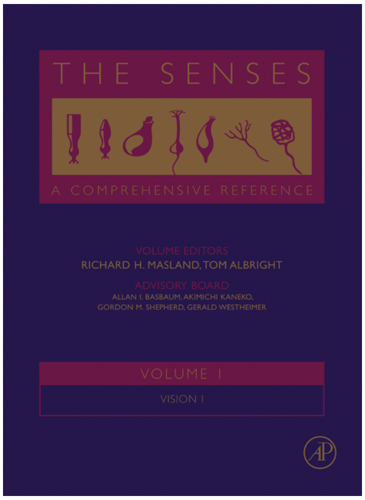

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1.30 Organization of Human Visual Cortex

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1.30.1 Introduction

The human visual system contains numerous visual areas that collectively occupy about 27% of the total extent of cerebral cortex (950 cm^2) (Van Essen, D. C., 2003). Typically, visual cortical areas can be identified by four main criteria: retinotopy, global functional properties, histology (cytoarchitecture and myeloarchitecture), and intercortical connectivity (Felleman, D. J. and Van Essen, D. C., 1991; Kaas, J. H., 1997; Tootell, R. B. *et al.*, 2003). Over the past decade, noninvasive neuroimaging methods, especially functional magnetic resonance imaging (fMRI), have greatly clarified the retinotopic organization and functional properties of the human visual system (Tootell, R. B. *et al.*, 1996; 1998b; 2003; Grill-Spector, K. and Malach, R., 2004). Several studies have also explored histological differences between human brain areas in postmortem specimens, but these data have been largely restricted to early visual areas (Horton, J. C. and Hedley-Whyte, E. T., 1984; Horton, J. C. *et al.*, 1990; Clarke, S., 1994a; 1994b; Tootell, R. B. and Taylor, J. B., 1995). More recently, anatomical MRI and diffusion tensor imaging (DTI) have revealed histological and connectional distinctions between areas as well (Conturo, T. E. *et al.*, 1999; Hagmann, P. *et al.*, 2003). Based on these criteria, human visual cortex can be tentatively parceled into more than a dozen distinct areas (Figure 1) (e.g., Tootell, R. B. *et al.*, 2003). In this chapter, we summarize our current understanding of visual cortical organization in humans. Visual areas will be classified and reviewed in four sections: occipital visual areas, ventral stream areas, dorsal stream areas, and frontal areas.

1.30.2 Occipital Visual Areas

The visual cortical hierarchy begins with occipital areas, which are involved in early visual processing. Topographic (retinotopic) mapping (Figure 2) is a

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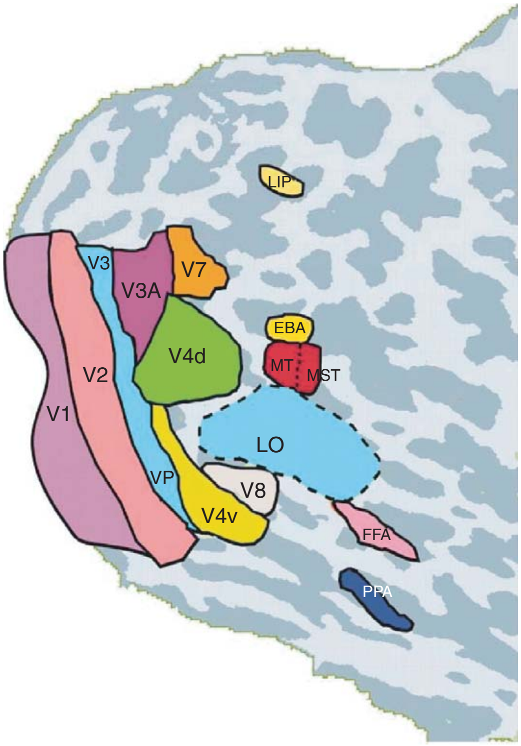

Figure 1 Map of reported areas in human visual cortex. Consensus is highest in lower-tier (generally, leftmost) areas; such areas tend to be evolutionarily more conserved, and the retinotopy is more easily resolved. Adapted from Tootell, R. B., Tsao, D., and Vanduffel, W. 2003. Neuroimaging weighs in: humans meet macaques in "primate" visual cortex. J. Neurosci. 23, 3981–3989.

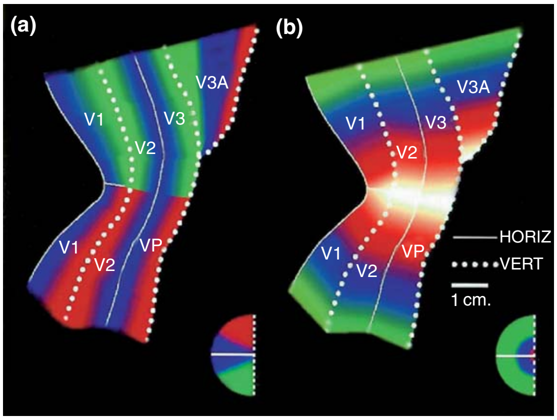

Figure 2 Principles of functional magnetic resonance imaging (fMRI) retinotopic mapping. (a) The polar angle retinotopy and (b) the eccentricity retinotopy. In (a), each of the red, blue, and green pseudocolor ranges represents retinotopically differentiable activation within a 60° subdivision of polar angle in the contralateral visual field (see *logo*, a). In (b), the red, blue, and green ranges correspond to activation within logarithmically equal subdivisions of the eccentricity range from 0.75 through ~15° in the visual field, centered at ~1.5° (red), 3.8° (blue), and 10.3° (green) (see *logo*, b). Adapted from Tootell, R. B., Mendola, J. D., Hadjikhani, N. K., Ledden, P. J., Liu, A. K., Reppas, J. B., Sereno, M. I., and Dale, A. M. 1997. Functional analysis of V3A and related areas in human visual cortex. J. Neurosci. 17, 7060–7078.

ubiquitous property of occipital visual areas in both human (Engel, S. A. *et al.*, 1994; Sereno, M. I. *et al.*, 1995; DeYoe, E. A. *et al.*, 1996; Engel, S. A. *et al.*, 1997a; Hadjikhani, N. K. *et al.*, 1998; Wandell, B. A., 1999; Tootell, R. B. and Hadjikhani, N. K., 2001) and non-human (Gattass, R. *et al.*, 1981; Van Essen, D. C., *et al.*, 1984; Gattass, R. *et al.*, 1988; Tootell, R. B. *et al.*, 1988; Brewer, A. A. *et al.*, 2002; Fize, D. *et al.*, 2003) primates. A visual cortical area is called retinotopic (or said to contain a retinotopic map) if nearby cortical regions receive inputs from nearby retinal regions. Mapping between the retina and the cortex can be best described as a log-polar transformation (Schwartz, E. L., 1977), in which standard axes in the retina are transformed into polar axes in the cortex: eccentricity (distance from fovea) and polar angle (angle from horizontal axis). The logarithmic component of the transformation accounts for the magnification of central representations in the cortex (Schwartz, E. *et al.*, 1985; Duncan, R. O. and Boynton, G. M., 2003).

Mapping the phase (angle) component of the retinotopic map reveals multiple horizontal and vertical meridian representations arranged in approximately parallel bands along the cortical surface. These vertical and horizontal meridian representations alternate and define the borders between mirror-symmetric retinotopic areas. Perpendicular to these bands lie isoeccentricity bands. In humans, the expanded foveal representation of low-level retinotopic areas converges in the occipital pole, in the confluent fovea. Flanking the confluent fovea, there are bands of parafoveal/peripheral representations present both ventrally and dorsally.

