'What' and 'where' in the human brain

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Multiple visual areas in the cortex of nonhuman primates are organized into two hierarchically organized and functionally specialized processing pathways, a 'ventral stream' for object vision and a 'dorsal stream' for spatial vision. Recent findings from positron emission tomography activation studies have localized these pathways within the human brain, yielding insights into cortical hierarchies, specialization of function, and attentional mechanisms.

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Introduction: visual processing streams in nonhuman primates

Vision is by far the most richly represented sensory modality in the cortex of nonhuman primates. Anatomical and physiological studies of Old World monkeys have revealed at least thirty separate visual cortical areas, occupying about one-half of the total cortex [1,2]. As shown in Fig. 1, these areas appear to be organized into two functionally specialized processing pathways, each having the striate cortex as the source of inital input [3,4]. The occipitotemporal pathway, or 'ventral stream', is crucial for the visual identification of objects, whereas the occipitoparietal pathway, or 'dorsal stream', is crucial for appreciating the spatial relationships among objects, as well as for the visual guidance of movements toward objects in space.

Recently, Young [5•] has analyzed the connectional topology for extrastriate cortical areas of Old World monkeys using multidimensional scaling, and has confirmed the segregation of these areas into dorsal and ventral processing streams — with limited cross-talk between them. Multiple visual areas in the cortex of New World monkeys appear to be similarly organized into separate dorsal and ventral streams [6], suggesting a common primate plan that probably extends to the organization of the human visual cortex as well. In this review, we will examine the results of recent work aimed at addressing this idea.

The original evidence for separate processing streams for object vision and spatial vision was the contrasting effects of inferior temporal and posterior parietal lesions in monkeys. Lesions of inferior temporal cortex cause severe deficits in performance on a wide variety of visual discrimination tasks (e.g. pattern, object, color) [7], but not on visuospatial tasks (e.g. visually guided reaching and judging which of two identical objects is located closer to a visual landmark; reviewed in [3]). In contrast, posterior parietal lesions do not affect visual discrimination performance, but instead cause severe deficits in visuospatial performance (for review, see [3]). Physiological evidence also supports this distinction, as neurons in areas (or modules of areas) along the occipitotemporal cortical pathway (areas V1, V2, V4, and inferior temporal areas TEO and TE) respond selectively to visual features relevant to object identification (i.e. 'what'), such as color and shape, whereas neurons in areas (or modules of areas) along the occipitoparietal cortical pathway (areas V1, V2, V3, middle temporal area (MT), medial superior temporal area (MST), and further stations in inferior parietal and superior temporal sulcal cortex) respond selectively to spatial aspects of stimuli (i.e. 'where'), such as direction of motion and velocity, as well as to tracking eye movements (for reviews, see [1,8]). Recent connectionist models have suggested that there may be computational advantages to segregate these 'what' and 'where' functions into separate anatomical pathways [9,10].

Although it had been proposed that the occipitotemporal and occipitoparietal pathways are the cortical extensions of separate subcortical 'parvo-' and 'magno-' processing systems [11], there is now considerable evidence that this is not the case. Although it is true that the input to the occipitoparietal pathway derives mainly from cells in the magnocellular layers of the lateral geniculate nucleus, the input to the occipitotemporal pathway derives from cells in both the magnocellular and parvocellular layers (for review, see [12••]).

Hierarchical organization of visual cortical areas

Areas along both the occipitotemporal and occipitoparietal pathways are organized hierarchically, such that low-level inputs are transformed into more useful representations through successive stages of pro-

Abbreviations

MRI—magnetic resonance imaging; **MST**—medial superior temporal area; **MT**—middle temporal area; **PET**—positron emission tomography; **rCBF**—regional cerebral blood flow.

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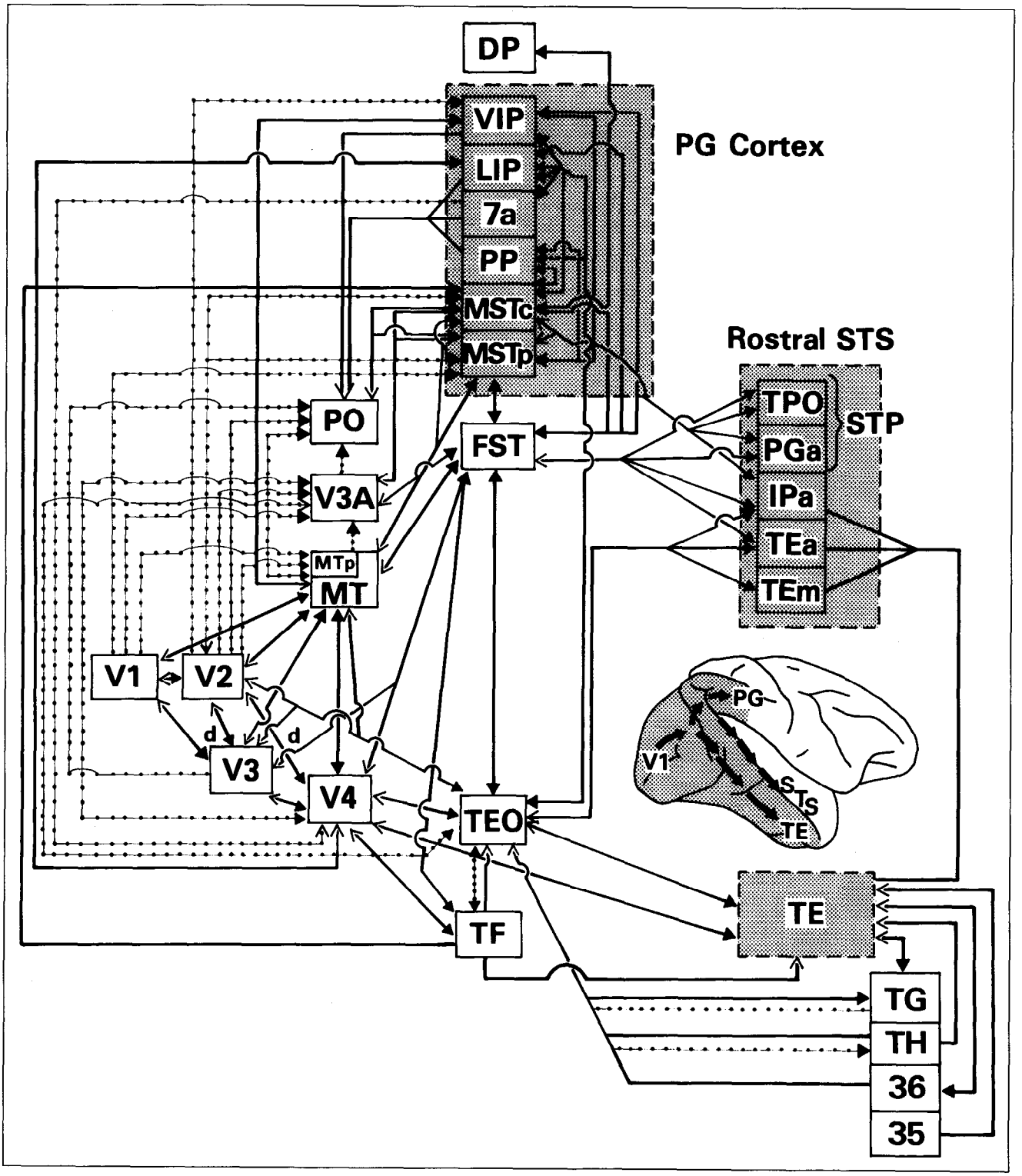

