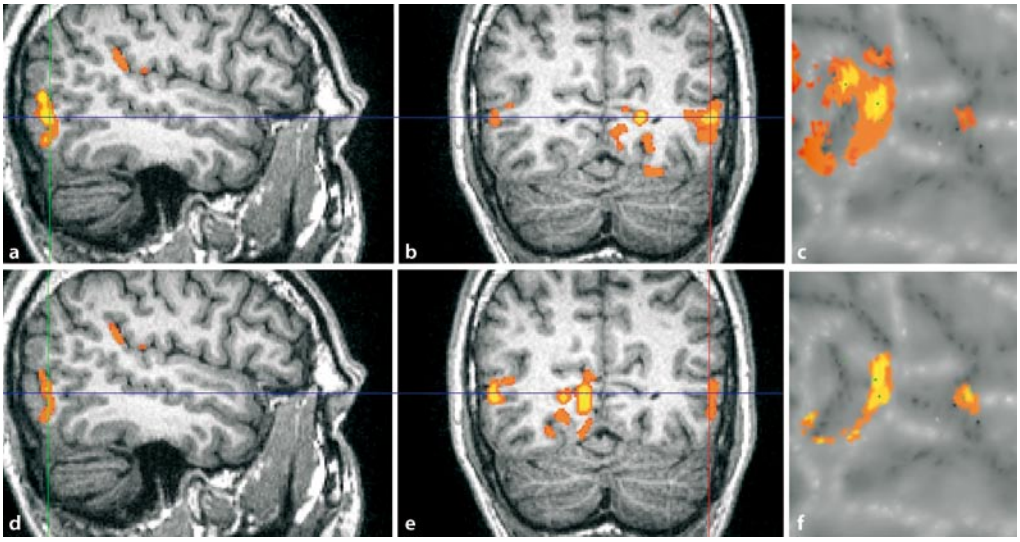

Fig. 8.5a–f. BOLD responses to lateralized random dot-motion stimuli presented in the left visual field (**a**–**c**) or in the right visual field (d–f). **a** Sagittal view of activation in the MT+ region in the right hemisphere. **b** Coronal view depicting the activation in both left and right hemispheres. **c** Zoomed flatmap of the activation in right MT+ when the stimuli were restricted to the left hemifield. **d**,**e**. As in **a**–**c** except now the activations are shown for motion stimuli restricted to the right (ipsilateral to right hemisphere). The *small green marks* help compare the locations in the flatmaps in **c** and **f** (adapted from Rutschmann and Greenlee, unpublished results)

Summary for the Clinician

- The human homolog of the primate region MT (also referred to as V5) lies in the ascending part of the inferior temporal gyrus in BA 37. Responses in MT/V5 to drifting gratings were higher than those for counterphase flickering gratings, suggesting inhibition from neurons tuned to opposite directions.
- Human MST can be delineated from MT by comparing responses to contralateral and ipsilateral visual stimulation: MST shows a response to ipsilateral stimuli, whereas MT does not.

8.12 Responses to Optic Flow

Although the size of the visual stimulus is restricted within the MR scanner, some authors have attempted to record the BOLD responses to optic flow stimuli. Optic flow is defined as the spatiotemporal pattern of stimulation that occurs when the subject moves within an otherwise stationary environment. One of the challenges of visual neuroscience is to understand how local object motion is discriminated from more global patterns of motion evoked by self-motion, navigation or exploratory eye/head movements (Logan and Duffy 2006; Raabe et al. 2006). Rutschmann et al. (2000) studied the effects of presenting optic flow patterns dichoptically to the left and right eye. These dot patterns were presented to create the sense of self motion in a virtual environment (composed only of dots) leading to expansion/contraction or spiral motion. The results indicate that areas in extrastriate cortex (V3a/V3b), but not MT+, responded selectively to motion-in-depth stimuli. Morrone et al. (2000) isolated an area dorsal to MT+ that responded selectively to changes in motion direction. Smith et al. (2006) presented optic flow stimuli to subjects and isolated responses from MT and MST. Their findings suggest that MST, with its larger receptive

fields, is more sensitive to changes in the global characteristics of optic flow stimuli.