1.30.2.1 Primary Visual Cortex

Area V1 (also known as primary visual cortex, striate cortex, or Brodmann's area 17) is the human visual cortical area with the most well-defined anatomical boundaries (Brodmann, K., 1909; Holmes, G. and Lister, W. T., 1916; Von Economo, C. and Koskinas, G. N., 1925; Polyak, S. A., 1933; Stensaas, S. S. *et al.*, 1974). In primates, area V1 plays a critical role in early visual information processing, because most visual information ultimately reaching the rest of visual cortex is first funneled through V1 (Felleman, D. J. and Van Essen, D. C., 1991). Presumably, this anatomically complicated routing task is partly why striate cortex is so markedly laminated. In fact, primate striate cortex has been anatomically subdivided into eleven identifiable laminar divisions (labeled 1, 2, 3, 4A, 4B, 4C alpha, 4C beta, 5A, 5B, 6A, and 6B) (Lund, J. S., 1988; Hendry, S. H. *et al.*, 1994) rather than the customary six layers described in most cortical areas. Sublamina 4C alpha receives most of the magnocellular input from the lateral geniculate nucleus (LGN) of thalamus, and sublamina 4C beta receives most of the input from the parvocellular LGN (Hubel, D. H. and Wiesel, T. N., 1972). The name striate cortex is derived from the *stria of Gennari*, a distinctive stripe that represents a dense concentration of myelinated fibers in cortical layer 4B. Recently, several groups have reported the in vivo detection of myelination patterns within the human V1 cortex using advanced MRI techniques (Barbier, E. L. *et al.*, 2002; Clare, S. and Bridge, H., 2005). Ocular dominance columns in human V1 have been also demonstrated by using multiple anatomical stains (Haseltine, E. C. *et al.*, 1979; Hitchcock, P. F. and Hickey, T. L., 1980; Horton, J. C. and Hedley-Whyte, E. T., 1984; Horton, J. C. *et al.*, 1990) and blood-oxygen-level dependent (BOLD)-based fMRI (Menon, R. S. *et al.*, 1997; Cheng, K. *et al.*, 2001).

The V1 is the largest known visual cortical area, and perhaps the largest cortical area, at least in macaques, where multiple cortical area boundaries are best known (Felleman, D. J. and Van Essen, D. C., 1991). In addition, one human fMRI study has estimated that neuronal receptive fields are smaller in V1, compared with those in higher-tier visual areas such as V2, V3/VP, V3A, and V4 (Smith, A. T. *et al.*, 2001).

It is well known that V1 normally extends over the depth and lips of the calcarine fissure. However, there is considerable individual variability in the size, location, and shape of V1, and even more variability in the shape of the calcarine fissure (Stensaas, S. S. *et al.*, 1974; Rademacher, J. *et al.*, 1993). Retinotopic lesion defects (Holmes, G. and Lister, W. T., 1916), electrically induced phosphenes (Penfield, W. *et al.*, 1954), and retinotopic maps in positron emission tomography (PET) (Fox, P. T. *et al.*, 1987) and fMRI (Engel, S. A. *et al.*, 1994; Sereno, M. I. *et al.*, 1995; DeYoe, E. A. *et al.*, 1996; Engel, S. A. *et al.*, 1997a; Tootell, R. B. *et al.*, 1998c) studies all confirm that human V1 has a well-defined topographic organization. Generally, the upper bank of the calcarine sulcus responds to the lower half of visual field, and the lower bank of the calcarine responds to the upper half of visual field. The horizontal meridian in the visual field is mapped onto the base of the calcarine sulcus, and the vertical meridian is represented rostrally at the border between V1 and V2. The central visual field activates the posterior tip of the calcarine sulcus, and the peripheral visual field activates anterior parts of the calcarine. Because of the cortical magnification factor (Engel, S. A. *et al.*, 1994; Sereno, M. I. *et al.*, 1995; Engel, S. A. *et al.*, 1997a), a large portion of V1 in the confluent fovea is devoted to the representation of small, central portion of visual field.

The correspondence between a given location in V1 and in the visual field is very precise: even the retinal blind spot is represented as a monocular region in V1 (Tootell, R. B. *et al.*, 1998c; Tong, F. and Engel, S. A., 2001). As one would predict from its location in the retina, the blind spot is located just inferior (superior in the visual field) to the cortical representation of the horizontal meridian, centered at the represented eccentricity near 15°.

The V1 has been generally considered as a feature preprocessing area where the neurons code for basic stimulus attributes, such as line orientation and motion direction. fMR-adaptation paradigms (Tootell, R. B. *et al.*, 1998c; Fang, F. *et al.*, 2005; Larsson, J. *et al.*, 2006; but see Boynton, G. M. and Finney, E. M., 2003) and pattern analysis of fMRI data (Kamitani, Y. and Tong, F., 2005; Haynes, J. D. and Rees, G., 2005) have confirmed that human V1 has strong first-order (luminance) orientation selectivity, as suggested by numerous studies in macaques (Hubel, D. H. and Wiesel, T. N., 1968). Recent fMRI studies also reveal the existence of asymmetric orientation sensitivity (including oblique effect and radial orientation bias) in human V1 cortex (Furmanski, C. S. and Engel, S. A., 2000; Sasaki, Y. *et al.*, 2006). Processing of first-order motion also originates in V1 (Smith, A. T. *et al.*, 1998; Seiffert, A. E. *et al.*, 2003; Nishida, S. *et al.*, 2003).

V1 also shows selectivity for stimulus color (Engel, S. A. *et al.*, 1997b) and spatial frequency (Tootell, R. B. *et al.*, 1998b). The systematic organization of spatial frequency preference in V1 is remarkably similar to that for retinotopic eccentricity (Tootell, R. B. *et al.*, 1998b).

One characteristic functional property of V1 is that its contrast response varies continuously and monotonically over contrasts greater than ~6% (Tootell, R. B. *et al.*, 1995b; Boynton, G. M. *et al.*, 1996). However, the contrast response in higher visual cortical areas (such as V3, MT, and LOC) is quite different, essentially saturated at contrasts higher than ~6% (Tootell, R. B. *et al.*, 1995b; 1998c; Avidan, G. *et al.*, 2002a).

Pathological damages to V1 usually lead to scotomas (e.g., hemianopia) restricted to corresponding regions of the visual field (Holmes, G., 1918). Interestingly, patients with scotomas are often able to make use of visual information presented to their scotomas, despite being unable to consciously perceive it – a phenomenon called blindsight (Stoerig, P. and Cowey, A., 1997).

1.30.2.2 V2/V3/VP

V2 (roughly, Brodmann's area 18) and V3 (even more roughly, Brodmann's area 19) are located adjacent to V1 and are part of extrastriate cortex, sometimes called the peristriate belt. As in V1, V2 and V3 have well-defined topographical (i.e., polar angle and eccentricity) representations of the contralateral visual hemifield (Engel, S. A. *et al.*, 1994; Sereno, M. I. *et al.*, 1995; DeYoe, E. A. *et al.*, 1996; Engel, S. A. *et al.*, 1997a). Each area has a dorsal part (V2d and V3d, above the calcarine fissure representing the lower visual field) and a ventral part (V2v and V3v/VP, below the calcarine representing the upper visual field). In macaques, there is an asymmetry in the size of V2v versus V2d; V2v is slightly wider than V2d (Olavarria, J. F. and Van Essen, D. C., 1997), but such an asymmetry has not been shown in humans.