Fig. 1. Summary diagram of the visual cortical hierarchy. Solid lines indicate connections originating from both central and peripheral field representations, whereas dotted lines indicate connections restricted to peripheral field representations. Solid arrowheads indicate feedforward connections, open arrowheads indicate feedback connections, and reciprocal solid arrowheads indicate intermediate-type connections. The diagram demonstrates the divergence in the flow of visual information into ventral and dorsal streams directed toward the inferior temporal (TE) and inferior parietal (PG) cortex, respectively, and possible sites for interaction between the two within the rostral superior temporal sulcus (STS) [85]. Reproduced with permission from [86•].

cessing. As one proceeds from one area to the next, both neuronal response latencies and average receptive field size increase steadily, and neuronal response properties become increasingly complex. Along the oc-

cipitotemporal pathway, for example, whereas many V1 cells function as local spatiotemporal filters, V2 cells may respond to 'virtual' or illusory contours of figures [13], some V4 cells respond only if a stimulus stands out from its background on the basis of a difference in color or form [14,15], and inferior temporal cells respond selectively to global or overall object features, such as shape [16–18], with a small proportion being specialized for faces ([17,19–21]; for reviews, see [22,23]). Similarly, as one proceeds from V1 to MT, to MST, and thence to areas in parietal cortex, new types of directional selectivity emerge. For example, whereas cells in V1 are sensitive to the direction of motion of the Fourier components of a complex pattern, many MT cells are sensitive to the global motion of the pattern, that is, the vector sum of the component motions [24]. Within MST, many cells are selective for rotation or for the expansion/contraction of the image of any object moving in depth [25,26], and whereas such motion selectivity has also been reported for parietal neurons, these neurons demonstrate even more complex spatial properties [27,28].

Thus, much of the neural mechanism for both object vision and spatial vision can be viewed as a 'bottom-up' process subserved by feedforward projections between successive pairs of areas within a pathway. Anatomical studies have shown, however, that each of these feedforward projections is reciprocated by a feedback projection [1,2]. Projections from higher-order processing stations back to lower-order ones could mediate some 'top-down' aspects of visual processing, such as the influence of selective attention. It has also been proposed that feedback, or re-entrant, projections could mediate perceptual completion effects or perceptual binding of stimulus attributes [29,30,31•].

The effects of focal brain lesions in humans

The differential visual impairments produced by focal lesions in clinical cases suggest that human visual cortex, like that of the monkey, may be similarly organized into two anatomically distinct and functionally specialized pathways: the ventral and dorsal streams [32–37]. In the most recent of these studies, for example, a double dissociation of visual recognition (face perception camouflaged by shadows) and visuospatial performance (stylus maze learning) was demonstrated in two men with lesions of occipitotemporal and occipitoparietal cortex, respectively — confirmed by postmortem examination [37]. The specific clinical syndromes produced by occipitotemporal lesions include visual object agnosia, prosopagnosia, and achromatopsia (for reviews, see [38,39]), whereas those produced by occipitoparietal lesions include optic ataxia (misreaching), visuospatial neglect, constructional apraxia, gaze apraxia, akinotopsia, and disorders of spatial cognition (see e.g. [40–42]; reviewed in [43]). Interestingly, imagery disorders involving descriptions of either objects (especially faces, animals, and colors of objects) or spatial relations (e.g. geographic directions) are also dissociable following temporal and parietal lesions [44].

Recently, Goodale, Milner and colleagues [45–47,48•] have proposed that the ventral and dorsal streams, rather than mediating 'what it is' versus 'where it is', are best understood as subserving the perception of objects versus the control of skilled actions directed toward those objects. It should be pointed out that, in its original formulation, the what and where model acknowledged the importance of the parietal cortex for mediating visually guided reaching [3]. However, what was central to the model was that, in the perceptual domain, parietal damage produces visuospatial rather than object-recognition impairments.

Nonetheless, Goodale and Milner [45–47,48•] have argued, largely on the basis of a single case, patient D.F., that separate object vision and spatial vision pathways cannot explain the ability of this patient to use the size and orientation of objects to appropriately control her visually guided grasping movements, despite her profound inability to describe or recognize these same features of the object. What is the evidence, however, that parietal cortex is mediating these visually guided movements? According to Goodale and Milner [45,46,48•], patient D.F. suffered an anoxic episode from carbon monoxide poisoning, resulting in diffuse brain damage, which was most apparent in cortical areas 18 and 19. These areas are the source of visual input to parietal, as well as temporal, cortex. Thus, it is not at all clear which brain regions are mediating patient D.F.'s intact abilities. They may even be subcortical. The crucial question is whether patients with parietal damage demonstrate visuospatial impairments that cannot be attributed to a primary visuomotor defect. The answer is clearly yes. In a recent review summarizing the results of testing 67 patients with focal parietal lesions confirmed with magnetic resonance imaging (MRI), von Cramon and Kerkhoff [49•] reported that the patients had impaired perception of horizontal and vertical axes, poor length and distance estimation, a deficit in orientation discrimination, as well as a deficit in position matching. Furthermore, there was some evidence that impaired perception of axes and angles was more closely associated with anterior parietal damage, whereas impaired perception of position and distance was more closely assoicated with posterior parietal damage. Thus, although visuospatial deficits may be accompanied by visuomotor impairments, they are not explained by them.