8.13 Disparity and Motion-in-Depth Stimulation

The ability to fuse left and right retinal images allows us to extract horizontal disparity in visual stimuli (Parker and Cummings 2001). Backus and colleagues studied the responses associated with binocular disparity and found selective responses that correlated with the disparity level of the stimuli. These responses were most robust in area V3A (Backus et al. 2001). Motion-in-depth stimuli were employed by Rutschmann et al. (2000) to determine the correspondence between responses in motion-sensitive areas to random dots presented dichoptically. Their results point to a region in the extrastriate cortex, probably corresponding to V3a/V3b, which selectively responded to the disparity and optic flow properties of motion displays. The relative disparity of random-dot stimuli indicated activation in dorsal stream areas (Tsao et al. 2003; Rutschmann and Greenlee 2004).

8.14 Interface Between Visual and Oculomotor Systems

The role of the visual cortex in the planning, programming and execution of visually guided saccades remains for the most part unknown. Indeed many prominent models of saccade control leave out the visual cortex completely (Leigh and Zee 2006). In several experiments we have studied the neural correlates of saccadic eye movements in fMRI. Kimmig et al. (2001) compared visually guided saccades performed at different rates and revealed a signal that increased with saccade frequency. Cornelissen et al. (2002) compared pro- and anti-saccades in a random event-related task. On each task, subjects were cued by a change in the colored fixation mark whether to perform a pro- or anti-saccade (i.e., to shift their gaze toward or away from the peripheral target). The results indicate similar activations in the frontal eye fields (FEF) and V1 during both tasks with evidence for anticipatory set effects (see also Connolly et al. 2002). Memory-guided saccades led to activation in FEF and additional areas in prefrontal cortex (Brown et al. 2004; Ozyurt et al. 2006). Applying dynamic causal modeling to explore the effective connectivity between regions in visual, parietal and prefrontal cortex, we recently reported evidence for a complex interactive network in the control of saccades and pursuit (Acs and Greenlee 2006). These new forms of data analysis open new insights into the processes occurring in several brain regions simultaneously.

Using an event-related design, Vallines and Greenlee (2006) recently determined the level of activation in V1 in the brief moments prior to the onset of the visually guided saccade. Subjects were requested to detect briefly flashed Gaussian-enveloped sinusoidal (Gabor) patterns located just above or below a lateral saccade target. By systematically varying the time between the onset of the Gabors and the onset of the saccade to the eccentric target, the authors found a significant reduction in the BOLD signal in V1 evoked by the transient stimuli. The time course of the effect was comparable to the time course of the drop in psychophysically determined contrast sensitivity to the same stimuli, suggesting that the changes in V1 reflect the changes in sensitivity that occur 50 ms prior to the onset of the visually guided (and planned) saccade. These results suggest that neural processes in V1, or prior to V1, are linked to saccadic suppression.

In a further study, Tse et al. (2007) compared V1 responses evoked by micro-saccades as well as visually guided saccades with amplitudes comparable to those of micro-saccades (the smallest being 0.13 visual degrees). Their results suggest that V1 activation is excited by small voluntary fixational eye movements that fall in the range of micro-saccades in V1, V2, V3, and MT. Moreover, the magnitude of the BOLD response increases parametrically in V1, V2, and V3 with the size of the small voluntary eye-movements. However, the BOLD signal response in MT remains constant regardless of the magnitude of the small saccade, suggesting that area MT´s response is not driven primarily by changes in the

image, since there is greater motion magnitude in the image with larger eye-movements. That microsaccades trigger an increase of the BOLD signal in retinotopic cortex suggests that saccadic suppression does not operate for microsaccades, which are involuntary.

This makes sense if one accepts the view that micro-saccades occur in order to counteract the loss of signal that accompanies the perceptual fading that would occur upon the maintenance of perfect visual fixation (see Martinez-Conde et al. 2004). The majority of fMRI experiments to date have been carried out without measuring micro-saccades in the scanner. If micro-saccade occurrence or rate is correlated more with one experimental condition than another, there could be a significant difference in the BOLD signal arising from one condition as compared to another, even though this difference arose because of the artifact of micro-saccades, and not as a function of the difference between experimental conditions. These studies reflect the urgent need to monitor eye movements and fixation behavior of subjects while they perform visual tasks.

8.15 Parietal Lobe Maps of Visuotopic Space

Sereno et al. (2001) discovered a region in the superior parietal cortex (Taliarach coordinates: $X = 32$, $Y = -68$, $Z = 46$ mm deviation from the anterior-posterior commissure) that showed robust visuotopic mapping of the remembered target angle. These authors suggested that this region contains a representation of the entire contralateral hemifield and, as such, could be a homolog of the lateral intraparietal area in macaque monkeys (Sereno et al. 2001). Figure 8.6 illustrates the main findings of the Sereno et al. (2001) study, which indicates contralateral visuotopic mapping of the target location for the planned saccade. Interestingly, neurons in the intraparietal cortex in monkeys have been shown to fire during the preparation of saccades (Bisley and Goldberg 2003). In a recent set of studies, Schluppeck et al. (2005, 2006) performed similar experiments and found a similar organization in posterior parietal cortex.