A long-unresolved controversy in macaques is whether V3d and VP (ventral posterior area) are independent cortical areas (Burkhalter, A. *et al.*, 1986; Felleman, D. J. and Van Essen, D. C., 1987) or two parts of a common area V3 (Gattass, R. *et al.*, 1988; Lyon, D. C. and Kaas, J. H., 2001). Thus far, these two regions are functionally indistinguishable in the human fMRI data, supporting the latter model. In macaques, areas V3 and VP are unusually thin, relative to the width of their neighboring counterparts V2, V4v, and V3A (Felleman, D. J. and Van Essen, D. C., 1991). However, in humans, V3/VP are just as wide as these neighboring retinotopic areas (Tootell, R. B. *et al.*, 1997; Dougherty, R. F. *et al.*, 2003).

The border between V1 and V2 is the representation of vertical meridian, whereas the border between V2 and V3 is the representation of horizontal meridian. Thereby, V2 and V3 (likewise, V1 and V2) have mirror-symmetric visuotopic organizations. It has been suggested that this mirror-symmetric organization might be crucial for optimizing the wiring length of interareal connections (Van Essen, D. C., 1997). V1, V2, and V3 share a common foveal region (foveal confluence) near the occipital pole. Parafoveal and peripheral field stimuli are represented at increasingly anterior positions, in both ventral and dorsal cortex.

Functionally, V2 and V3 have many properties in common with V1. Cells are tuned to simple properties such as orientation, spatial frequency, and color. In macaques, the responses of many V2 neurons are also modulated by more complex properties, such as illusory contours and figure–ground relationships (von der Heydt, R. *et al.*, 1984; Zhou, H. *et al.*, 2000). FMRI suggests that human V2 may be relatively less sensitive to the illusory contours (Mendola, J. D. *et al.*, 1999) – but alternatively, this could be another case in which single units were simply not tested in the most activated areas (as measured by fMRI).

1.30.2.3 V4/V8

In ventral cortex, the border between V3v and V4v is defined by an upper vertical meridian. Currently, there is debate about what constitutes the anterior border of V4 (Figure 3) (Zeki, S. *et al.*, 1991; Hadjikhani, N. K. *et al.*, 1998; Wandell, B. A., 1999; Bartels, A. and Zeki, S., 2000; Wade, A. R. *et al.*, 2002; Tootell, R. B. *et al.*, 2003; Brewer, A. A. *et al.*, 2005). One proposal is that there is a complete hemifield representation, termed human V4 (hV4), adjacent and anterior to V3v, which might be complementary to the dorsal V3A representation (McKeefry, D. J. and Zeki, S., 1997; Kastner, S. *et al.*, 2001; Wade, A. R. *et al.*, 2002; Brewer, A. A. *et al.*, 2005). In contrast, Tootell and colleagues suggest that V4v has a quarter-field representation, and there is a separate area termed V8, consisting of a hemifield representation, which is located anterior to V4v and rotated relative to V4v (Hadjikhani, N. K. *et al.* 1998). In the V8 model, this area has its own representation of the fovea, quite distinct from the foveal representation in adjacent area V4v. All data place the human color-selective region well inferior to the topographic homologue of dorsal V4, which was the originally proposed site of color processing in macaques (e.g., Zeki, S. M., 1973; Zeki, S., 1980).

Clinical studies reveal that color vision loss (achromatopsia) is correlated with damage in the ventral occipito-temporal cortex (Pearlman, A. L. *et al.*, 1979; Damasio, A. *et al.*, 1980; Zeki, S. A.,

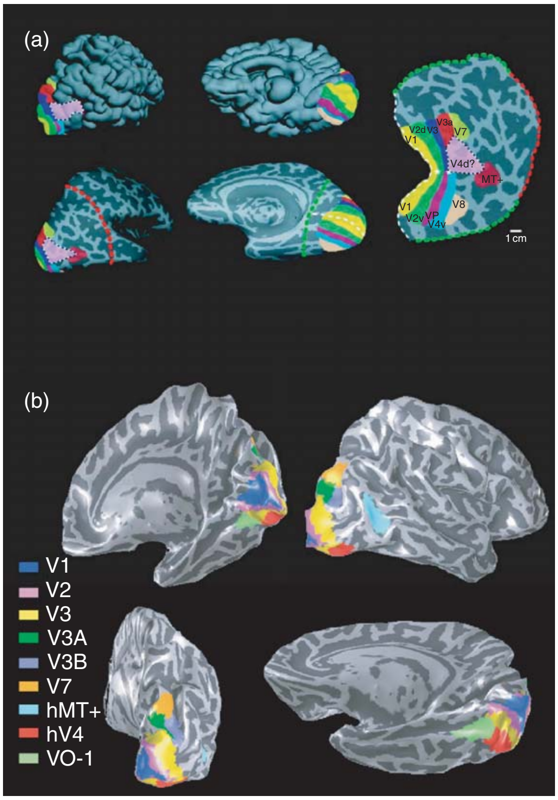

Figure 3 Two proposed models for the retinotopic organization of V4 in humans. The V8 model (a) specifies a quarter-field map, termed V4v, adjacent to the V3v. Anterior to V4v, the model proposes a rotated hemifield representation, termed V8. The hV4 (human V4) model (b) specifies a hemifield map, termed hV4, adjacent to the V3v. Anterior to hV4, the model proposes a cluster of hemifield maps in ventral occipital cortex (VO cluster). The region in the expected location of dorsal V4 (based on macaque V4d) has been assigned a variety of labels such as V4d-topo (a) or V3B (b). Several observations suggest that this region is functionally heterogeneous. (a) Adapted from Tootell, R. B. and Hadjikhani, N. K. 2001. Where is "dorsal V4" in human visual cortex? Retinotopic, topographic and functional evidence. Cereb. Cortex 11, 298–311. (b) Adapted from Wandell, B. A., Brewer, A. A., and Dougherty, R. F. 2005. Visual field map clusters in human cortex. Philos. Trans. R. Soc. Lond. B Biol. Sci. 360, 693–707, with permission.

1990). Neuroimaging studies have also shown regions in the vicinity of V4v (but not V4v itself) that respond more strongly to colored patterns than to luminance-defined patterns. These regions are referred to as V8 (Hadjikhani, N. K. *et al.*, 1998; Tootell, R. B. and Hadjikhani, N. K., 2001), the V4 complex (Lueck, C. J. *et al.*, 1989; McKeefry, D. J. and Zeki, S., 1997; Bartels, A. and Zeki, S., 2000), or the ventral occipital (VO) cluster (Wandell, B. A., 1999; Brewer, A. A. *et al.*, 2005). One study has reported that the cortical region V8 is also preferentially activated by color afterimages (Hadjikhani, N. K. *et al.*, 1998). In the V4-complex scheme, this area has been subdivided into two color-selective subdivisions: a posterior structure termed V4 and an anterior one termed V4 alpha (Beauchamp, M. S. *et al.*, 1999; Bartels, A. and Zeki, S., 2000). In the VO-cluster scheme, this cluster has two separate hemifield maps termed VO1 and VO2 (Brewer, A. A. *et al.*, 2005).

1.30.2.4 V5 (Human MT+)

Human MT+ (hMT+) is located at the temporo-parietal occipital junction (Watson, J. D. *et al.*, 1993; Tootell, R. B. *et al.*, 1995b). This region is a central motion-selective locus in the human brain and is a well-accepted homologue of the macaque motion-sensitive area called MT/V5 (Heeger, D. J. *et al.*, 2000; Rees, G. *et al.* 2000; Sereno, M. I. and Tootell, R. B., 2005). hMT+ is selectively activated by moving versus stationary stimuli and exhibits high contrast sensitivity (Tootell, R. B. *et al.*, 1995b). Consistent with psychophysical and electrophysiological findings, fMRI activity in this area decreases when moving color-varying stimuli are equated in luminance (Tootell, R. B. *et al.*, 1995b).