PET–rCBF studies of dorsal and ventral streams in human cortex

By measuring local hemodynamic changes associated with specific visual processes, functional brain imaging makes it possible to map the organization of human extrastriate cortex with far greater precision than is possible with human lesion studies, and without the

confounding influence of compensatory responses to brain injury. In experiments designed to investigate the possible existence of separate object vision and spatial vision pathways in humans, changes in regional cerebral blood flow (rCBF) were measured using positron emission tomography (PET) while subjects performed object identity and spatial location matching-to-sample tasks [50,51•]. In the object identity task, the subject indicated which of the two (choice) faces matched the sample face, whereas in the spatial location task, the subject indicated which of two (choice) stimuli contained a small square (or a dot) in the same location, relative to a double line, as the small square (or dot) in the sample stimulus. For some conditions, the small squares contained faces, such that identical stimuli were used for face and location matching, with only the task requirements changing.

The results identified specific occipitotemporal and occipitoparietal regions associated with face and location matching, respectively, and specific posterior occipital regions associated with both visual functions (Fig. 2). Within the occipitotemporal cortex, areas in the posterior and mid-fusiform gyrus (Brodmann areas 19 and 37) were selectively activated by the face-matching task [51•]. Within occipitoparietal cortex, areas in the dorsolateral occipital cortex (Brodmann area 19), superior parietal cortex, and the cortex near the fundus of the intraparietal sulcus (both Brodmann area 7) were selectively activated by the location-matching task [51•]. In addition, regions in right inferior prefrontal (Brodmann areas 45 and 47) and right dorsal premotor (Brodmann area 6) cortex were activated selectively by face- and location-matching, respectively (JV Haxby, unpublished data). These findings, thus, indicate the existence in humans, as in monkeys, of two functionally specialized and anatomically segregated visual processing pathways and further suggest the extensions of each into the frontal lobe. As shown in Fig. 2, the locations of the occipitoparietal and premotor foci activated by the spatial location matching-to-sample task have been corroborated in two recent studies of visuospatial processing, one of which employed a spatial attention task [52••] and the other of which employed a spatial working memory task [53•]. Similarly, the locations of occipitotemporal foci activated during face perception have also been corroborated ([54••]; see below).

Hierarchical organization of face processing in the ventral stream

Having identified dorsal and ventral processing streams in human cortex, it is possible to use different experimental paradigms to explore the functional specialization of areas within them. For example, whereas multiple regions within occipitotemporal and ventral temporal cortex are activated during 'face' tasks, the locations of these activations are task dependent. As shown in Fig. 2, identification based on facial features, as in face matching [50,51•] or gender discrimination [54••], activates the posterior fusiform gyrus, whereas identification of a unique individual's face activates the mid-fusiform gyrus, and retrieving knowledge about an individual, such as in naming the individual's profession, activates even more anterior regions in the parahippocampal gyrus, midtemporal gyrus, and temporal pole [54••]. These results suggest a hierachical organization as one proceeds from posterior to anterior extrastriate areas in the ventral stream. Posteriorly, facial features appear to be extracted in order to construct, in more anterior regions, a unique representation of a face. Yet more anteriorly, this representation can be associated and stored with knowledge about that individual. This hierarchical scheme, derived from PET studies, fits well with the clinical literature on the kinds of face-recognition impairments produced by selective temporal lobe lesions [55].

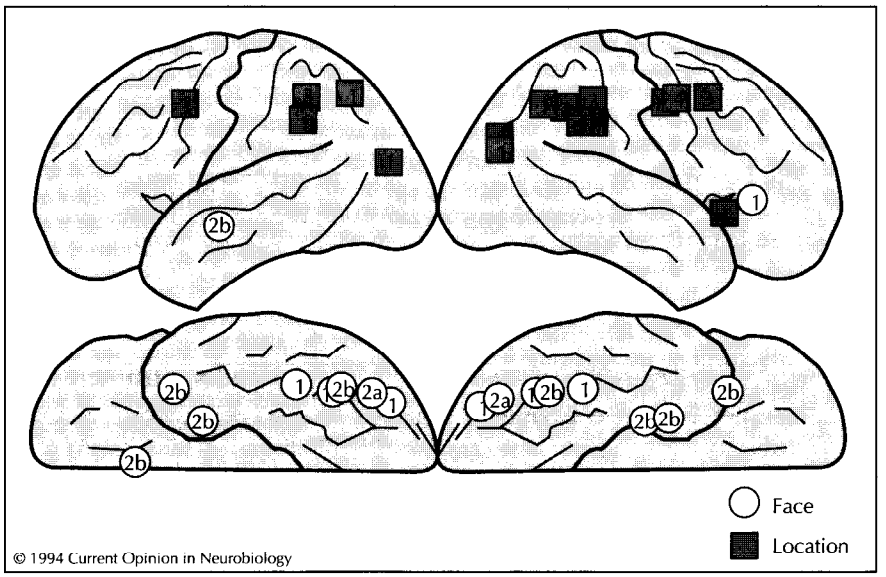

Fig. 2. Cortical regions in human dorsal and ventral streams selectively activated by perception of location or faces, as demonstrated by increased rCBF, measured with PET. The two top diagrams depict the left and right lateral views of each of the two cortical hemispheres, and the two bottom diagrams represent the left and right ventral views. Numbers in symbols indicate the study reporting each activated focus: 1 — face and location matching-to-sample ([51•]; JV Haxby, unpublished data); 2a — gender discrimination [54••]; 2b —face identity [54••]; 3 — shifting attention to spatial locations [52••]; and 4 — spatial working memory [53•]. In some instances, multiple nearby foci are shown as a single focus, representing their center of gravity.

Areas MT and V4 in the human brain?

In the monkey, a major route by which visual information is transmitted to inferior temporal cortex is via area V4, whereas a major route to inferior parietal cortex is via area MT, also known as area V5 (Fig. 1). PET studies have indicated the locations of possible homologues of these areas in the human brain.

