abilities in adult owl monkeys performing a tactile frequency discrimination task *J. Neurophysiol*. 67, 1015–1030

10 Recanzone, G.H., Merzenich M.M. and Jenkins, W.M. (1992) Frequency discrimination training engaging a restricted skin surface results in an emergence of a cutaneous response zone in cortical area 3a *J. Neurophysiol*. 67, 1057–1070

11 Recanzone, G.H. *et al.* (1992) Topographic reorganization of the hand representation in cortical area 3b of owl monkeys trained in a frequency-discrimination task *J. Neurophysiol*. 67, 1031–1056

12 Recanzone, G.H., Merzenich, M.M. and Schreiner, C.E. (1992) Changes in the distributed temporal response properties of SI cortical neurons reflect improvements in performance on a temporally based tactile discrimination task *J. Neurophysiol*. 67, 1071–1091

13 Pascual-Leone, A. and Torres, F. (1993) Sensorimotor cortex representation of the reading finger of Braille readers: an example of activity-induced cerebral plasticity in humans *Brain* 116, 39–52

14 Rauschecker, J.P. *et al.* (1992) Crossmodal changes in the somatosensory vibrissa/barrel system of visually deprived animals *Proc. Natl. Acad. Sci. U. S. A*. 89, 5063–5067

15 Pascual-Leone, A. *et al.* (1993) Modulation of motor cortical outputs to the reading hand of Braille readers *Ann. Neurol.* 34, 33–37

16 Karni, A. *et al.* (1995) Functional MRI evidence for adult motor cortex plasticity during motor skill learning *Nature* 377, 155–158

17 Sadato, N. *et al.* (1996) Activation of primary visual cortex by Braille reading in blind subjects *Nature* 380, 526–528

18 Pascual-Leone, A. *et al.* (1995) The role of reading activity on the modulation of motor cortical outputs to the reading hand in Braille readers *Ann. Neurol*. 38, 910–915

19 Pascual-Leone, A., Grafman, J. and Hallett, M. (1994) Modulation of cortical motor output maps during development of implicit and explicit knowledge *Science* 263, 1287–1289

20 Pascual-Leone, A. *et al.* (1995) Modulation of human cortical motor outputs during the acquisition of new fine motor skills *J. Neurophysiol.* 74, 1037–1045

21 Pascual-Leone, A. *et al.* Neuroplasticity in adjustment to blindness, in *Neuroplasticity: Building a Bridge From the Laboratory to the Clinic*, Springer-Verlag (in press)

22 Walsh, V. and Cowey, A. (1998) Magnetic stimulation studies of visual cognition *Trends Cognit. Sci.* 2, 103–110

23 Cohen, L.G. *et al.* (1997) Functional relevance of cross-modal plasticity in blind humans *Nature* 389, 180–183

24 Phillips, J.R. *et al.* (1988) Spatial pattern representation and transformation in monkey somatosensory cortex *Proc. Natl. Acad. Sci. U. S. A.* 85, 1317–1321

25 Haenny, R.E., Maunsell, J.H. and Schiller, P.H. (1988) State dependent activity in the monkey visual cortex: II. Retinal and extraretinal factors in V4 *Exp. Brain Res.* 69, 245–259

26 Uhl, F. *et al.* (1991) On the functionality of the visually deprived occipital cortex in early blind persons *Neurosci. Lett.* 124, 256–259

27 Uhl, F. *et al.* (1993) Increased regional cerebral blood flow in inferior occipital cortex and the cerebellum of early blind humans *Neurosci. Lett.* 150, 162–164

28 Pascual-Leone, A. *et al.* (1994) Responses to rapid-rate transcranial magnetic stimulation of the human motor cortex *Brain*, 117, 847–858

29 Pascual-Leone, A. *et al.* (1997) Effects of repetitive transcranial magnetic stimulation on motor cortex activity during a rate controlled motor task as measured by functional magnetic resonance imaging *Neurology* 48, A106

30 Tergau, F. *et al.* (1997) Effects of repetitive transcranial magnetic stimulation on cortico-spinal and cortico-cortical excitability *Neurology* 48, A107

31 Chen, R. *et al.* (1997) Depression of motor cortex excitability by low-frequency transcranial magnetic stimulation *Neurology* 48, 1398–1403

32 Sacks, O. (1995) *An Anthropologist on Mars*, Random House

33 Cohen, L.G. *et al.* (1991) Attenuation in detection of somatosensory stimuli by transcranial magnetic stimulation *Electroencephalogr. Clin. Neurophysiol.* 81, 366–376

34 Pascual-Leone, A. *et al.* (1994) Differentiation of sensorimotor neuronal structures responsible for induction of motor evoked potentials, attenuation in detection of somatosensory stimuli, and induction of sensation of movement by mapping of optimal current directions *Electroencephalogr. Clin. Neurophysiol.* 93, 230–236

From retinotopy to recognition: fMRI in human visual cortex

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Recent advances in functional magnetic resonance imaging (fMRI) have furnished increasingly informative and accurate maps of the retinotopy and functional organization in human visual cortex. Here we review how information in those sensory-based maps is topographically related to, and influenced by, more cognitive visuo-spatial dimensions, such as mental imagery, spatial attention, repetition effects and size perception.

As cognitive science evolves, the initial psychological observations that established this field will increasingly be explained in terms of specific brain mechanisms. Such reductive explanations will undoubtedly take many forms, including those of electrophysiology, psychophysics and neuroimaging. Among these techniques, the neuroimaging of cognitive mechanisms in the human brain might be especially informative at present.

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At the scale of individual neurons, the primate brain is almost unmanageably large. The cerebral cortex alone contains an estimated 20 thousand million neurons[1] – far more than any electrophysiologist could possibly record from. In such a situation it is optimal to localize first where relevant activity occurs in the brain, before one begins more expensive and time-consuming experiments in specifically-chosen smaller brain regions of experimental animals, using microelectrodes or anatomical tracers – other classical neurobiological techniques. Neuroimaging results obtained from the human brain (in which cognition demonstrably occurs) can tell us exactly where to look for such activity. Of course, when one tries to make linking hypotheses between neuroimaging results in humans and invasive, microelectrode-based results from experimental animals, a fundamental question arises: which areas in humans correspond to which regions of the brain in a given species of experimental animal?