It has been reported that hMT+ contains two distinct subregions, as one might expect from studies of the corresponding region in nonhuman primates. The first subregion (putative hMT) has retinotopic organization but shows little response to peripheral ipsilateral stimulation, indicating smaller receptive fields (Dukelow, S. P. *et al.*, 2001; Huk, A. C. *et al.*, 2002). Conversely, the second subregion within hMT+ (putative human MST or MSTd) has no clear retinotopic organization but responds to peripheral stimuli in both the ipsilateral and contralateral visual hemifields, indicating larger receptive fields (Tootell, R. B. *et al.*, 1998d; Dukelow, S. P. *et al.*, 2001; Huk, A. C. *et al.*, 2002). Retinotopic organization and the relative position of these two subregions in hMT+ are similar to those in the macaque motion areas MT (middle temporal area) and MST (medial superior temporal area) (Gattass, R. and Gross, C. G., 1981; Albright, T. D. and Desimone, R., 1987; Maunsell, J. H. and Van Essen, D. C., 1987). In addition, Dukelow S. P. *et al.* (2001) have reported activity in the anterolateral subsection of the MT+ complex when subjects perform nonvisual pursuit of a self-generated somatosensory target in darkness, suggesting that this region receives extraretinal nonvisual signals, and thereby corresponds to the human homologue of MSTl (lateral). Some evidence also suggests that there is a functional subregion within the hMT+, which selectively responds to particular radial and circular motion patterns (rather than simple translation) and thus may be involved in calculating optic flow (Morrone, M. C. *et al.*, 2000). Anteroventral to macaque MT/MST, there is another motion-selective area called fundus of the superior temporal sulcus (STS) (FST) (Erickson, R. G. and Dow, B. M., 1989). Currently, no study has reported a human homologue of macaque FST.

Several studies have shown that fMRI activity in hMT+ increases during the perceptual illusion of the motion aftereffect (Tootell, R. B. *et al.*, 1995a; He, S. *et al.*, 1998; Culham, J. C. *et al.*, 1999; Taylor, J. G. *et al.*, 2000; but see Huk, A. C. *et al.*, 2001). Because the motion aftereffect is direction specific, this indicates that hMT+ probably contains direction-selective neural populations, similar to findings in macaques (Maunsell, J. H. and Newsome, W. T. 1987; Britten, K. H. *et al.*, 1992; Salzman, C. D. *et al.*, 1992; Hegger, D. J. *et al.*, 1999). Furthermore, the activation within hMT+ increases linearly with the coherence of motion in random dot patterns (Rees, G. *et al.*, 2000), implying that this area has strong direction selectivity.

hMT+ seems to be mainly involved in global motion processing (Castelo-Branco, M. *et al.*, 2002). For example, hMT+ adapts to patterned motion, in contrast to lower visual areas, which adapt to component motion (Huk, A. C. and Heeger, D. J., 2002). Interestingly, human MT/MST is also activated by static images with implied motion (Kourtzi, Z. and Kanwisher, N., 2000a). Finally, activation of this area is enhanced when subjects attend to or track motion (Buchel, C. *et al.*, 1998; Culham, J. C. *et al.*, 1998).

Thus, converging evidence shows that hMT+ response properties parallel both the response properties of macaque single neurons (Rees, G. *et al.*, 2000) and perception (Muckli, L. *et al.*, 2002). This inference is further supported by clinical studies revealing that akinetopsia (the failure to perceive motion) is associated with lesions in the vicinity of hMT+ (see Zeki, S., 1991, for review).

Adjacent to hMT+, other motion-related cortical sites have been reported. Orban and colleagues described an area termed the kinetic-occipital area (KO) (Dupont, P. *et al.*, 1997; Van Oostende, S. *et al.*, 1997), which is located posterior to hMT+ and specializes in the processing of kinetic boundaries created by discontinuities in motion direction (but see Zeki, S. *et al.*, 2003; Tyler, C. W. *et al.*, 2006). Increasing evidence also suggests a distinct area specialized for perceiving biological motion. This hypothetical area is located within a small region on the posterior STS (STSp) (lateral and anterior to human MT/MST/KO) and is selectively activated during viewing of light-point-defined moving figures (Grossman, E. *et al.*, 2000; Vaina, L. M. *et al.*, 2001; Grossman, E. D. and Blake, R., 2002), but not by the random movement or inverted motion of the same dots that composed the light-point figures. This region is also activated by other types of biological motion such as movies of people walking (Pelphrey, K. A. *et al.*, 2003) or of hand, eye, or mouth movements (Puce, A. and Perrett, D., 2003), or perhaps even implied biological motion (see below).

1.30.2.5 V3A/V3B

After cortical visual areas V3 and V4 were identified and named in macaque monkeys, another region was discovered between them, named V3A (V3 accessory) (Van Essen, D. C. and Zeki, S. M., 1978; Zeki, S. M., 1978a; 1978b). fMRI studies in humans have also revealed a human homologue of V3A (Tootell, R. B. *et al.*, 1997; 1998a; Culham, J. C. *et al.*, 1998; Hasnain, M. K. *et al.*, 1998; Baseler, H. A. *et al.*, 1999; Boynton, G. M. *et al.*, 1999; Mendola, J. D. *et al.*, 1999; Somers, D. C. *et al.*, 1999; Sunaert, S. *et al.*, 1999; Wandell, B. A., 1999). As in macaques, human V3A is regarded as a cortical area that is entirely independent and distinct from its similarly named neighbor, V3, in terms of its retinotopy and functional properties (Tootell, R. B. *et al.*, 1997). Unlike other retinotopic areas in superior occipital cortex (i.e., V1d, V2d, and V3), human V3A has a distinctive, continuous map of the entire contralateral hemifield immediately anterior to area V3 (including a retinotopic representation of both lower and upper visual fields). The inferior vertical meridian is mapped posteriorly (bordering V3), and the superior vertical meridian is mapped at the anterior border of V3A (Tootell, R. B. *et al.*, 1997). The foveal representation is mapped inferiorly, and the periphery is mapped superiorly. In some cases, the V3A foveal representation is displaced from, and located superior to, the confluent foveal representations of V1, V2, V3, and VP (Tootell, R. B. *et al.*, 1997). These properties of human V3A are generally consistent with those described previously in macaque V3A (Tootell, R. B. *et al.*, 2003).

In both macaques and humans, V3A has large receptive fields (Gattass, R. *et al.*, 1988; Tootell, R. B. *et al.*, 1997), which are apparently involved in wide-field visual computations. Such calculations include the processing of binocular disparity (Backus, B. T. *et al.*, 2001; Tsao, D. Y. *et al.*, 2003b; Neri, P. *et al.*, 2004), and illusory contours (Mendola, J. D. *et al.*, 1999). Human V3A is moderately motion-selective, whereas human V3 is less so (Tootell, R. B. *et al.*, 1997; Braddick, O. J. *et al.*, 2001). As in hMT+, contrast sensitivity appears quite high in area V3A (Tootell, R. B. *et al.*, 1997).

Smith A. T. *et al.* (1998) have proposed that V3A (as defined by Tootell, R. B. *et al.*, 1997) may actually consist of two areas, V3A-proper and V3B. In this scheme, both V3A and V3B are located anterior to V3, but V3A borders the peripheral V3 representation, whereas V3B borders the foveal V3 representation. There is no correlate of proposed human area V3B in macaque cortex. Some studies have described a full contralateral hemifield representation in V3B (Press, W. A *et al.*, 2001; Wandell, B. A. *et al.*, 2005; Silver, M. A. *et al.*, 2005), while other groups have reported only a lower contralateral visual quadrant representation in this area (Smith, A. T. *et al.*, 1998; Dumoulin, S. O. *et al.*, 2003). Reportedly, V3B shares a parafoveal representation with V3A. It has motion and disparity specificity like V3A (Smith, A. T. *et al.*, 1998; Greenlee, M. W., 2000) and largely overlaps with the KO area (Zeki, S. *et al.*, 2003).