Area MT

Area MT in the monkey is characterized by a high proportion of neurons selective for the direction of visual motion [56]. In Old World monkeys, the area is located on the lateral bank and floor of the caudal superior temporal sulcus, whereas in New World monkeys it is located in the middle part of the temporal lobe; in both Old and New World monkeys, it is distinguished from surrounding areas by heavy myelination (e.g. [57–61]).

PET studies have identified a region within the lateral occipitotemporoparietal cortex of humans that is selectively activated by the perception of motion [62,63,64••] (Fig. 3). A detailed study of the neuroanatomical location of this area in 12 subjects, mapped onto structural MRI scans, showed that it is consistently located in the ascending limb of the inferior temporal sulcus [64••]. It has recently been reported that visual activation of presumably the same region can be detected using functional MRI (RBH Tootell, KK Kwong, JW Belliveau, JR Baker, CE Stern, *et al.*, *Soc Neurosci Abstr* 1993, 19:1500). Importantly, in this study, low contrast stimuli were as effective as high contrast stimuli in activating the area, just as one would predict if the area were MT, as the inputs to this area are derived from the magnocellular layers of the lateral geniculate nucleus. Finally, a postmortem study of human brain has identified a heavily myelinated zone in the lateral occipitotemporoparietal cortex [65], providing further evidence for the hypothesis that this region is the human homologue of area MT. It should be pointed out, however, that, in addition to MT, the monkey contains numerous areas in parietal cortex and the superior temporal sulcus that are selective for motion, and some of these areas (e.g. area MST) are also heavily myelinated [25,26,66,67]. Thus, the identification of the homologue of MT in human cortex remains tentative.

Area V4

Area V4 in the monkey contains neurons selective for many different features relevant for object recognition, including color and shape [14,15,68,69•]. In Old World monkeys, the area is located dorsally in the hemisphere (mainly on the prelunate gyrus), where the lower visual field is represented, and it extends ventrally into occipitotemporal cortex, where the upper visual field is represented [70]. On the basis of anatomical connections and receptive field properties, it has been proposed that the homologous area in New World monkeys is DL, the dorsolateral area [71,72].

The perception of color in humans has been associated with activation of a ventromedial occipital area (in the collateral sulcus or lingual gyrus) in three separate PET studies [62,63,73] (Fig. 3). Because V4 contains color-selective cells, it has been speculated that this area is the homologue of V4 [63,74]. The location of this area agrees well with the location of lesions associated with achromatopsia [75], and is close but medial to the posterior fusiform area activated by faces (compare Figs. 2 and 3). That these color- and face-selective areas are close to each other, but not identical, is supported by recent studies of evoked potentials measured on the cortical surface in presurgical epilepsy patients [76,77]. The proximity of color- and face-selective areas would explain the frequent association of achromatopsia with prosopagnosia [75,78].

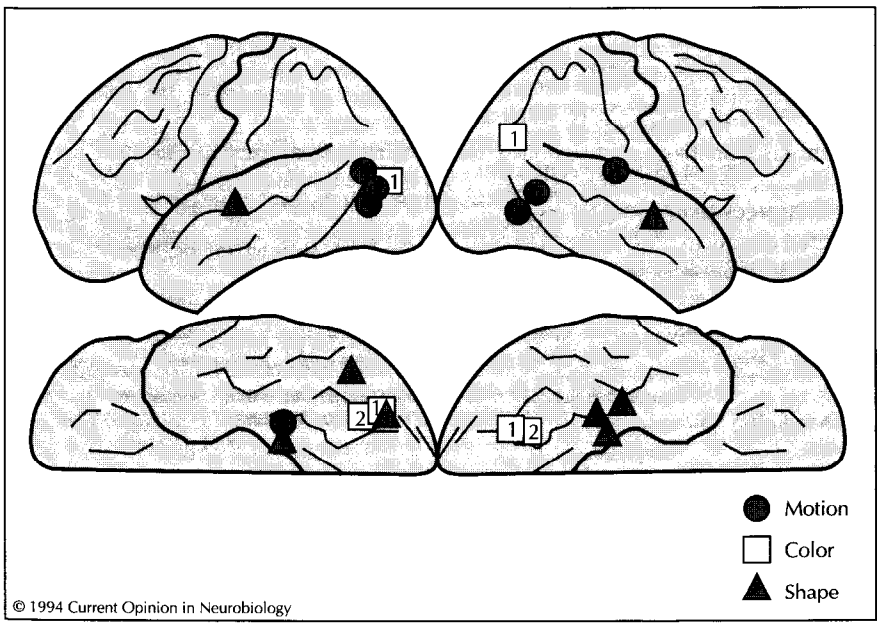

Fig. 3. Human extrastriate cortical regions (identified by PET–rCBF studies) associated with the perception of color, shape, and motion. The two top diagrams depict the left and right lateral views of each of the two cortical hemispheres, and the two bottom diagrams represent the left and right ventral views. Numbers in symbols indicate the study reporting each activated focus: 1 — selective attention to color, shape, and velocity [62]; 2 — passive perception of color and motion [63]; and 3 — passive perception of motion [64••]. In some instances, multiple nearby foci are shown as a single focus, representing their center of gravity.

What is the evidence that the color-selective area in humans is the homologue of monkey area V4? If it were, then the area should also be activated by shape, like V4 neurons. Of the two PET studies examining color and shape, one found that shape perception also activated this ventromedial occipitotemporal region [62], but the other did not [73]. Even more troublesome is the finding of additional color-selective foci in lateral occipital cortex [62] (Fig. 3). But perhaps the most compelling evidence against the idea that these areas are homologous comes from the different effects of lesions. V4 lesions in monkeys do not produce the profound and permanent color impairment that is seen in patients with achromatopsia ([79,80,81•]; reviewed in [82•]). Moreover, V4 lesions produce significant impairments in form perception ([80,81•,83]; R Desimone, L Li, S Lehky, LG Ungerleider, M Mishkin, *Soc Neurosci Abstr* 1990, 16:621), but form perception is usually intact in patients with achromatopsia. Thus, there appears to be an area in ventromedial occipital cortex of humans that is especially important for color vision, but this area may not be the homologue of V4.