Summary for the Clinician

- Optic flow is defined as the spatiotemporal pattern of stimulation that occurs when the subject moves within an otherwise stationary environment. Recent studies have tried to better understand how local object motion is discriminated from more global patterns of motion evoked by self-motion, navigation or exploratory eye/head movements.
- MST has neurons with large receptive fields and these are more sensitive to changes in the global characteristics of optic flow stimuli.
- The combination of flow field stimuli with binocular disparity creates a sense of motion in depth. Extrastriate areas V3a/V3b respond selectively to the disparity and optic flow properties of these motion displays.
- Several studies have explored the responses in visual, parietal and prefrontal cortex during the planning, programming and execution of visually guided saccades. Similar activations in FEF and V1 during pro- and anti-saccade tasks were evident, suggesting the existence of anticipatory set effects. Memory-guided saccades lead, on the other hand, to additional activation in prefrontal cortex.

8.16 Working Memory for Visual Stimuli

Visual working memory is the ability to use information from prior visual stimulation to perform discrimination or recognition tasks. Recent studies suggest that this information may be stored in neural circuits that are also involved in the encoding of the sensory stimuli (Pasternak and Greenlee 2005). A further form of visual working memory is related to the ability to form vivid visual imagery, and these processes may involve early visual cortex (Kosslyn et al. 1999). Although the exact role of early visual cortex in visual imagery remains to be determined (Knauff et al. 2000; Kosslyn and Thompson 2003), more