Tootell R. B. and Hadjikhani N. K. (2001) have discussed a topographic (rather than functional) homologue of macaque dorsal V4 (the V4d topologue), based on neighborhood relations among visual areas (i.e., anterior to V3A, posterior to hMT+, and superior to ventral V4) (Figure 3). V4d-topo incorporates both V3B and KO and hence responds selectively to kinetic motion boundaries. Unlike some previous reports in macaque V4d (Zeki, S. M., 1973; Zeki, S., 1980), human V4d-topo is not significantly color-selective (Tootell, R. B. and Hadjikhani, N. K., 2001).

1.30.2.6 V7

Anterior to V3A lies another representation of polar angle that includes both upper and lower visual fields and is mirror-symmetric to that in V3A. This area has been called V7 (Tootell, R. B. *et al.*, 1998a; 1998b; Tootell, R. B. and Hadjikhani, N. K., 2000; Press, W. A. *et al.*, 2001; Wandell, B. A. *et al.*, 2005; Tyler, C. W. *et al.*, 2005). V7 has a distinct foveal representation (Press, W. A. *et al.*, 2001), and it exhibits robust activity during spatial attention (Tootell, R. B. *et al.*, 1998a; Culham, J. C. *et al.*, 1998). This area may be homologous to the macaque dorsal prelunate (DP) area (Andersen, R. A. *et al.*, 1990; Tootell, R. B. *et al.*, 1998a).

Recently, more topographically organized areas have been reported adjacent and anterior to V7. These areas, labeled IPS1 and IPS2 (IPS: intraparietal sulcus), completely represent the contralateral hemifield and are separated from each other and from V7 by reversals in visual field orientation (Silver, M. A. *et al.*, 2005; Schluppeck, D. *et al.*, 2005). IPS1 and IPS2 are mainly activated during covert shifts of attention or saccadic eye movements (Silver, M. A. *et al.*, 2005; Schluppeck, D. *et al.*, 2005).

1.30.3 Ventral Stream Areas

Cortex anterior to V4 is generally considered part of the ventral (or 'what') processing stream (Ungerleider, L. G. and Mishkin, M., 1982; Mishkin, M. *et al.*, 1983). In macaque, this cortical region includes a cluster of inferotemporal areas that are implicated mainly in pattern recognition and form analysis (Tanaka, K., 1997; Desimone, R. and Ungerleider, L. G., 1989). Similarly, a complex of several subdivisions within human occipito-temporal cortex shows functional specialization in object representation and recognition (Figure 4), so that damage to these regions results in severe visual recognition deficit or agnosia (Farah, M., 1990). Nonetheless, the exact nature of representation in object-related areas is not yet understood. Functional imaging results in humans indicate that object recognition is mediated by both distributed and localized representations. For example, objects such as chairs can be distinguished based on the distributed and overlapping brain activity they elicit, even though no one claims a chair area in cortex (Haxby, J. V. *et al.*, 2001; Spiridon, M. and Kanwisher, N., 2002). However, there are reports of specialized regions in human cortex dedicated to the processing of particular categories such as faces (Kanwisher, N. *et al.*, 1997), places (Epstein, R. and Kanwisher, N., 1998), and body parts (Downing, P. *et al.*, 2001). Malach and colleagues have recently proposed that topographical organization of these specialized regions follows principles of eccentricity mapping (Levy, I. *et al.*, 2001; Malach, R. *et al.*, 2002; Hasson, U. *et al.*, 2002; 2003b; Levy, I. *et al.*, 2004). According to this model, different object categories have specific eccentricity biases (e.g., faces, letters,

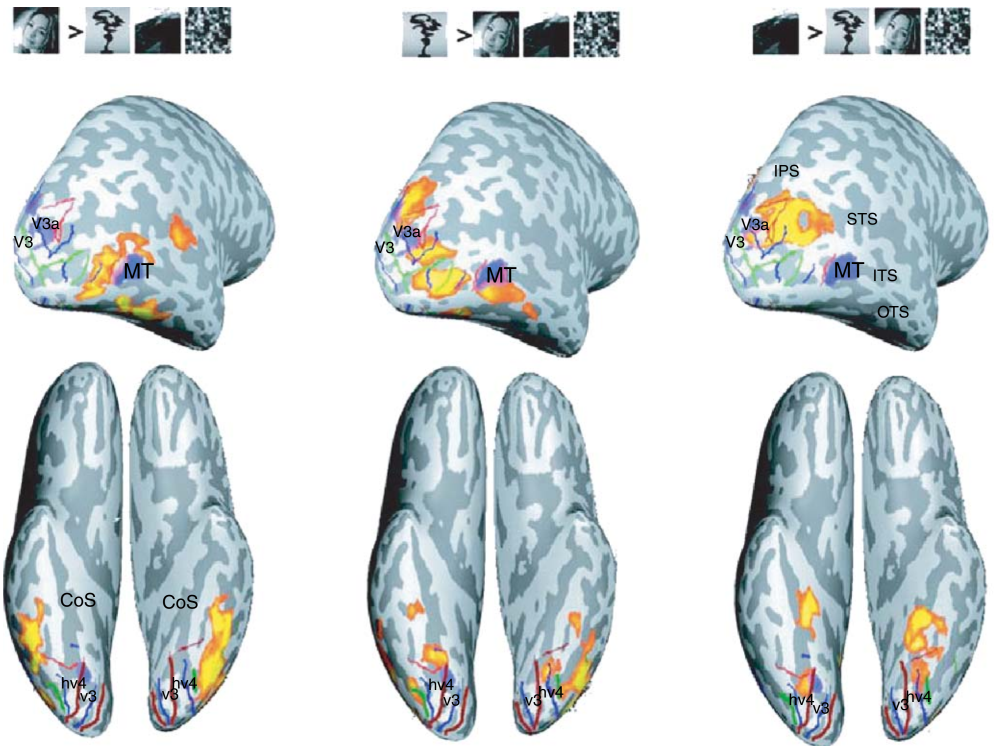

Figure 4 Face-, object-, and place-selective regions in the human brain displayed on an inflated cortical surface. Icons indicate the comparison done in the statistical tests. *Left*: Areas responding more strongly to faces than objects, places, or textures. *Center*: Areas responding more strongly to objects than faces, places, or textures. *Right*: Areas responding more strongly to places (scenes) than faces, objects, or textures. Yellow and orange indicate statistical significance. Colored lines indicate borders of retinotopic visual areas. Blue indicates area hMT+ that responds more strongly to moving versus stationary low-contrast gratings. Adapted from Grill-Spector, K. and Malach, R. 2004. The human visual cortex. Annu. Rev. Neurosci. 27, 649–677, with permission.

and words appear to be associated with central visual field bias, whereas buildings are associated with a peripheral one) (Figure 5). Another putative organizational rule for representation in high-order object areas is that different object categories are topographically represented based on shape-related differences (Fujita, I. *et al.*, 1992; Tanaka, K., 2003). Currently, no systematic investigation has addressed this possibility in human cerebral cortex.