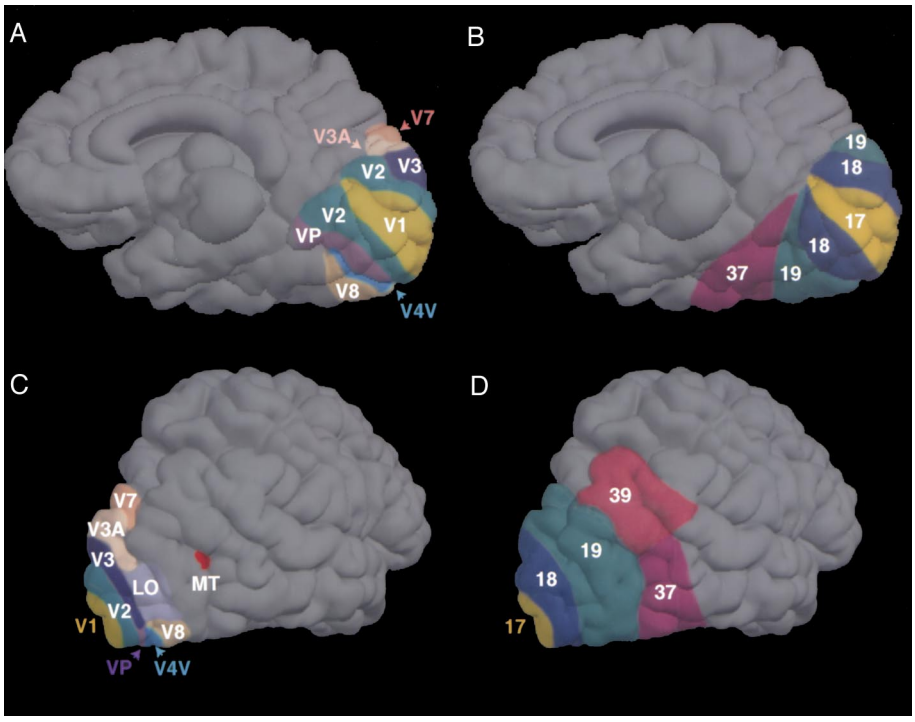

Fig. 1 Location of human visual cortical areas. (A) and **(C)** show the location of visual cortical areas, defined by fMRI and specific visual stimulation, in one representative subject (NH). The areas were defined by tests for motion and retinotopy, and painted onto the brain of the same subject, as reconstructed from anatomical MR images. (A) is a view of the medial bank, from a slightly inferior vantage point; the posterior brain axis is shown to the left, and anterior to the right. (C) is a view of the same brain, from a posterior-lateral vantage point. **(B)** and **(D)** show identical views of the same brain. The cortical 'areas' painted onto it have been extrapolated from the drawings of Brodmann[35]. Except in the location of area V1, there is very little correspondence between the Brodmann-based and the fMRI-based maps.

Comparisons are easiest between species that are evolutionarily close to each other, with similar brains, such as the macaque monkey and humans. However, even in the lower-level sensory areas, there are clear differences between brain areas in these two species. This is not surprising, since the human brain is about tenfold larger in size and quite different in shape from the macaque brain. In higher-order areas involved in cognitive function, evolutionary differences might be even more pronounced. Thus it is essential to test in humans any conclusions drawn from monkey studies, and vice versa. Human neuroimaging furnishes half of this comparison, at least at a global level. Some have argued that human fMRI experiments do not fully reveal cognitive mechanisms, instead stopping at a frustrating 'halfway' stage in which neural mechanisms are localized but not really understood. However, recent improvements in the temporal resolution of the neuroimaging signals[2,3] have begun to clarify the nature of brain activity, in addition to improvements in the localization of that activity. This makes it possible to ask a correspondingly wider range of experimental questions.

Current fMRI results also need to be evaluated in historical context. Functional MRI is a relatively new technique. Growth in the number of fMRI studies has been exponential since it was demonstrated six years ago[4,5], roughly doubling during the last two years[6]. One can expect, among the initial over-profusion of results, genuine insights into the working of the human brain, fueled by the many new researchers recruited from a wide range of disciplines, and by the constant pressure of ongoing technical improvements.

This review covers cognitive fMRI experiments from the visual cortex. This is an especially tractable part of the brain in which to study cognitive processes, for two main reasons. First, it is a sensory system, so that one can systematically manipulate the inputs in order to study cognitive outputs. Secondly, a great deal is known about the visual cortex in both humans and non-human primates. We first describe anatomical maps of human visual areas. Then we trace the flow and transformation of information between those areas, insofar as it is known. Finally, we compare these sensory maps with several examples of activity maps in higher-order cognitive processes. Such comparisons reveal aspects of the relationship between lower-level areas and higher-level processes – that is, what happens when retinotopy meets recognition. In this brief overview, many of these topics are illustrated with data available from our laboratory, although other laboratories are also producing important results.

Visual cortical areas

In daily life, one would normally begin exploring a new geographical region only after first consulting the most accurate available map of that region. Analogously, to make progress exploring human visual cortex, we first need to have an accurate map of the areas which exist there. Here we refer to cortical 'areas' in the rigorous sense, meaning regions of cortex with consistent topography across individuals, which differ from each other along sharp and genuine boundaries, in terms of their retinotopy, connections, histology, and/or global functional properties (e.g. Ref. 7).

Figures 1 and 2 show the areas known with most certainty in human visual cortex, revealed by fMRI tests in a single