Visual selective attention and the extrastriate cortex

By holding stimuli constant, two PET studies have examined the effect of manipulating the subject's attention to different aspects of the visual display [51•,62]. The results of these studies showed that selective attention to a particular attribute of a visual stimulus — such as color, motion, shape, face identity, or spatial location — activates the same area of extrastriate cortex that is activated during the perceptual processing of that attribute [51•,62]. Thus, selective attention to one aspect of a visual stimulus may be mediated, in part, by the selective increase in activity of neural systems that process that type of information. Additionally, it has been found that shifting attention to different spatial locations activates the same occipitoparietal and frontal areas associated with the perception of spatial location [51•,52••] (Fig. 2). Thus, although it has been proposed that these parietal and frontal areas constitute a system for spatially directed attention [84], an alternative possibility is that they are simply perceptual processing areas, in this instance for spatial location, that are modulated by selective attention in the same way that other functionally specialized areas are. If so, then an unanswered question is which neural systems drive the selection process.

Conclusion

With the advent of brain imaging techniques, considerable progress has been made in understanding the organization of the human brain. As in monkeys, the human cortex possesses separate cortical visual streams for processing object identity and spatial location information. There is emerging evidence for hierarchical processing and functional specialization within these two streams, although this work is still in an early stage and homologies with cortical areas in the monkey remain tentative. It is clear, however, that processing within extrastriate areas is strongly modulated by selective attention, as it is in the monkey. Although brain imaging cannot reveal the workings of the cortex at the level of individual neurons, it can be used to test hypotheses generated by work in animals and to advance into areas of cognition that are unique to the human brain.

References and recommended reading

Papers of particular interest, published within the annual period of review, have been highlighted as:

- • of special interest
- •• of outstanding interest

1. DESIMONE R, UNGERLEIDER LG: **Neural Mechanisms of Visual Processing in Monkeys.** In *Handbook of Neuropsychology*, vol 2. Edited by Boller F, Grafman J. Amsterdam: Elsevier; 1989:267–300.

2. FELLEMAN DJ, VAN ESSEN DC: **Distributed Hierarchical Processing in the Primate Cerebral Cortex.** *Cereb Cortex* 1991, 1:1–47.

3. UNGERLEIDER LG, MISHKIN M: **Two Cortical Visual Systems.** In *Analysis of Visual Behavior.* Edited by Ingle DJ, Goodale MA, Mansfield RJW. Cambridge, MA: MIT Press; 1982:549–586.

4. MISHKIN M, UNGERLEIDER LG, MACKO KA: **Object Vision and Spatial Vision: Two Cortical Pathways.** *Trends Neurosci* 1983, 6:414–417.

5. • YOUNG MP: **Objective Analysis of the Topological Organization of the Primate Cortical Visual System.** *Nature* 1992, 358:152–154.

This study reports the results of multidimensional scaling to analyze the connectional topology of extrastriate visual cortical areas. The results support the idea that these areas are segregated into 'dorsal' and 'ventral' streams with limited cross-talk, that the streams converge in area 46 of prefrontal cortex and within the polysensory cortex of the superior temporal sulcus, and that the system is hierarchically organized.

6. WELLER RE: **Two Cortical Visual Systems in Old World and New World Primates.** In *Progress in Brain Research*, vol 75. Edited by Hicks TP, Benedek G. Amsterdam: Elsevier; 1988:293–306.

7. GAFFAN D, HARRISON S, GAFFAN EA: **Visual Identification Following Inferotemporal Ablation in the Monkey.** *Q J Exp Psychol [B]* 1986, 38:5–30.

8. MAUNSELL JHR, NEWSOME WT: **Visual Processing in Monkey Extrastriate Cortex.** *Annu Rev Neurosci* 1987, 10:363–401.

9. RUECKL JG, CAVE KR, KOSSLYN SM: **Why Are "What" and "Where" Processed by Separate Cortical Visual Systems? A Computational Investigation.** *J Cogn Neurosci* 1989, 1:171–186.

10. OTTO I, GRANDGUILLAUME P, BOUTKHIL L, BURNOD Y: **Direct and Indirect Cooperation Between Temporal and Parietal Networks for Invariant Visual Recognition.** *J Cogn Neurosci* 1992, 4:35–57.

11. LIVINGSTONE MS, HUBEL DH: **Anatomy and Physiology of a Color System in the Primate Visual Cortex.** *J Neurosci* 1987, 7:3371–3377.

12. MERIGAN WH, MAUNSELL JHR: How Parallel are the Primate Visual Pathways? *Annu Rev Neurosci* 1993, 16:369–402.
•• This review summarizes the recent work on the functional distinctions between the magnocellular and parvocellular pathways, and evaluates the degree to which these subcortical pathways remain segregated in cortex. The authors conclude that the pathway to parietal cortex is largely (though not entirely) dependent on magnocellular inputs, but that the pathway to temporal cortex receives major contributions from both magnocellular and parvocellular inputs.

13. VON DER HEYDT R, PETERHANS E, BAUMGARTNER G: Illusory Contours and Cortical Neuron Responses. *Science* 1984, 224:1260–1262.

14. DESIMONE R, SCHEIN SJ: Visual Properties of Neurons in Area V4 of the Macaque: Sensitivity to Stimulus Form. *J Neurophysiol* 1987, 57:835–868.

15. SCHEIN SJ, DESIMONE R: Spectral Properties of V4 Neurons in the Macaque. *J Neurosci* 1990, 10:3369–3389.

16. SCHWARTZ EL, DESIMONE R, ALBRIGHT TD, GROSS CG: Shape Recognition and Inferior Temporal Neurons. *Proc Natl Acad Sci USA* 1983, 80:5776–5778.

17. DESIMONE R, ALBRIGHT TD, GROSS CG, BRUCE C: Stimulus Selective Properties of Inferior Temporal Neurons in the Macaque. *J Neurosci* 1984, 4:2051–2062.

18. TANAKA K, SAITO H, FUKUDA Y, MORIYA M: Coding Visual Images of Objects in the Inferotemporal Cortex of the Macaque Monkey. *J Neurophysiol* 1991, 66:170–189.

19. BAYLIS GC, ROLLS ET, LEONARD CM: Selectivity Between Faces in the Responses of a Population of Neurons in the Cortex in the Superior Temporal Sulcus of the Monkey. *Brain Res* 1985, 342:91–102.