1.30.3.1 Lateral Occipital Complex

Lateral occipital complex (LOC) is a complex of multiple areas in lateral occipital cortex that responds more strongly to a variety of object shapes, as compared with textures, noise patterns, scrambled objects, or scrambled Fourier phase information (which maintains the spatial frequency spectrum) (Malach, R. *et al.*, 1995; Grill-Spector, K. *et al.*, 1998b; 2001). These regions lie anterior and lateral to early retinotopic cortex. Based on fMRI data, the LOC can be divided into at least two putative subdivisions: a dorsal region (LO: lateral occipital) and a more ventral region (LOa: lateral occipital anterior) or pFs (posterior fusiform), along the posterior fusiform gyrus (Grill-Spector, K. *et al.*, 2001). fMRI results in LOC are generally consistent with earlier human PET studies, which had revealed selective activation of ventral and temporal regions associated with the recognition of objects (Haxby, J. V. *et al.*, 1991; Sergent, J. *et al.*, 1992; Kanwisher, N. *et al.*, 1996). This lateral occipital region can be strongly driven by ipsilateral as well as contralateral stimuli (Tootell, R. B. *et al.*, 1998d), and it may have a crude retinotopy (Larsson, J. *et al.*, 2006). The response in LOC is equivalent for familiar and unfamiliar shapes, so the response cannot be obviously accounted for in terms of matching to stored visual representations, or semantic/verbal coding of the stimuli (Malach, R. *et al.*, 1995; Kanwisher, N. *et al.*, 1996; Kanwisher, N., 2003).

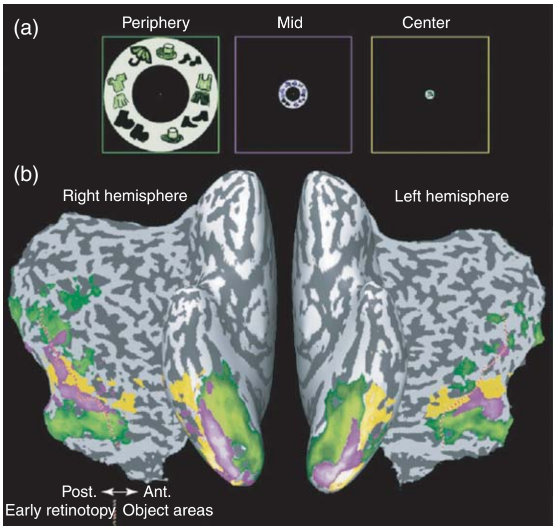

Figure 5 Eccentricity organization of human visual areas. The representations of center (yellow), mid (purple), and peripheral (green) visual field stimuli (a) are shown on a ventral view of the inflated hemispheres and on flattened cortical format (b). The eccentricity mapping is present even in the occipito-temporal cortex. Adapted from Malach, R., Levy, I., and Hasson, U. 2002. The topography of high-order human object areas. Trends Cogn. Sci. 6, 176–184, with permission.

Many studies have shown that the activation in object-selective cortex shows perceptual invariance. Object-selective regions in the ventral stream are activated when subjects view objects defined by luminance (Grill-Spector, K. *et al.*, 1998a), texture (Grill-Spector, K. *et al.*, 1998a; Kastner, S. *et al.*, 2000), motion (Grill-Spector, K. *et al.*, 1998a; Kriegeskorte, N. *et al.*, 2003), or depth cues (Kourtzi, Z. and Kanwisher, N., 2000b; 2001; Gilaie-Dotan, S. *et al.*, 2002), but not when subjects view textures, stationary dot patterns, coherently moving dots, or gratings defined by either motion or stereo. Other studies have shown that activation is independent of object format (photographs or line drawings) (Ishai, A. *et al.*, 2000) and that these regions are also activated when subjects perceive simple shapes created via illusory contours (Mendola, J. D. *et al.*, 1999; Stanley, D. A. and Rubin, N., 2003). Object-selective regions in the ventral stream represent shapes rather than contours or local features (Hasson, U. *et al.*, 2001; Kourtzi, Z. and Kanwisher, N., 2001; Andrews, T. J. *et al.*, 2002; Lerner, Y. *et al.*, 2002) and are more sensitive to the presentation of three-dimensional (3D) volumes relative to 2D shapes (Moore, C. and Engel, S. A., 2001; Kourtzi, Z. *et al.*, 2003a; Welchman, A. E. *et al.*, 2005). However, the unified perception of a global shape (or good Gestalt) may involve both LOC and lower visual areas (V1 and V2) (Murray, S. O. *et al.*, 2002; Altmann, C. F. *et al.*, 2003; Kourtzi, Z. *et al.*, 2003b). Interestingly, some regions within LO even show cross-modality convergence, with stronger activation to objects than textures, for both visually and haptically sensed objects (Amedi, A. *et al.*, 2001; James, T. W. *et al.*, 2002b).

fMR-adaptation paradigms (Grill-Spector, K. and Malach, R., 2001; Avidan, G. *et al.*, 2002b) have revealed more subtle aspects of LOC areas in invariant shape representations. Regions in the occipito-temporal sulcus (OTS) and fusiform gyrus (but not LO) show size and position invariance (Grill-Spector, K. *et al.*, 1999; 2001). In addition, two recent studies show some degree of viewpoint invariance for the representation of objects in ventral occipito-temporal (VOT) when using small rotation angles (James, T. W. *et al.*, 2002a; Vuilleumier, P. *et al.*, 2002; but see Grill-Spector, K. *et al.*, 1999).

Several studies have demonstrated a correlation between object perception and brain activation in lateral and ventral object areas such as LO (Grill-Spector, K. *et al.*, 2000; James, T. W. *et al.*, 2000; Bar, M. *et al.*, 2001; Avidan, G. *et al.*, 2002a; Kleinschmidt, A. *et al.*, 2002; Grill-Spector, K., 2003). In contrast, activity in lower-tier visual areas is not correlated with subjects' percepts in tasks requiring object recognition.

1.30.3.2 Fusiform Face Area

Neuroimaging studies have shown a specific region within the fusiform gyrus that is significantly more active when viewing faces (Sergent, J. and Signoret, J. L., 1992; Haxby, J. V. *et al.*, 1996) compared to other nonface stimuli such as objects (Kanwisher, N. *et al.*, 1997), letter strings (Puce, A. *et al.*, 1996), or houses (Tong, F. *et al.*, 2000). This area has been termed the fusiform face area (FFA) (Kanwisher, N. *et al.*, 1997). Human FFA appears to be topographically homologous to the macaque face patches located in the middle of the STS (Tsao, D. Y. *et al.*, 2003a; 2006). The FFA shows a higher response to upright than inverted faces (Yovel, G. and Kanwisher, N., 2005; but see Epstein, R. A. *et al.*, 2006), suggesting that upright faces are processed holistically in the FFA (see Tanaka, J. W. and Farah, M., 2003, for review). Holistic/configural aspects of face processing may be observed preferentially in the right FFA (Rossion, B. *et al.*, 2000; but see Yovel, G. and Kanwisher, N., 2004). Recently, fMR-adaptation paradigms have elegantly revealed that the FFA contains subpopulations of neurons, which are selectively tuned to face identity (Rotshtein, P. *et al.*, 2005; Loffler, G. *et al.*, 2005).

FFA activation correlates well with successful face processing but not with successful object processing (Grill-Spector, K. *et al.*, 2004). Other experiments have also used bistable phenomena such as binocular rivalry (Tong, F. *et al.*, 1998), and the Rubin face-vase illusion (Hasson, U. *et al.*, 2001; Andrews, T. J. *et al.*, 2002) to show the correlation of FFA activation with different perceptual states.