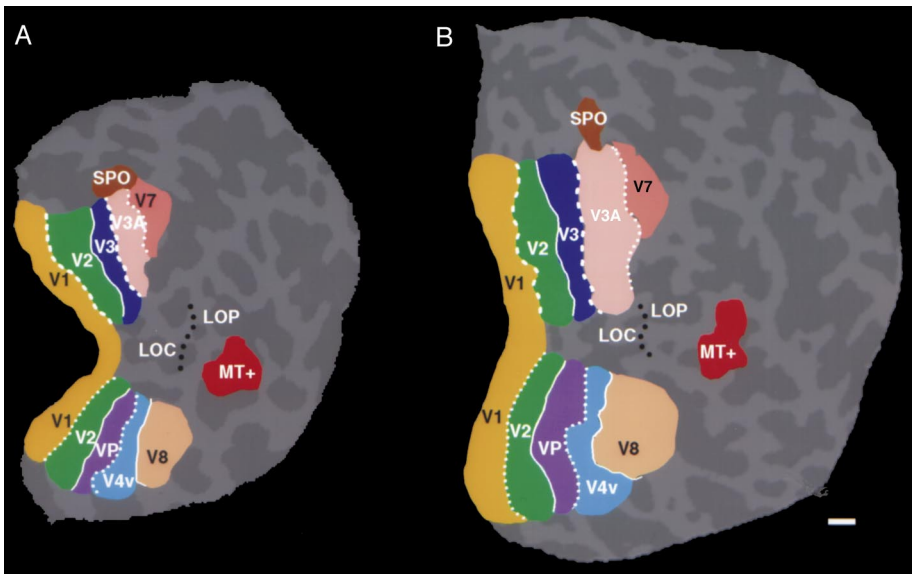

Fig. 2 Two-dimensional maps of the cortical visual areas in different subjects. Each map is based on visual tests and fMRI activity acquired from the same subjects. Areas V1, V2, V3, VP, V3A and V4v are classically retinotopic areas. Areas V7, V8 and LOC/LOP are 'fringe' retinotopic areas. We have adopted the term 'MT+', introduced by others[10], to include area MT and adjacent motion-selective satellite areas such as MST. The first map is taken from the hemisphere also shown in Fig. 1 (subject NH). The second map is taken from a different subject (BK). The orientation of the brain is as described in Refs 8,12,13. In different subjects, there are some overall differences in the size of the brain and visual areas, and in the exact area topography and area-sulcal/gyral relationships. However the areas revealed by the different area-labelling tests are remarkably similar across individual MR subjects.

subject, in a normal view of the brain (Fig. 1A,C) and in flattened cortical format (Fig. 2A). Figure 2B shows the topography of the same visual areas, revealed by the same fMRI tests, in a different subject. Although there is some variability in the exact topography between subjects, the general topography and the locations of each area relative to the others is consistent, across these and other individuals.

The organization of human visual areas is also similar to the organization in macque cortex in lower-tier areas, but some differences exist, especially in higher-order areas[8–13]. Such similarities and differences between human and macaque maps would be expected, based on comparisons of cortical maps in other mammalian species. Essentially all mammals tested show an area V1 and V2, but the maps in different species become progressively more divergent in rough accord with the evolutionary gap between them.

In general, higher-level cortical areas are more difficult to map. Even within a given species such as the rhesus macaque, technical and interpretive differences have led various investigators to draw slightly discrepant cortical maps in higher-level areas. So it is not surprising that other neuroimaging groups have drawn slightly different human maps, compared with those shown in Figs 1 and 2. Based on slice data from non-flattened cortex, without polar coordinate retinotopic mapping, McKeefry and Zeki discount the presence of V4v, and they use the name 'V4' for the region we describe as 'V8'. Orban and colleagues[14,15] describe an area ('KO') which is reported to respond preferentially to kinetic motion boundaries. Extrapolations from their data would place 'KO' near LOC in Fig. 2. Malach *et al.*[16] described a lateral occipital (LO) region (not necessarily an area), which shows higher activity in response to views of intact objects, compared with various control tests. In Fig. 2, LO would co-localize roughly with the fringe retinotopic areas (including LOC/LOP and V8). In our own maps, areas V7, V8 and LOC/LOP have been demonstrated only recently, using more sensitive retinotopic mapping and high-field scanning. Additional candidate areas (see below) have been proposed based on sensitivity to specific object classes such as faces and places.

What does each area do?

By combining data from the human maps with anatomical and single-unit data from macaques, we can construct a model of how visual and cognitive information interacts in its transition through human visual cortex. Most visual information arrives in the cortex via connections from the LGN to V1 (also known as primary visual cortex, striate cortex, or Brodmann's area 17). Those inputs are arranged to form a very specific reflection of retinal geometry; that is, the information is 'retinotopic' (e.g. Refs 17,18). Although the local neighborhood relations of the visual image are faithfully duplicated in the cortical map, the global cortical representation is transformed by the 'cortical magnification factor' (CMF), similar to that from Cartesian to polar coordinates. The center of the eye, where photoreceptors are most densely packed, is the center of this polar coordinate system. These geometric differences in the CMF are tightly linked to corresponding variations in receptive field size (and corresponding visual acuity, or spatial resolution) at different distances from the center of gaze (see Box 1).

Except for these systematic variations in retinotopy and sampling resolution, information arrives in primary visual cortex in relatively undifferentiated form. Nevertheless, a few specific properties present in single units from macaque V1 have also been revealed by neuroimaging in human V1. Such examples include selectivity for stimulus orientation[18], ocular dominance[18,19], color[20], spatial frequency (see Box 1), contours[12,13,21], and low contrast sensitivity[9,22]. The representation of the visual field in V1 is replicated (and often mirror-reflected or bisected), like xerox copies of the V1 map in each of the next retinotopic areas (V2, V3/VP, V3A and V4v). In V2, V3/VP and V4v, the visual field retinotopy is subdivided into quarter-field representations. Pathological damage to such areas undoubtedly underlies the quarter-field visual field losses ('quadranopsia' or 'quadrantanopia') reported in clinical studies, as suggested elsewhere[23]. In other areas such as V1 and V3A, the retinotopy is mapped into contiguous half-fields. Damage to these latter areas, and/or combinations of quarter-field areas, underlies the more common pathology of half-field loss ('hemianopsia' or 'hemianopia').

Receptive fields become larger in progressively higher-level visual areas in humans[13] and macaques[24]. However, the spatial frequency tuning does not decrease correspondingly