20. ROLLS ET, BAYLIS GC, LEONARD CM: Role of Low and High Spatial Frequencies in the Face-Selective Responses of Neurons in the Cortex in the Superior Temporal Sulcus in the Monkey. *Vision Res* 1985, 25:1021–1035.

21. PERRETT DI, MISTLIN AJ, CHITTY AJ: Visual Neurones Responsive to Faces. *Trends Neurosci* 1987, 10:358–364.

22. DESIMONE R: Face-Selective Cells in the Temporal Cortex of Monkeys. *J Cogn Neurosci* 1991, 3:1–8.

23. PERRETT DI, HIETANEN JK, ORAM MW, BENSON PJ: Organization and Functions of Cells Responsive to Faces in the Temporal Cortex. *Philos Trans R Soc Lond [Biol]* 1992, 335:23–30.

24. MOVSHON JA, ADELSON EH, GIZZI MS, NEWSOME WT: The Analysis of Moving Visual Patterns. In *Pattern Recognition Mechanisms*. Edited by Chagas C, Gattass R, Gross C. Vatican City: Pontifical Academy of Sciences; 1985:117–151.

25. TANAKA K, SAITO H: Analysis of Motion of the Visual Field by Direction, Expansion/Contraction, and Rotation Cells Clustered in the Dorsal Part of the Medial Superior Temporal Area of the Macaque Monkey. *J Neurophysiol* 1989, 62:626–641.

26. DUFFY CJ, WURTZ RH: Sensitivity of MST Neurons to Optic Flow Stimuli. I. A Continuum of Responsive Selectivity to Large-Field Stimuli. *J Neurophysiol* 1991, 65:1329–1345.

27. ANDERSEN RA, BRACEWELL RM, BARASH S, GNADT JW, FOGASSI L: Eye Position Effects on Visual Memory, and Saccade-Related Activity in Areas LIP and 7a of Macaque. *J Neurosci* 1990, 10:1176–1196.

28. DUHAMEL J-R, COLBY CL, GOLDBERG ME: The Updating of the Representation of Visual Space in Parietal Cortex by Intended Eye Movements. *Science* 1992, 255:90–92.

29. FINKEL LH, EDELMAN GM: Integration of Distributed Cortical Systems by Reentry: a Computer Simulation of Interactive Functionally Segregated Visual Areas. *J Neurosci* 1989, 9:3188–3208.

30. TONONI G, SPORNS O, EDELMAN GM: Reentry and the Problem of Integrating Multiple Cortical Areas: Simulation of Dynamic Integration in the Visual System. *Cereb Cortex* 1992, 2:310–355.

31. ZEKI S: *A Vision of the Brain*. Oxford: Blackwell Scientific Publications; 1993.
• One man's view of the history of visual neuroscience. The focus is on color vision and achromatopsia.

32. NEWCOMBE F, RUSSELL WR: Dissociated Visual Perceptual and Spatial Deficits in Focal Lesions of the Right Hemisphere. *J Neurol Neurosurg Psychiatry* 1969, 32:73–81.

33. RATCLIFF G, DAVIES-JONES GAB: Defective Visual Localization in Focal Brain Wounds. *Brain* 1972, 95:49–60.

34. RATCLIFF G, NEWCOMBE F: Spatial Orientation in Man: Effects of Left, Right, and Bilateral Posterior Cerebral Lesions. *J Neurol Neurosurg Psychiatry* 1973, 36:448–454.

35. DAMASIO H, BENTON AR: Impairment of Hand Movements Under Visual Guidance. *Neurology* 1979, 29:170–174.

36. DAMASIO AR, DAMASIO H, VAN HOESEN GW: Prosopagnosia: Anatomic Basis and Behavioral Mechanisms. *Neurology* 1982, 32:331–341.

37. NEWCOMBE F, RATCLIFF G, DAMASIO H: Dissociable Visual and Spatial Impairments Following Right Posterior Cerebral Lesions: Clinical, Neuropsychological and Anatomical Evidence. *Neuropsychologia* 1987, 25:149–161.

38. DAMASIO AR, TRANEL D, DAMASIO H: Disorders of Visual Recognition. In *Handbook of Neuropschology*, vol 2. Edited by Boller F, Grafman J. Amsterdam: Elsevier; 1989:317–332.

39. FARAH MJ: *Visual Agnosia*. Cambridge, MA: MIT Press; 1990.

40. EGLIN M, ROBERTSON LC, KNIGHT RT: Visual Search Performance in the Neglect Syndrome. *J Cogn Neurosci* 1989, 1:372–385.

41. VAINA L, LEMAY M, BIENFANG DC, CHOI AY, NAKAYAMA K: Intact "Biological Motion" and "Structure from Motion" Perception in a Patient with Impaired Motion Mechanisms: a Case Study. *Vis Neurosci* 1990, 5:353–369.

42. ZIHL J, VON CRAMON D, MAI N, SCHMID C: Disturbance of Movement Vision After Bilateral Posterior Brain Damage. *Brain* 1991, 114:2235–2252.

43. NEWCOMBE F, RATCLIFF G: Disorders of Visuospatial Analysis. In *Handbook of Neuropsychology*, vol 2. Edited by Boller F, Grafman J. Amsterdam: Elsevier; 1989:333–356.

44. LEVINE DN, WARACH J, FARAH M: Two Visual Systems in Mental Imagery: Dissociation of "What" and "Where" in Imagery Disorders Due to Bilateral Posterior Cerebral Lesions. *Neurology* 1985, 35:1010–1018.

45. GOODALE MA, MILNER AD, JAKOBSON LS, CAREY DP: A Neurological Dissociation Between Perceiving Objects and Grasping Them. *Nature* 1991, 349:154–156.

46. GOODALE MA, MILNER AD: Separate Visual Pathways for Perception and Action. *Trends Neurosci* 1992, 15:20–25.

47. .GOODALE MA: Visual Pathways Supporting Perception and Action in the Primate Cerebral Cortex. *Curr Opin Neurobiol* 1993, 3:578–585.