Currently, there is debate whether the function of the FFA is truly specific to faces, or whether it instead involves a domain-general operation that could in principle be applied to other stimulus categories. Gauthier and colleagues have argued that the right FFA is an expertise center, responding better to any overtrained visual stimuli, including (but not limited to) faces (Tarr, M. J. and Gauthier, I., 2000). For instance, the FFA is reportedly activated by cars in car experts and by birds in bird experts (Gauthier, I. *et al.*, 2000a). The FFA is also more active when participants become expert at distinguishing computer-generated nonsense shapes known as greebles (Gauthier, I. *et al.*, 1999). These evidence led Tarr M. J. and Gautier I. (2000) to reinterpret the name FFA as the flexible fusiform area. Additional evidence that has challenged the role of FFA in face processing is apparently normal face-related fMRI activation in the FFA in congenital prosopagnosic individuals who are markedly impaired at face processing (Hasson, U. *et al.*, 2003a; Avidan, G. *et al.*, 2005; Behrmann, M. and Avidan, G., 2005).

Early studies of face-selective activation in the cortex have reported that, in addition to the FFA, other cortical areas are selectively active for faces, specifically in the STS and in the inferior and mid-occipital gyri (e.g., Kanwisher, N. *et al.*, 1997; Halgren, E. *et al.*, 1999; Haxby, J. V. *et al.*, 1999; Vaina, L. M. *et al.*, 2001), although in some studies these areas appeared to be less systematically activated (e.g., Kanwisher, N. *et al.*, 1997) or showed a weaker face-selective response (Gauthier, I. *et al.*, 2000b) than did the FFA. Gauthier I. *et al.* (2000b) termed the face-selective inferior occipital area that falls within the larger LOC region, the occipital face area (OFA).

1.30.3.3 Parahippocampal Place Area

The parahippocampal gyrus is a cortical region in the medial temporal lobe that surrounds the hippocampus and plays an important role in both spatial memory (Squire, L. R. and Zola-Morgan, S., 1991) and navigation (Aguirre, G. K. *et al.*, 1996; Maguire, E. A. *et al.*, 1996). The parahippocampal place area (PPA) is a subregion in posterior parahippocampal and anterior lingual cortex that responds preferentially to indoor/outdoor scenes and also to houses/buildings, but not to faces or objects (Epstein, R. and Kanwisher, N., 1998; Aguirre, G. K. *et al.*, 1998). It has been recently demonstrated that the PPA represents scenes in a viewpoint-specific manner (Epstein, R. *et al.*, 2003) and processes the spatial structure of the currently visible environment (Epstein, R. *et al.*, 1999). In addition, activity in the PPA correlates with the scene/house percept (Tong, F. *et al.*, 1998; but see Marois, R. *et al.*, 2004). The evidence for the PPA is supported by neuropsychological patients with topographic disorientation associated with damage in parahippocampal cortex (Habib, M. and Sirigu, A., 1987; Bohbot, V. D. *et al.*, 1998; Aguirre, G. K. and D'Esposito, M., 1999; Epstein, R. *et al.*, 2001).

Recently, Bar and colleagues have shown that the parahippocampal cortex mediates the representation and processing of familiar contextual associations in general, rather than places *per se* (Bar, M. and Aminoff, E., 2003; Bar, M., 2004), and therefore, this region is activated when people recognize highly contextual objects (e.g., a traffic light, houses).

1.30.3.4 Extrastriate Body Area

Downing P. *et al.* (2001) have described a distinct cortical region in humans that responds selectively to images of nonface body parts. This region is located in the lateral occipitotemporal cortex, adjacent to motion-selective MT/MST area, in or near region(s) reportedly activated by the perception of biological motion (Grossman, E. *et al.*, 2000). Peelen M. V. and Downing P. E. (2005) have also reported a fusiform region, so-called the fusiform body area (FBA), which is adjacent to and partially overlaps with the FFA and responds more strongly to headless bodies than to objects (see also Schwarzlose, R. F. *et al.*, 2005).

1.30.4 Dorsal Stream Areas

The human parietal lobes (excluding somatosensory regions) traditionally fall into the category of association cortex because of their complex and multimodal responses (see Zeki, S. M., 1993, for review). Regions of parietal cortex form a major component of the dorsal stream, which is involved in spatial localization (the 'where' system) (Ungerleider, L. G. and Mishkin, M., 1982) and the control of action (the 'how' system) (Goodale, M. A. and Milner, A. D., 1992). Neuropsychological studies show that patients with parietal damage have attentional disorders (such as hemispatial neglect and simultanagnosia), spatial localization disorders, and sensorimotor coordination problems (Feinberg, T. E. and Farah, M. J., 1997). Single-neuron recordings in macaques also demonstrate numerous regions in parietal cortex that perform highly specialized spatial and sensorimotor functions (Andersen, R. A., 1989; Colby, C. L. and Goldberg, M. E., 1999). Recent neuroimaging studies have identified putative human homologues of macaque parietal regions (particularly regions in the IPS) (Figure 6) (Culham, J. C. and Kanwisher, N. G., 2001; Orban, G. A. *et al.*, 2004; 2006).

1.30.4.1 Caudal Intraparietal Sulcus

Monkey caudal intraparietal sulcus (cIPS) contains neurons selective for binocular disparity and 3D surface orientation and may provide information for the visual guidance of hand action (Sakata, H. *et al.*, 1997; 1998; 1999). Human neuroimaging has identified a region in the caudal end of the IPS that is activated during stereoscopic processing (Tsao, D. Y. *et al.*, 2003b), during object matching and grasping (Faillenot, I. *et al.*, 1997), as well as during discriminations of object size and surface orientation (Faillenot, I. *et al.*, 1999; Shikata, E. *et al.*, 2001). This area might be homologous to monkey cIPS.

1.30.4.2 Parieto-Occipital Cortex/V6

The anterior bank of the parieto-occipital (PO) sulcus of the macaque monkey (classically considered as part of Brodmann's area 19) contains two functionally distinct areas: a ventral, purely visual area, V6, and a dorsal area, V6A, containing visual neurons and neurons related to the control of reaching movements (Colby, C. L. *et al.*, 1988; Galletti, C. *et al.*, 1996; 2005). Macaque V6 contains a topographical representation of the contralateral (both upper and lower) visual field, up to an eccentricity of at least 80° (Galletti, C. *et al.*, 1999). Recent findings suggest that the likely