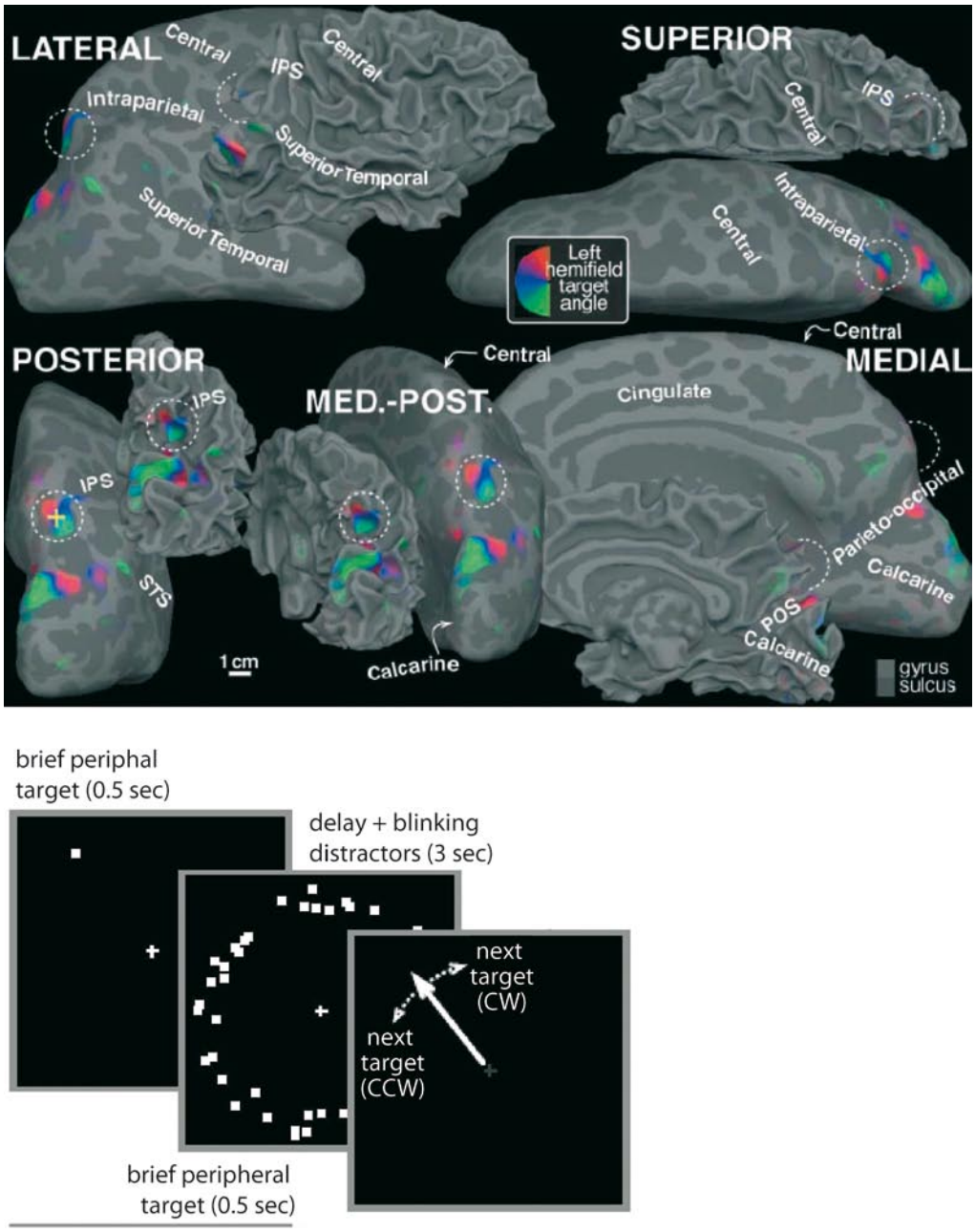

Fig. 8.6. Results of the Sereno et al. (2001) study that employed a delayed saccade task to map the retinotopic organization of a small region in the superior parietal cortex of a single subject. The subject was instructed to maintain central fixation while a peripheral target (*lower panel*) was flashed. The target was followed by a ring of flickering distractor dots. After 3 s the subject was asked to perform a memory-guided saccade to the location where the target dot had been flashed. Using the phase-angle encoding method, Sereno et al. could apply Fourier techniques to extract the relative phase of the T2*-signal at the stimulus frequency, which was assigned one of three colors (see *inset, upper panel*) corresponding to the relative location in the contralateral visual field (adapted from Sereno et al. 2001 with permission)

recent work indicates that the precuneus is an important area for visual memory and visual imagery (Cavanna and Trimble 2006).

In a delayed orientation discrimination task, we recently tested the theory that the precuneus is involved in the storage and recall of visual information (Rothmayr et al. 2007). Figure 8.7 shows the main findings of this study. Subjects compared two sequentially presented Gabor stimuli that varied randomly in their orientation. To test the so-called dual-coding theory of visual imagery (Paivio 1986), we instructed subjects to use verbal codes (e.g., tilted left) to aid them in the delayed discrimination task. The results under this instruction set were compared to the results when the instructions informed them to use visual imagery to perform the task (activations shown in green and red, respectively, in Fig. 8.7).

8.17 Role of V1 in Visual Consciousness

One of the deepest questions in neuroscience concerns the role of individual cortical areas in the neural processing underlying consciousness. An experimental paradigm used to explore the role of early visual areas in conscious perception is binocular rivalry (Blake and Logothetis 2002). In these experiments the subjects are presented with a different image in the left and right eye, such as a horizontal grating presented solely to the left eye and a vertical one solely to the right eye. The subject typically oscillates between perceiving the image available to the left and that available to the right eye, but not both. During brain imaging, the subject signals when he or she consciously perceives the left- or right-eye image. Using statistical methods based on the response distributions in the different visual areas, Haynes et al. (2005) reported that individual voxels within V1 correlated significantly over time with the conscious perception of the subjects, such that the recorded activation could be used to predict which retinal image the subject was perceiving. Tse et al. (2005) used metacontrast masking as a probe to determine neural correlates of the visibility of simple bar stimuli. In metacontrast masking a target bar can be rendered visible or invisible by flanking bar stimuli, depending on the temporal relationships among target and flanker bar onsets and offsets. Moreover, targets and flankers can be presented to either the same eye or to different eyes. Monoptic visual masking was found in all visual retinotopic areas, whereas dichoptic masking was only found in retinotopic areas beyond V2. This finding represents a lower bound for the neural correlates of visual consciousness of simple stimuli such as bars. Moreover, they found that those neural correlates lie within the occipital lobe, placing a corresponding upper bound on the neural correlates of bar visibility, as indicated in Fig. 8.8.