48. MILNER AD, GOODALE MA: Visual Pathways to Perception and Action. In *The Visually Responsive Neuron: From Basic Neurophysiology to Behavior. Progress in Brain Research*, vol 95. Edited by Hicks TP, Molotchnikoff S, Ono T. Amsterdam: Elsevier; 1993:317–338.
• This chapter summarizes the anatomical, physiological, and behavioral evidence indicating the existence of separate 'dorsal' and 'ventral' processing streams. On the basis of this evidence, the authors propose that the ventral stream mediates the perception of objects, whereas the dorsal stream mediates actions directed toward those

objects. This formulation (see also [45–47]) is presented as an alternative to the 'what' versus 'where' model [3,4].

49. • VON CRAMON D, KERKHOFF G: **On the Cerebral Organization of Elementary Visuo-Spatial Perception.** In *Functional Organisation of the Human Visual Cortex.* Edited by Gulyás B, Ottoson D, Roland PE. Oxford: Pergamon Press; 1993:211–231.

The results of testing 67 patients with focal parietal lesions (confirmed with MRI) indicated that the patients had impaired perception of basic visuospatial functions, including horizontal and vertical axes, length and distance, orientation, and position. Impaired perception of axes and angles was more closely associated with anterior parietal damage, whereas impaired perception of position and distance was more closely associated with posterior parietal damage.

50. HAXBY JV, GRADY CL, HORWITZ B, UNGERLEIDER LG, MISHKIN M, CARSON RE, HERSCOVITCH P, SCHAPIRO MB, RAPOPORT SI: **Dissociation of Spatial and Object Visual Processing Pathways in Human Extrastriate Cortex.** *Proc Natl Acad Sci USA* 1991, 88:1621–1625.

51. • HAXBY JV, GRADY CL, HORWITZ B, SALERNO J, UNGERLEIDER LG, MISHKIN M, SCHAPIRO MB: **Dissociation of Object and Spatial Visual Processing Pathways in Human Extrastriate Cortex.** In *Functional Organisation of Human Visual Cortex.* Edited by Gulyás B, Ottoson D, Roland PE. Oxford: Pergamon Press; 1993:329–340.

This PET study demonstrates the existence of separate processing pathways for object vision and spatial vision in human cortex. Multiple, bilateral areas were identified in occipitotemporal and occipitoparietal cortex that were selectively activated, respectively, by face identity and spatial location tasks. Given that the stimuli for both tasks were identical, the results show that selective attention to face identity and spatial location is mediated, at least in part, by increased activity in extrastriate areas associated with the perception of those attributes.

52. •• CORBETTA M, MIEZIN FM, SHULMAN GL, PETERSEN SE: **A PET Study of Visuospatial Attention.** *J Neurosci* 1993, 13:1202–1226.

This study identified regions in human parietal and frontal cortex that were activated (as indicated by rCBF changes measured with PET) when subjects shifted attention to different locations within one visual hemifield. The finding that right parietal cortex has distinct foci for attention to the right and left hemifields, with no such distinction in left parietal cortex, may help explain differences between neglect syndromes associated with right and left parietal injury.

53. • JONIDES J, SMITH EE, KOEPPE RA, AWH E, MINOSHIMA S, MINTUN MA: **Spatial Working Memory in Humans as Revealed by PET.** *Nature* 1993, 363:623–625.

Right dorsolateral occipital, parietal, and frontal regions activated by a test of working memory for visuospatial locations were identified using PET by measuring rCBF changes. Correspondence between these results and those from studies of location perception [51•] and visuospatial attention [52••] suggests that the regions associated with visuospatial perception, attention, and working memory either lie in close proximity to each other or are, perhaps, co-extensive.

54. •• SERGENT J, OHTA S, MACDONALD B: **Functional Neuroanatomy of Face and Object Processing: a Positron Emission Tomography Study.** *Brain* 1992, 115:15–36.

Two tests of face perception, one (gender discrimination) requiring only structural processing and the other (profession identification) requiring the perception of unique individuality and face memory, activated different regions of ventral occipitotemporal cortex. The results suggest a hierarchical organization of processing in the ventral stream and demonstrate remarkable correspondence with other studies of face perception in human cortex [51•,76,77].

55. DAMASIO AR, TRANEL D, DAMASIO H: **Face Agnosia and the Neural Substrates of Memory.** *Annu Rev Neurosci* 1990, 13:89–109.

56. ZEKI SM: **Functional Organization of a Visual Area in the Posterior Bank of the Superior Temporal Sulcus of the Rhesus Monkey.** *J Physiol (Lond)* 1974, 236:549–573.

57. ALLMAN JM, KAAS JH: **A Representation of the Visual Field in the Caudal Third of the Middle Temporal Gyrus of the Owl Monkey.** *Brain Res* 1971, 31:85–105.

58. UNGERLEIDER LG, MISHKIN M: **The Striate Projection Zone in the Superior Temporal Sulcus of *Macaca mulatta*: Location and Topographic Organization.** *J Comp Neurol* 1979, 188:347–366.

59. GATTASS R, GROSS CG: **Visual Topography of Striate Projection Zone (MT) in Posterior Superior Temporal Sulcus of the Macaque.** *J Neurophysiol* 1981, 46:621–638.

60. VAN ESSEN DC, MAUNSELL JHR, BIXBY JL: **The Middle Temporal Visual Area in the Macaque: Myeloarchitecture, Connections, Functional Properties and Topographic Organization.** *J Comp Neurol* 1981, 199:293–326.

61. KRUBITZER LA, KAAS JH: **Cortical Connections of MT in Four Species of Primates: Areal, Modular, and Retinotopic Patterns.** *Vis Neurosci* 1990, 5:165–204.

62. CORBETTA M, MIEZIN FM, DOBMEYER S, SHULMAN GL, PETERSEN SE: **Selective and Divided Attention During Visual Discriminations of Shape, Color, and Speed: Functional Anatomy by Positron Emission Tomography.** *J Neurosci* 1991, 11:2383–2402.

63. ZEKI S, WATSON JPG, LUECK CJ, FRISTON K, KENNARD C, FRACKOWIAK RSJ: **A Direct Demonstration of Functional Specialization in Human Visual Cortex.** *J Neurosci* 1991, 11:641–649.

64. •• WATSON JD, MYERS R, FRACKOWIAK RSJ, HAJNAL JV, WOODS RP, MAZZIOTTA JC, SHIPP S, ZEKI S: **Area V5 of the Human Brain: Evidence from a Combined Study Using Positron Emission Tomography and Magnetic Resonance Imaging.** *Cereb Cortex* 1993, 3:79–94.