Box 1. Map of preferred spatial frequency in human visual cortex

Previous data from animal models suggests that the sensitivity to peak spatial frequency (roughly, stimulus size) varies systematically with retinotopic eccentricity, in rough parallel with the cortical magnification factor, in classically retinotopic areas of human visual cortex. To illustrate this, imagine the following example. If you are staring at someone's nose, the representation of that nose becomes enormously enlarged in your brain, because it is temporarily the center of this near-polar coordinate system. Correspondingly, you will be able to see very fine spatial details (e.g. pores, or small veins) when you stare at that nose. However, these details become invisible when you look away from it, because then you center the detail-resolving central visual machinery on another object, located elsewhere. This systematic variation in spatial-frequency selectivity with retinal eccentricity can be revealed by fMRI, using sinusoidal gratings as visual stimuli. Panel A (Fig.) shows a map of the peak responses to different spatial frequencies, from the flattened right hemisphere of one representative subject. In this experiment, the subject fixated the center of a sinusoidal grating, which was continually counterphase-reversing. The grating varied systematically in spatial frequency, in a phase-encoded paradigm. The pseudocolor map reveals where fMRI responses were maximal in response to spatial frequencies of about 3 cycles per degree (cpd) (red), 1.5 cpd (blue) and 0.75 cpd (green) (see key). The location of the classical retinotopic areas (V1, V2, V3/VP, V3A and V4v) were labeled in the same subject, in additional experiments using phase-encoded retinotopy and field sign analysis (see panel C). These visual area borders are drawn in white lines in panels A and B (solid white lines = from horizontal meridian; dotted white lines = from upper vertical meridian; dashed white lines = from lower vertical meridian; see key). The representation of the center of gaze (fovea) is represented by white asterisks. Panel B shows a phase-encoded map of retinotopic eccentricity. Visual field locations closest to the center of gaze are coded red, those slightly further away are coded blue, and those most peripheral are coded green (see key). The systematic organization of spatial frequency preference (panel A) is remarkably similar to that for retinotopic eccentricity (panel B).

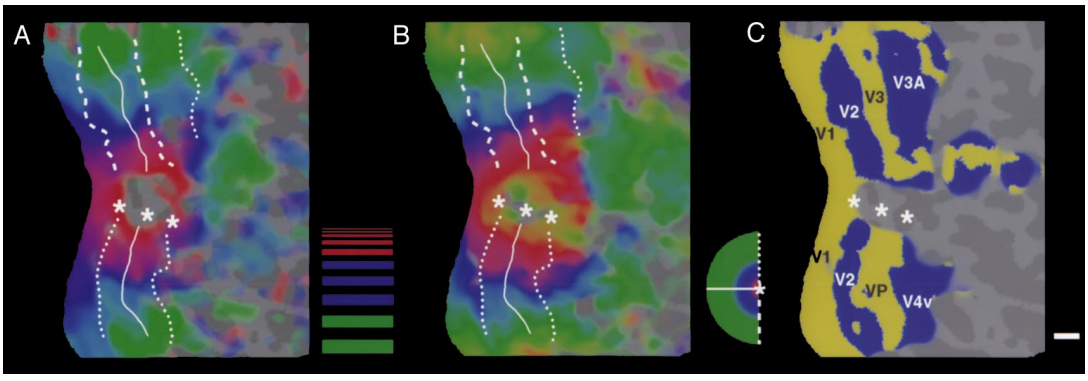

Fig. fMRI of peak responses to different visual spatial frequencies (see text for details).

(see Box 1). This suggests that the larger receptive fields in higher-order areas are constructed by converging input from more and more subunits, where each subunit has a size equivalent to those at lower levels, at equivalent eccentricity.

Several differences exist between human versus macaque maps in these retinotopic areas. In macaque, areas V3/VP are unusually thin, relative to the width of their neighboring counterparts V2, V4v and V3A (Ref. 7). However in humans, V3/VP are proportionately just as wide as in these neighboring retinotopic areas[13]. Another difference arises in nearby area V3A. In humans, V3A responds better to moving stimuli. However in macaque, it is instead area V3 that is predominantly motion-selective[13]. Such prominent map differences might well have functional implications, but direct comparisons have not yet been made to reveal them.

Anterior to the classically retinotopic areas there is a 'fringe' region of areas showing crude retinotopy (V7, LOC/LOP, and V8) (unpublished observations; see Figs 1 and 2). Anterior to these fringe areas, visual areas do not have demonstrable retinotopy. In the absence of retinotopic distinctions, visual areas must instead be distinguished based on global functional criteria. Specific areas have been reported that are globally sensitive to: visual motion[9,25–28], color[25,26] faces (see below), places[29], and kinetic motion boundaries[14].

In combination with macaque data[7], the nature of the global functional specificity in each human area can be used to subdivide human areas into tentative parietal and temporal information processing 'streams' in humans. Presumably, areas MT+, SPO, and perhaps V3A and V7, lie in a human parietal ('dorsal') stream involved in motion perception and space perception. LOC/LOP, V8, FFA and the 'PA' would be included in a temporal ('ventral') stream involved in color and form perception. However, several caveats should be added. First, it is technically quite difficult to trace connections in human cortex, so these functional 'streams' have not yet been confirmed by connectional evidence. Secondly, area borders are somewhat uncertain when they are drawn based on global fMRI tests, since adjacent areas may have a common response to a given functional test.

For instance in macaque, both MT and MST might respond to moving visual stimuli, though they are clearly different areas based on many other criteria. It is for this reason that many neuroimaging studies in humans have adopted the name 'MT+' (leaving room for the present imaging ambiguity) rather than the early version 'MT' or 'V5'. Such

a concern does not exist in retinotopically-defined areas, because the retinotopy itself reveals whether one is dealing with one or two maps of the visual field.

Beyond Brodmann

The fMRI boundaries described by different investigators agree quite well with each other, in a 'core' group of visual areas (V1, V2, V3/VP, V3A, V4v and MT+). These areas also correspond reasonably well with recent histological studies of human cortex[30,31]. However, the fMRI maps do not correspond well to the maps of extrastriate visual areas published almost a century ago by Konstantin Brodmann (see Fig. 1B,D). With hindsight this is not surprising. As anyone who has done such staining can attest, the histological differences on which Brodmann based his diagrams are extremely subtle. Except along the V1/V2 border (which is obvious even in unstained tissue), the cortical cytoarchitectonic differences are so subtle that the maps drawn by subsequent anatomists, based on similar staining experiments[32–34], show little relationship to the map drawn by Brodmann[35].

Similarly, when cortical areas were defined much later, with great accuracy and using modern techniques in macaque monkey[7], those maps also bore little resemblance to Brodmann's cytoarchitectonic map of cortical areas in the Old World monkey[35]. Thus in visual cortex, Brodmann's diagrams are increasingly disregarded in favor of the new maps based on neuroimaging and modern histology. Analogously, in future studies of non-visual cortex, we can expect that Brodmann's 'area' distinctions will be supplanted when better information is available about actual area boundaries, in each cortical region.

Visual imagery

After accurately mapping the visual cortical areas, it becomes possible to ask where different cognitive processes occur relative to those fMRI-based areas – and this is the question of real interest. One issue with clear topographic predictions is the location of activity during visual imagery. When we imagine a visual image, where does that mental activity take place? Because this process involves recalling an image from memory, it might produce activity only in higher-order ('association') areas, beyond retinotopic areas, or at least beyond primary visual cortex (V1). On the other hand, perhaps we can 'see' those mental images only when that representation is projected back into the lowest-level, most retinotopically-specific areas, such as V1.