Summary for the Clinician

- Recent studies suggest that this information may be stored in neural circuits that are also involved in the encoding of the sensory stimuli.
- During a delayed orientation discrimination task, subjects exhibit significant clusters of BOLD activation in the precuneus and the posterior parietal cortex.
- Binocular rivalry has been used to study the neural mechanisms underlying visual consciousness. It has been shown that V1 activation correlates significantly over time with the conscious perception.
- Monoptic and dichoptic visual masking are techniques that reveal how information combined from the two eyes contributes to conscious perception. Using these techniques, the effects of monoptic visual masking was found in all visual retinotopic areas, whereas dichoptic masking was only found in retinotopic areas beyond V2.

8.18 Summary

This chapter has reviewed the current literature on brain imaging studies related to the way the visual image is encoded in primary and extrastriate visual cortex. The results from several laboratories converge to form a clear map of human visual cortex consisting of V1, V2, V3, V4, V5 and visual areas in the precuneus

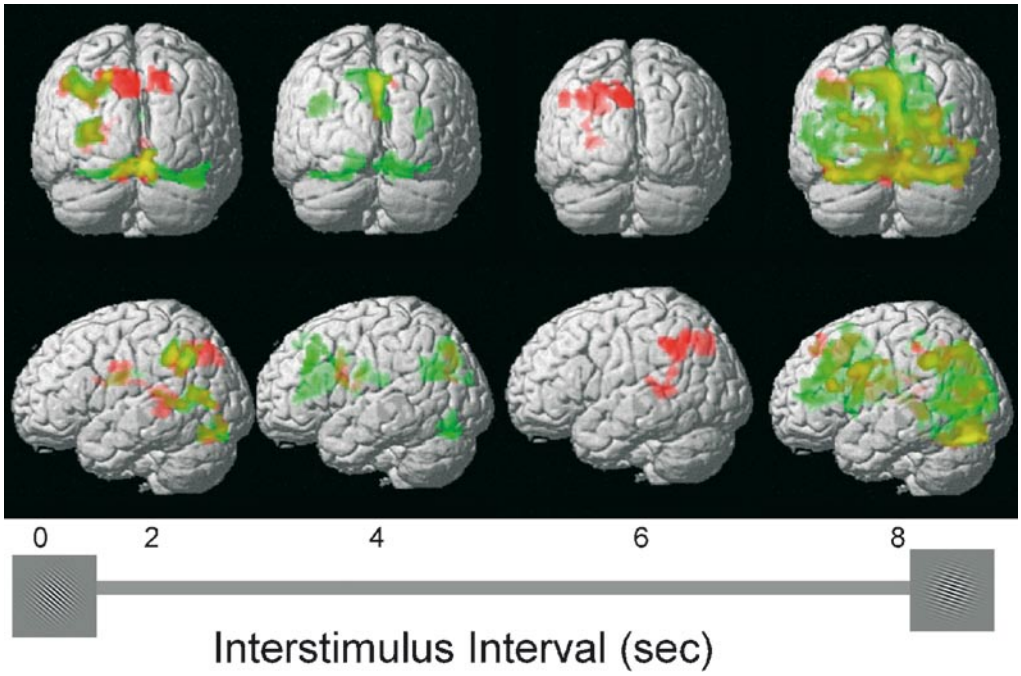

Fig. 8.7. Results of the Rothmayr et al. (2007) study that employed a delayed orientation discrimination task to map the cortical activation related to the storage of pattern information. The subjects were instructed to use either a verbal code to aid them in the memory task (*green*), or visual imagery to store and recall the first pattern (red). Overlap between the activation from these conditions is indicated by *yellow*. The brain images from *left* to right illustrate how the activation develops over the 8-s interstimulus interval of the working memory task. The upper row presents posterior views of the brain and the *lower row* shows a lateral view of the left hemisphere. Although there is considerable overlap in the activations in these two experiments, responses in the imagery condition (*red*) were more pronounced in the precuneus and lateral parts of the posterior parietal cortex, whereas language-related regions in the left hemisphere (*green*) were more active in the verbal encoding condition (adapted from Rothmayr et al. 2007)

and posterior parietal cortex along the dorsal pathway, as well as – although not discussed here – in the lateral occipital (LO) area and the inferior temporal cortex along the ventral pathway. Damage to these areas leads to selective impairment in visual function (Goodale and Milner 1992). Higher cognitive processes based on visual stimulus input are now becoming better understood. These functions are related to visual imagery, visual working memory and visual consciousness. These higher levels of cognition pose a challenge to modern visual neuroscience, and new research approaches promise to provide novel insights into the neural circuitry underlying these processes. Functional MRI will continue to provide some of the best information available to neuroscientists in their attempts to understand visual processing in the human brain.