The location of a human cortical area activated by passive perception of motion was identified in 12 subjects by measuring rCBF changes with a high sensitivity PET scanner and mapping the activations to each individual's structural MRI scan. The results demonstrate individual variations in the stereotactic brain atlas coordinates for a functionally defined extrastriate area, and associate this area with an anatomical landmark, namely, the ascending limb of the inferior temporal sulcus. It is suggested that this area is the human homologue of area MT/V5 in the monkey.

65. CLARKE S, MIKLOSSY J: **Occipital Cortex in Man: Organization of Callosal Connections, Related Myelo- and Cytoarchitecture, and Putative Boundaries of Functional Visual Areas.** *J Comp Neurol* 1990, 298:188–214.

66. PERRETT DI, SMITH PAJ, MISTLIN AJ, CHITTY AJ, HEAD AS, POTTER DD, BROENNIMANN R, MILNER AD, JEEVES MA: **Visual Analysis of Body Motion by Neurons in the Temporal Cortex of the Macaque Monkey: a Preliminary Report.** *Behav Brain Res* 1985, 16:153–170.

67. DESIMONE R, UNGERLEIDER LG: **Multiple Visual Areas in the Caudal Superior Temporal Sulcus of the Macaque.** *J Comp Neurol* 1986, 248:164–189.

68. ZEKI SM: **Functional Specialization in the Visual Cortex of the Rhesus Monkey.** *Nature* 1978, 274:423–428.

69. • GALLANT J, BRAUN J, VAN ESSEN DC: **Selectivity for Polar, Hyperbolic, and Cartesian Gratings in Macaque Visual Cortex.** *Science* 1993, 259:100–103.

Recordings from neurons in area V4 of macaque monkeys indicated that 16% responded significantly more to polar or hyperbolic (non-Cartesian) gratings than to conventional sinusoidal (Cartesian) gratings. The authors suggest that such neurons may play an intermediate role in pattern recognition and the representation of object shape.

70. GATTASS R, SOUSA APB, GROSS CG: **Visuotopic Organization and Extent of V3 and V4 of the Macaque.** *J Neurosci* 1988, 8:1831–1845.

71. BAKER JF, PETERSEN SE, NEWSOME WT, ALLMAN JM: **Visual Response Properties of Neurons in Four Extrastriate Visual**

Areas of the Owl Monkey (*Aotus trivirgatus*): a Quantitative Comparison of Medial, Dorsomedial, Dorsolateral, and Middle Temporal Areas. *J Neurophysiol* 1981, 45:397–416.

72. WELLER RE, KAAS JH: Cortical Projections of the Dorsolateral Visual Area in Owl Monkeys: the Prestriate Relay to Inferior Temporal Cortex. *J Comp Neurol* 1985, 234:35–39.

73. GULYÁS B, ROLAND PE: Cortical Fields Participating in Form and Colour Discrimination in the Human Brain. *Neuroreport* 1991, 2:585–588.

74. LUECK CJ, ZEKI S, FRISTON KJ, DEIBER MP, COPE P, CUNNINGHAM VJ, LAMMERTSMA AA, KENNARD C, FRACKOWIAK RSJ: The Color Centre in the Cerebral Cortex of Man. *Nature* 1989, 340:386–389.

75. DAMASIO A, YAMADA T, DAMASIO H, CORBETT J, MCKEE J: Central Achromatopsia: Behavioral, Anatomical and Physiologic Aspects. *Neurology* 1980, 30:1064–1071.

76. ALLISON T, BEGLEITER A, MCCARTHY G, ROESSLER E, NOBRE AC, SPENCER DD: Electrophysiological Studies of Color Processing in Human Visual Cortex. *Electroencephalogr Clin Neurophysiol* 1993, 88:343–355.

77. ALLISON T, GINTER H, MCCARTHY G, NOBRE AC, PUCE A, LUBY M, SPENCER DD: Face Recognition in Human Extrastriate Cortex. *J Neurophysiol* 1994, 71:821–825.

78. RIZZO M, NAWROT M, BLAKE R, DAMASIO A: A Human Visual Disorder Resembling Area V4 Dysfunction in the Monkey. *Neurology* 1992, 42:1175–1180.

79. HEYWOOD CA, COWEY A: On the Role of Cortical Area V4 in the Discrimination of Hue and Pattern in Macaque Monkeys. *J Neurosci* 1987, 7:2601–2617.

80. SCHILLER PH, LEE K: The Role of Primate Extrastriate Area V4 in Vision. *Science* 1991, 251:1251–1253.

81. • HEYWOOD CA, GADOTTI A, COWEY A: Cortical Area V4 and Its Role in the Perception of Color. *J Neurosci* 1992, 12:4056–4065.

This behavioral study demonstrates the ability of monkeys with V4 lesions to perform well on the kinds of color discrimination tasks on which patients with achromatopsia typically fail.

82. • MERIGAN WH: Human V4? *Curr Biol* 1993, 3:226–229.

This paper argues, largely on differences in lesion effects, that the ventromedial area in human cortex associated with color vision in PET studies, and with achromatopsia in clinical cases, is not the homologue of monkey area V4.

83. WALSH V, BUTLER SR, CARDEN D, KULIKOWSKI JJ: The Effect of V4 Lesions on the Visual Abilities of Macaques: Shape Discrimination. *Behav Brain Res* 1992, 50:115–126.

84. POSNER MI, PETERSEN SE: The Attention System of the Human Brain. *Annu Rev Neurosci* 1989, 13:25–42.

85. BAIZER JS, UNGERLEIDER LG, DESIMONE R: Organization of Visual Inputs to the Inferior Temporal and Posterior Parietal Cortex in Macaques. *J Neurosci* 1991, 11:168–190.

86. • DISTLER C, BOUSSAOUD D, DESIMONE R, UNGERLEIDER LG: Cortical Connections of Inferior Temporal Area TEO in Macaques. *J Comp Neurol* 1993, 334:125–150.

In this anatomical study, the cortical connections of inferior temporal area TEO were examined in rhesus monkeys. The results indicate that TEO forms an important link in the occipitotemporal pathway for object vision.

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