This question has been asked a number of times using neuroimaging techniques. Some studies concluded that activity occurs only in higher-order areas beyond V1[36–38]. Other studies attributed activity to V1 itself[39,40]. However no study has yet compared the location of the obtained activity to the actual retinotopic maps of cortical visual areas, so such conclusions remain preliminary. Because current fMRI techniques reveal the retinotopy itself, it is now possible to ask whether the mental image is represented in retinotopic coordinates themselves, as well as asking in which visual areas (retinotopic or non-retinotopic) the mental activity occurs (see Box 2). This is important, because elegant psychophysical experiments[41–43] strongly suggest that mental imagery is represented in retinotopic coordinates.

Overall, the following model is suggested. Visual images are drawn from memory storage sites beyond primary visual cortex (perhaps ventral prefrontal cortex, and/or anterior inferotemporal cortex[44,45]). This information is projected back into the retinotopic visual areas via centrifugal connections. Such connections (from higher-order to lower-order) occur routinely at all levels of the visual hierarchy, and they are usually point-to-point[7] (i.e. preserving retinotopy). The recalled images are thus projected in a topographically coherent fashion onto the retinotopic mental 'screen' of those visual areas, during the conscious re-perception of those images. It is not completely clear which of the multiple retinotopic areas are necessary and/or sufficient to visualize mental images, but areas V2 and V3/VP are probably included (Box 2).

Visual spatial attention

It is well-accepted that spatial visual attention (informally, the 'spotlight of attention') can modulate the sensitivity to specific locations in the visual field (see Refs 46–49 for reviews). Using covert attention paradigms, neuroimaging studies have reported a modulation of activity in the hemisphere contralateral to the attended target[49,50]. However, several more detailed questions can now be addressed using the flattened cortical maps. For example, which visual areas show such modulation? Are such effects more prominent in higher-level areas than lower-level areas, as one would expect from single unit reports (e.g. Ref. 51)? Assuming these effects are retinotopic, does the spotlight of attention vary in cortical extent (1) with the cortical magnification factor?, (2) in different areas?, and (3) at the representation of different eccentricities, as does the size of the underlying cortical receptive fields? Several imaging laboratories are actively working on these issues, so it is hoped that they should be clarified soon.

Stimulus repetition

Another relevant paradigm is that of memory-related activation in visual cortex. Experiments in this field hinge on the logic that novel stimuli become 'familiar' only by reference to intact memories of their prior presentation. Therefore, by comparing activation in response to familiar versus novel visual stimuli, it should be possible to reveal which cortical areas are modulated by input from memory, and which visual areas are not. Such experiments are generally equivalent to tests of stimulus priming or repetition effects.

This issue has extensive roots in other experimental contexts. Single units recorded from macaque anterior inferotemporal cortex commonly show response attenuation as stimuli are repeatedly presented; as the stimuli become more 'familiar' to the individual neurons[52–55]. An apparently similar enhancement of responses to novel stimuli has been shown in human EEG studies[56], although the signal source is less clear in such studies. Why should these neural responses decrease with time? One idea is that orientation to novel stimuli has survival value. There are obvious dangers posed by predators approaching stealthily in the underbrush, or their modern equivalents. It is less critical to orient to stimuli that the person or animal has already seen, deemed safe, and incorporated into a working model of its immediate environs (i.e. familiar stimuli).

Box 2. Mapping of imagined stimuli in retinotopic coordinates

When we imagine visual stimuli, do those images activate lower-level visual areas in retinotopic coordinates, as would actual visual stimuli? We can test this hypothesis using fMRI and the flattened cortical maps (in an extension of a PET experiment by Kosslyn *et al.*[a]). Panel A (Fig.) shows the approximate stimuli imagined by one representative subject. In one set of alternating 32-second epochs, the subject imagined small letters (first A, then B, then C, then D, and so on through the alphabet; see top row of stimuli). In the alternating set of 32 second epochs, the subject imagined a large field of letters in the same alphabet sequence, but sparing a small central region (see bottom row of letters). These stimuli were chosen because the retinotopic prediction from such stimuli is very straightforward. If these letters were actual rather than imaginary stimuli, the small letters would produce activation in the foveal region in the maps of retinotopic eccentricity (see Fig. panels B,D). However, the large imaginary letters should produce activation over a much more extensive area, corresponding to the wider range of retinotopic eccentricities stimulated by actual large letters. Panel C shows the results of this task, in the right hemisphere. This task produced significant positive activation in phase with the imaging of small letters (shown by red-yellow), and significant positive activation in phase with the imaging of large letters (blue-cyan). The activation during imaging of small letters was more prominent. Panels B and D show control activation produced by actual (not imaginary) visual stimuli. The subject viewed a very small moving ring that was either present around the central fixation spot (top row) or absent (bottom row), in alternating epochs. This stimulus thus activated the cortical representation of the center of gaze (panel D), in V2, V3/VP, V4v, V8 and other visual areas. Activation was also produced in foveal V1 and V3A, although the threshold is set high in this particular example to indicate peak activity (see key).

The prominent patches of foveal activation (from panel D) have been outlined in green and transferred to panel C. In general, the retinotopy of imagined visual stimuli produced activation which was entirely consistent with the retinotopy of actual visual stimuli (panel C). In the classical retinotopic extrastriate areas (e.g. areas V3/VP, V4v, etc.), and in at least one fringe reginotopic area (V8), the prominent patch of activation in response to imagining small letters (yellow/red in panel C) coincides with the representation of the retinotopic center of gaze. The foveal representation in and around MT+ was not activated while imagining small letters, which is consistent with the fact that the letters were imagined while stationary, not moving. Although it was small, the activation produced while imagining larger letters was also consistent with the more peripheral extent of these images. The differences in the amplitudes of small-versus-large activation suggest that neural activity is concentrated much more when the subjects imagined small central letters, but 'diluted' over a much wider cortical region when the subjects imagined a wide field of many disparate letters. Such mental images are perceptually faint and ephemeral, compared to actual visual stimuli. However the (correspondingly fainter) activity in the fMRI was signal-averaged to yield statistically robust maps worthy of study. The data used in the figure represents the average of many images of alternating imagery (4096 images for small, 4096 images for large). Thus, the regions of peak activity in panel C would be produced by chance only one time in 10 million.