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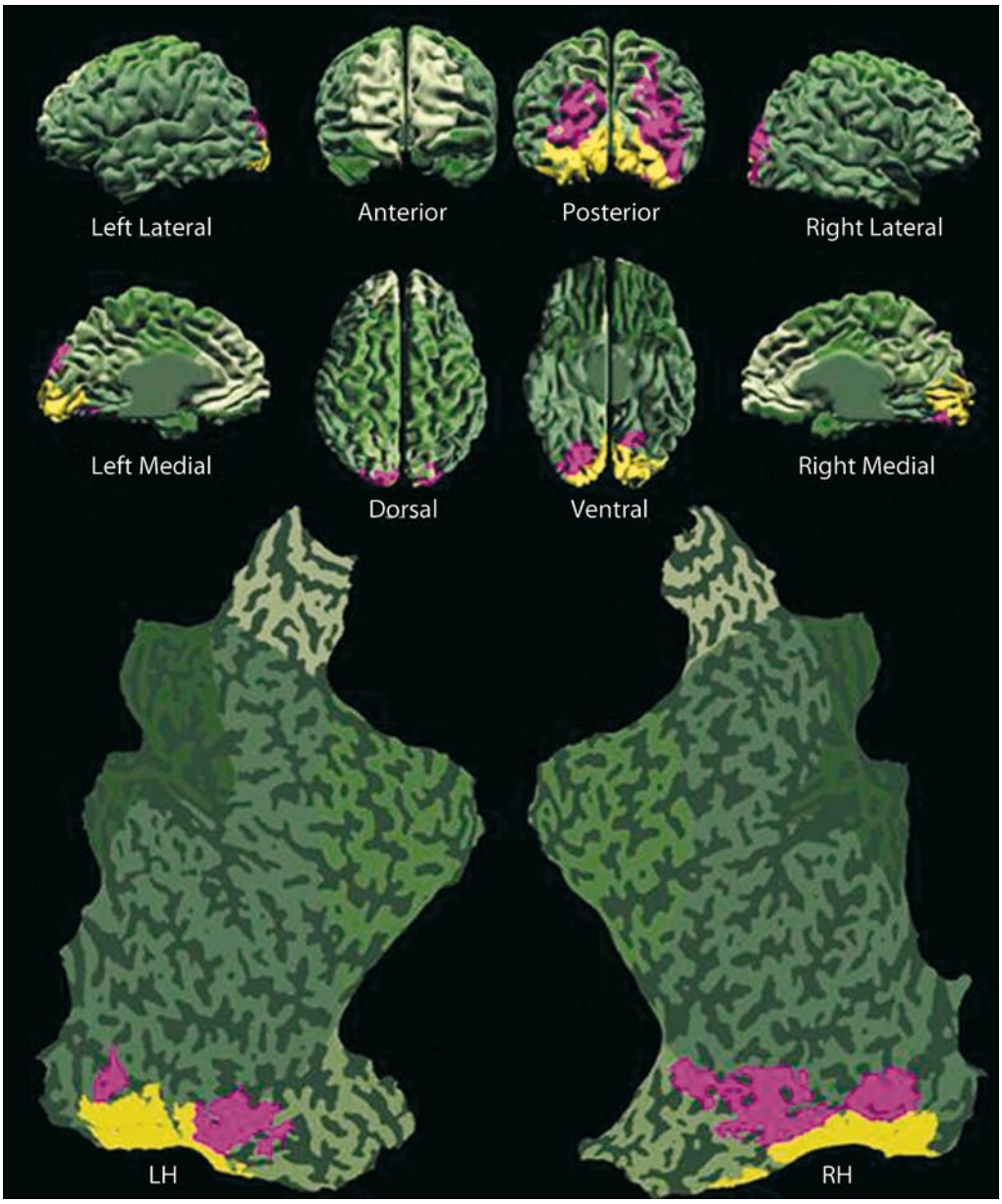

Fig. 8.8. Layout of retinotopic areas that potentially maintain awareness of simple targets. An individual brain model from all perspectives, including both hemispheres flat-mapped, overlaid with the functional activation from one typical subject. The *yellow-shaded areas* are those portions of the brain that did not show significant dichoptic masking and thus are ruled out for maintaining visual awareness of simple targets. The *pink-colored voxels* represent the cortical areas that exhibited significant dichoptic masking and thus are potential candidates for maintaining awareness of simple targets (adapted from Tse et al. 2005 with permission)

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