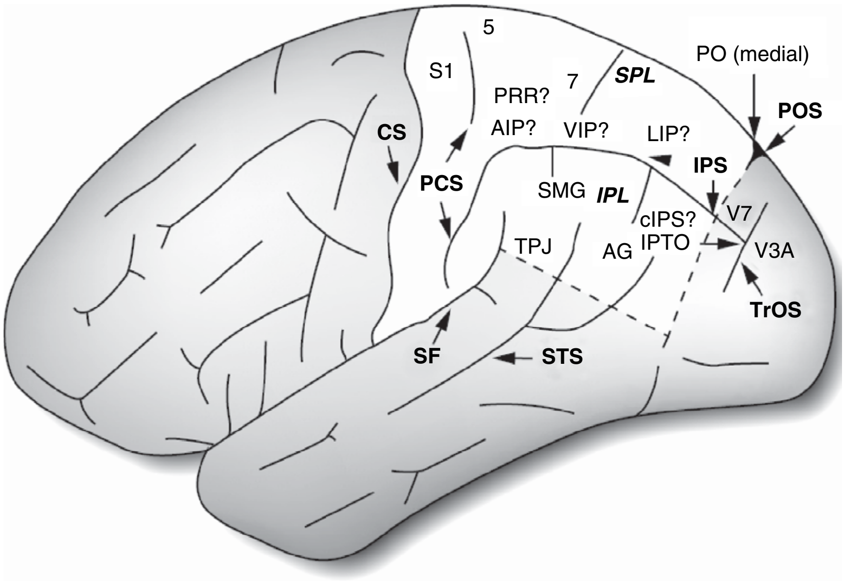

Figure 6 Dorsal stream areas in human parietal lobes. Major sulci, lobules, and functional or anatomical areas have been shown in the lateral view of human brain. Parietal boundaries are based on anatomical landmarks including central sulcus (CS), Sylvian fissure (SF), and parieto-occipital sulcus (POS). The intraparietal sulcus (IPS) divides the parietal lobe into the superior parietal (SPL) and inferior parietal (IPL) lobules. The IPS is located between the transverse occipital sulcus (TrOS near the POS) and the postcentral sulcus (PCS). Several human areas have been proposed to be putative human homologues of monkey areas in the anterior (AIP), ventral (VIP), medial (MIP), lateral (LIP), and caudal (cIPS) sections of the IPS, and also in the parieto-occipital (PO) region. Other areas without clear homologies include the supramarginal (SMG) and angular (AG) gyri, functional areas at the IPS/TrOS junction (IPTO), and the temporo-parietal junction (TPJ). Medial parietal areas have not been well characterized in humans. Adapted from Culham, J. C. and Kanwisher, N. G. 2001. Neuroimaging of cognitive functions in human parietal cortex. Curr. Opin. Neurobiol. 11, 157–163.

human homologue of the macaque V6 is also located in the parieto-occipital sulcus (anteromedial cuneus) (Dechent, P. and Frahm, J., 2003). Human V6 responds strongly to luminance flicker (Portin, K. and Hari, R., 1999; Vanni, S. *et al.*, 2001; Dechent, P. and Frahm, J., 2003). The topography of V6 has not yet been established in humans (Portin, K. and Hari, R., 1999; Dechent, P. and Frahm, J., 2003).

1.30.4.3 Parietal Reach Region

Monkey parietal reach region (PRR) includes both area V6A and the medial intraparietal area (MIP) (Galletti, C. *et al.*, 1997; Snyder, L. H. *et al.*, 1997; Galletti, C. *et al.*, 2003). Neuroimaging studies have also reported activation in the human IPS during reaching and pointing movements (Kertzman, C. *et al.*, 1997; Connolly, J. D. *et al.*, 2000). Reach activity has been reported anterior to saccade activity (Kawashima, R. *et al.*, 1996), whereas pointing-related activation seems to be more medial to a saccade-related region (Connolly, J. D. *et al.*, 2000). A reach-related region in the anterior IPS is modulated by eye position (Baker, J. T. *et al.*, 1999; DeSouza, J. F. X. *et al.*, 2000) and could be the human homologue of the monkey PRR (Andersen, R. A. *et al.*, 1985).

1.30.4.4 Anterior Intraparietal Area

Neurons in monkey anterior intraparietal area (AIP) are involved in fine grasping (Sakata, H. and Taira, M., 1994). The human anterior IPS is also activated during visually guided grasping (Faillenot, I. *et al.*, 1997; Binkofski, F. *et al.*, 1998; Shikata, E. *et al.*, 2003; Culham, J. C. *et al.*, 2003), although grasping activity appears to overlap with reach-related activity. This area is a probable human homologue of monkey AIP. Other studies have reported that this region is also activated by action observation (Iacoboni, M. *et al.*, 1999; Buccino, G. *et al.*, 2001; Muhlau, M. *et al.*, 2005), mental rotation (Bonda, E. *et al.*, 1995), cross-modal processing of object features (Grefkes, C. *et al.*, 2002), tactile manipulation of objects (Binkofski, F. *et al.*, 1999a; 1999b), and even by passive viewing of graspable objects, namely tools (Chao, L. L. and Martin, A., 2000).

1.30.4.5 Ventral Intraparietal Area

Monkey ventral intraparietal area (VIP) responds to motion in any sensory modality (Colby, C. L. *et al.*, 1993; Duhamel, J. R. *et al.*, 1998). Bremmer F. *et al.* (2001) have identified a region in the depth (fundus) of the human IPS that responds multimodally to visual, tactile, and auditory moving stimuli. They propose that this area might be the human equivalent of monkey area VIP. This region is also activated by 3D structure from motion (Orban, G. A. *et al.*, 1999; Vanduffel, W. *et al.*, 2002). In addition, human VIP may play a crucial role in the representation of quantity and number processing (Dehaene, S. *et al.*, 2003; Hubbard, E. M. *et al.*, 2005).

1.30.4.6 Lateral Intraparietal Area

Sereno M. I. *et al.* (2001) have identified a region of the posterior IPS that is thought to be homologous to monkey lateral intraparietal area (LIP) (Colby, C. L. *et al.*, 1996). This region is active when humans make visually guided saccades (Muri, R. M. *et al.*, 1996). Putative LIP contains a retinotopic map of saccade direction (Sereno, M. I. *et al.*, 2001), similar to macaque LIP (Ben Hamed, S. *et al.*, 2001). In addition, recent studies have shown that this region in the IPS is jointly activated by attending, pointing, and making saccades to peripheral targets (Astafiev, S. V. *et al.*, 2003). Another parallel between macaque and human area LIP is the involvement of these areas in spatial updating and representing the spatial location of targets in eye-centered coordinates (Medendorp, W. P. *et al.*, 2003; Merriam, E. P. *et al.*, 2003).

1.30.4.7 Superior Parietal Lobule and Inferior Parietal Lobule

The parietal lobe above the IPS and below the IPS is called superior parietal lobule (SPL) and inferior parietal lobule (IPL), respectively. Human SPL is believed to be homologous to area 7 in macaque cortex (Andersen, R. A., 1988). Human SPL and IPL (including the supramarginal gyrus) along with regions in the IPS, the postcentral sulcus, and the temporo-parietal junction are activated in attention-related tasks (Corbetta, M. *et al.*, 1993; 1998; Wojciulik, E. and Kanwisher, N., 1999; Donner, T. *et al.*, 2000; Corbetta, M. *et al.*, 2000; Hopfinger, J. B. *et al.*, 2000; Perry, R. J. and Zeki, S., 2000; Culham, J. C. *et al.*, 2001). So far, the precise role of these parietal regions in attention is a matter of substantial debate; however, several studies have strengthened the evidence that regions in parietal cortex (particularly SPL and in some cases IPL) are a source of attentional control signals (Kastner, S. *et al.*, 1999;

Shulman, G. L. *et al.*, 1999; Corbetta, M., *et al.*, 2000; Hopfinger, J. B. *et al.*, 2000).

1.30.5 Frontal Areas

Felleman D. J. and Van Essen D. C. (1991) have classified macaque areas 8 (FEF: frontal eye field) and 46 as part of visual cortex. However, little is known about the visual properties of frontal and prefrontal cortical areas in humans. Recently, one study has shown that working memory-related areas in human dorsolateral prefrontal cortex contain a topological map of visual space (Hagler, D. J., Jr. and Sereno, M. I., 2006).

1.30.6 Conclusions

Over the past several decades, the intense and comprehensive study of visual cortical areas in monkeys and other mammals has resulted in what are arguably the best-understood regions of mammalian cortex. This body of work has formed the basis of well-informed models of how sensory information is processed on its way to higher-order integration.

Over most of that time span, very little was known about the workings of visual cortex in humans, except for a few hints from histology and neuropsychology about V1, and a few higher-order visual processing regions. However, with the advent of modern, non-invasive neuroimaging techniques, and with a more systematic comparison of information from macaques and humans, our understanding of human visual cortex is maturing nicely. The next few decades promise to be even more revealing.

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