Reference

a Kosslyn, S.M. *et al.* (1993) Visual mental imagery activates topographically organized visula cortex: PET investigations *J. Cogn. Neurosci.* 5, 263–287

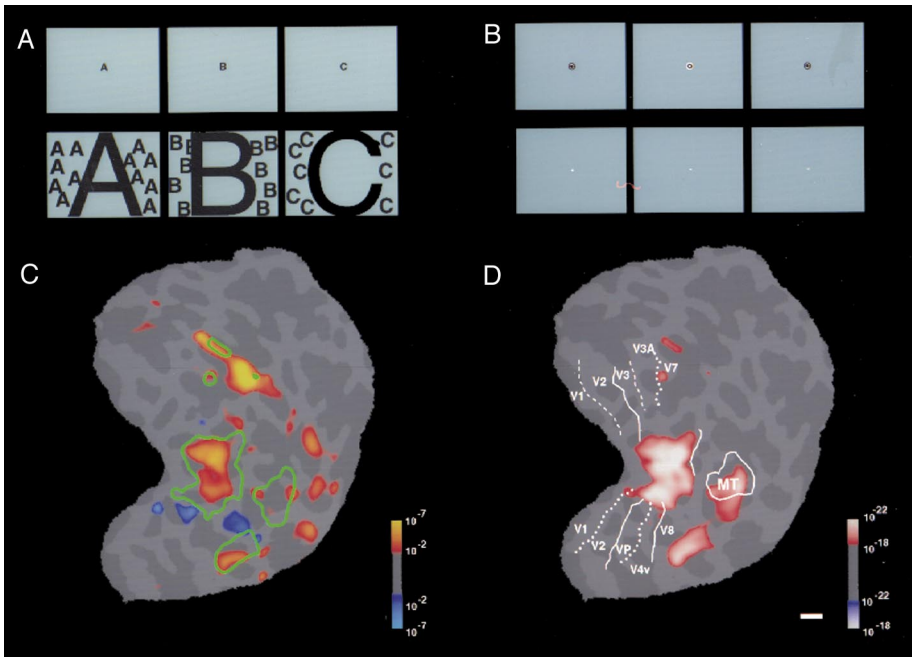

Fig. fMRI of imagined visual images (see text for explanation).

Thus, it is unsurprising that novel stimuli are perceived more readily[57,58] and are more difficult to ignore[59]. Presumably the higher firing rates of inferotemporal neurons in response to novel stimuli gives those stimuli a competitive advantage driving orienting mechanisms, as suggested elsewhere (e.g. Ref. 60). Thus the organism naturally orients to (looks at) novel stimuli, thereby aligning the most concentrated neural processing array (i.e. the fovea) on that novel stimulus (see Box 3).

Box 3. Activation produced by novel stimuli in two higher-order regions of human visual cortex

A wide range of data suggest that novel stimuli produce more neural activity than previously-seen stimuli, in certain brain areas. To study this, most neuroimaging studies of repetition effects have compared words or letter strings[a–c], focusing on memory-related activation in frontal cortex. However, visual images have also been used (Ref. f and data reported by A. Martin, *Soc. Neurosci. Abstr.* 1995, Vol. 21, p. 1497). The figure shows the comparison of novel versus familiar pictures, in four representative right hemispheres, in visual cortex. The subjects in these experiments were shown images of naturalistic scenes, in either of two alternating conditions: (1) novel images; or (2) images that the subject had already seen multiple times (familiar images). The stimuli were equated as far as possible for differences in lower-level visual cues (e.g. retinotopic extent), and for possible differences in attention coupled with the novel vs. familiar differences. Areas in which the novel stimuli produced more activation than the familiar stimuli are shown in red-through-white (see key). No areas showed more activation to the previously-seen stimuli, compared with the novel stimuli. In the early retinotopic areas such as V1, V2 and V3, the activity produced by these two stimuli was essentially equal: this suggests that the stimuli were successfully matched for lower-order visual cues, and that there was no additional modulation by input from memory in these areas. The lack of memory-related modulation in early visual areas is consistent with results from electrophysiology and connection experiments in macaques (for review, see Ref. g). Anterior to that, the novel stimuli produced more activity than the familiar stimuli. This novelty bias was not rigidly linked to particular cortical area boundaries. However, it was often localized in two general patches, apparently divided between temporal and parietal streams. One region was located in the inferior aspect of anterior occipital cortex, similar in location to the regions showing novelty-biased cells in macaque. In the human data, comparison to the retinotopic maps from the same subjects revealed that this novel-biased region usually includes area(s) V4v, V8, and areas anterior and inferior to those such as FFA, PA, etc. (see Figs 1,2 in main article).

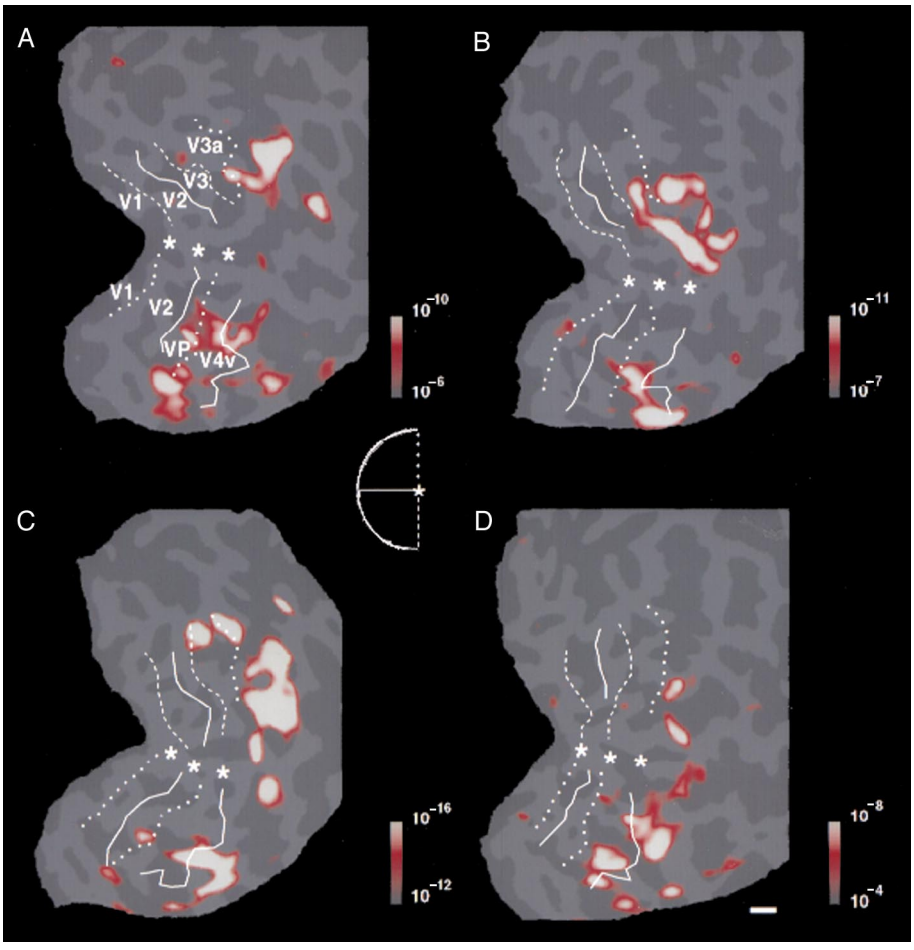

Fig. Maps of neural activity in the right hemispheres of four subjects (A–D) in response to novel visual images.

The second novel-biased region was located more laterally, including area LOP. LOP is a peripheral retinotopic representation, which also shows high activity in a range of other tests sensitive to comparisons across wide regions of the visual field (unpublished observations). In macaque, the topographically corresponding region is probably the peripheral and anterior extents of dorsal V4, and regions further anterior. Single units there have not been extensively sampled with regard to stimulus repetition. However, the human data suggests that such units should show decreases in response to repeated stimuli, similar to those in inferotemporal cortex.

References

a Squire, L.R. *et al.* (1992) Activation of the hippocampus in normal humans: A functional anatomical study of memory *Proc. Natl. Acad. Sci. U. S. A.* 89, 1837–1841

b Buckner, R.L. *et al.* (1995) Functional anatomical studies of explicit and implicit memory retrieval tasks *J. Neurosci.*15, 12–29

c Schacter, D.L. *et al.* (1996) Conscious recollection and the human hippocampal formation; evidence from positron emission tomography *Proc. Natl. Acad. Sci. U. S. A.* 93, 321–325

d Raichle, M.E. *et al.* (1994) Practice-related changes in human brain functional anatomy during nonmotor learning *Cereb. Cortex* 4, 8–26

e Demb, J.B. *et al.* (1995) Semantic encoding and retrieval in the left inferior prefrontal cortex: A functional MRI sudy of task difficulty and process specificity *J. Neurosci.* 15, 5870–5878

f Buckner, R.L. *et al.* Functional-anatomical correlates of object priming in humans revealed by rapid presentation event-related fMRI *Neuron* (in press)

g Desimone, R. and Duncan, J. (1995) Neural mechanisms of selective visual attention *Annu. Rev. Neurosci.* 18, 193–222

The fusiform face-selective area

Another active topic is the clarification of face-selective responses in or near the fusiform gyrus. Previous data from human intracranial electrophysiology[61,62], PET imaging[63,64], and single unit electrophysiology from non-human primates[65,66] suggested that a similar region of the temporal lobe is selectively responsive to faces. That data is supported by the well-known neurological syndrome of prosopagnosia, a selective difficulty identifying faces (for reviews, see Refs 67,68). Although the brain damage that produces prosopagnosia is

typically quite extensive, it normally includes the middle and anterior parts of the fusiform gyrus, where recent fMRI studies also suggest that face-selective activity occurs[69–71]. In both the imaging and the clinical data, the face-selectivity appears preferentially in the right hemisphere[71]. Lateralizations such as this do not appear in the more posterior, presumptively lower-level areas.

Reflecting the location of this area and its apparent functional properties, this face-selective area has been dubbed 'FF' or 'FFA', the fusiform face area[71], although it is not certain to be a single cortical area. Examples of such activation are shown from four subjects in Fig. 3. In the flattened map (Fig. 2), this region would be located just to the right of area V8. So far, this face-selective region appears non-retinotopic.

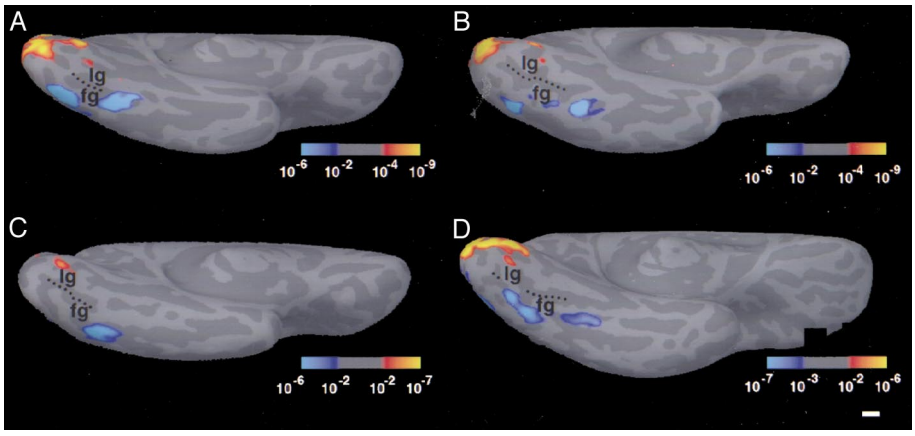

Fig. 3 Localization of the 'face area' and related regions. Inferior views from the right hemisphere of four representative subjects **(A–D)**. To reveal the activity within sulci, the brains are presented in cortically 'inflated' format. In the brains shown, the medial bank is uppermost, lateral is below, anterior is to the right and posterior to the left. Each subject was presented with images of faces, compared with scrambled images of those same faces, in alternating epochs. It is known from stimulation with various control stimuli that this paradigm produces activity in areas selective for intact presentation of objects in general (areas towards the left), as well as faces specifically (the rightmost area in each panel). The latter 'face' area (FFA) is typically located on or near the middle of the fusiform gyrus (fg). (lg, lingual gyrus; dotted lines represent the fundus of the collateral sulcus.) (The stimuli used in these experiments were generated by E. Halgren and colleagues.)

The FFA is now the focus of a classic nature-versus-nurture controversy. Since we are highly social primates who communicate extensively with our faces, sensitivity to different faces and their subtle expressions is important for survival. However, it is not clear whether the apparent face-selectivity in FFA represents an instinctive, innate hypersensitivity to faces, or if it is simply a region specialized for making any subtle object-based discrimination, which has been trained to discriminate faces (as well as other familiar and important visual stimuli) during many years of social learning. By exploiting the potential of fMRI to acquire unlimited numbers of stimulus comparisons in the same subjects, one recent study[71] clarified the range of stimulus selectivity in the FFA. Almost by definition, these investigators found that the 'face-selective' area responded more to faces, but varying levels of sub-maximal modulation were also produced by the different control stimuli.

Somewhat paradoxically, the responses to the control stimuli clarify the actual nature of the 'face' processing in FFA. For instance, significant MR responses were produced by cat faces in FFA, although the responses were smaller than those to human faces. This could be interpreted as an expression of evolutionary flexibility – presumably, the FFA responses in our long-distant ancestors were optimally tuned for quite different faces, more ape-like than human.

New evidence also suggests that one or more regions located medial to FFA respond to complementary visual stimuli. These regions might include selectivity for places[29], or objects related to spatial organization (e.g. houses, chairs; preliminary data reported by A. Ishai *et al.*, *Soc. Neurosci. Abstr.* 1997, Vol. 23, p. 2229). This apparent selectivity for additional object classes strongly supports the 'nature' side of the argument. On the 'nurture' side of the argument, one recent fMRI experiment trained subjects to make subtle discriminations not in faces but in more arbitrary objects ('greebles'), which resulted in 'face-like' patterns of activation in FFA after training[72,73]. Another striking piece of evidence on the nurture side arises from patients in which damage including the FFA reduced a pre-existing, trained familiarity to individual mountain peaks (in a climber) or individual cows (in a farmer)[74,75]. Such patients exhibited symptoms similar to prosopagnosia, except that the selective blindness affected a set of non-human objects, rather than human faces, owing to a specialized history in each of these patients.

Conclusion

The approaches described here, in which higher-order brain activity is related to the location of cortical areas, should help organize and interpret the increasing flood of neuroimaging data from human visual cortex. Similar approaches should be equally helpful in additional cortical regions including frontal cortex[76], where fMRI evidence also is beginning to reveal reliable areas. This should allow us to peer into the 'black box' of human cognition with greatly increased clarity.

References

1 Braitenberg, V. and Schuz, A. (1991) *Anatomy of the Cortex: Statistics and Geometry*, Springer-Verlag

2 Rosen, B.R., Buckner, R.L. and Dale, A.M. (1998) Event-related functional MRI: past, present and future *Proc. Natl. Acad. Sci. U. S. A.* 95, 773–780

3 Dale, A.M. and Buckner, R.L (1997) Selective averaging of rapidly presented individual trials using fMRI *Hum. Brain Mapp.* 5, 329–340

4 Kwong, K.K. *et al.* (1992) Dynamic magnetic resonance imaging of human brain activity during primary sensory stimulation *Proc. Natl. Acad. Sci. U. S. A.* 89, 5675–5679

5 Ogawa, S. *et al.* (1992) Intrinsic signal changes accompanying sensory stimulation: functional brain mapping with magnetic resonance imaging *Proc. Natl. Acad. Sci. U. S. A.* 89, 5951–5955

6 Fox, P.T. (1997) The growth of human brain mapping *Hum. Brain Mapp.* 5, 1–2

7 Felleman, D.J. and Van Essen, D.C. (1991) Distributed hierarchical processing in primate cerebral cortex *Cereb. Cortex* 1, 1–47

8 Sereno, M.I. *et al.* (1995) Borders of multiple visual areas in humans revealed by functional magnetic resonance imaging *Science* 268, 889–893

9 Tootell, R.B.H. *et al.* (1995) Functional analysis of human MT and related visual cortical areas using magnetic resonance imaging

J. Neurosci. 15, 3215–3230

10 DeYoe, E.A. *et al.* (1996) Mapping striate and extrastriate visual areas in human cerebral cortex *Proc. Natl. Acad. Sci. U. S. A.* 93, 2382–2386

11 Engel, S.A., Glover, G.H. and Wandell, B.A. (1997) Retinotopic organization in human visual cortex and the spatial precision of functional MRI *Cereb. Cortex* 7, 181–192

12 Tootell, R.B.H. *et al.* (1996) New images from human visual cortex *Trends Neurosci.* 19, 481–489

13 Tootell, R.B.H. *et al.* (1997) Functional analysis of V3A and related areas in human visual cortex *J. Neurosci.* 17, 7076–7078

14 Van Oostende, S. *et al.* (1997) The kinetic occipital (KO) region in man: an fMRI study *Cereb. Cortex* 7, 690–701

15 Dupont, P. *et al.* (1997) The kinetic occipital region in human visual cortex *Cereb. Cortex* 7, 283–292

16 Malach, R. *et al.* (1995) Object-related activity revealed by functional magnetic resonance imaging in human occipital cortex *Proc. Natl. Acad. Sci. U. S. A.* 92, 8135–8139

17 Tootell, R.B.H. *et al.* (1988) Functional anatomy of macaque striate cortex: II. Retinotopic position *J. Neurosci.* 8, 1531–1568

18 Tootell, R.B.H. *et al.* (1998) Functional analysis of primary visual cortex (V1) in humans *Proc. Natl. Acad. Sci. U. S. A.* 95, 811–817

19 Menon, R.S. *et al.* (1997) Ocular dominance in human V1 demonstrated by functional magnetic resonance imaging *J. Neurophysiol.* 77, 2780–2787

20 Engel, S., Zhang, X. and Wandell, B. (1997) Colour tuning in human visual cortex measured with functional magnetic resonance imaging *Nature* 388, 68–71

21 Reppas, J.B. *et al.* (1997) Motion boundaries are represented in retinotopic human visual cortical area *Nature* 388, 175–179

22 Boynton, G.M. *et al.* (1996) Linear systems analysis of functional magnetic resonance imaging in human V1 *J. Neurosci.* 16, 4207–4221

23 Horton, J.C. and Hoyt, W.F. (1991) Quadrantic visual field defects: a hallmark of lesions in extrastriate (V2/V3) cortex *Brain* 114, 1703–1718

24 Boussaoud, D., Desimone, R. and Ungerleider, L.G. (1991) Visual topography of area TEO in the macque *J. Comp. Neurol.* 306, 554–575

25 Lueck, C.J. *et al.* (1989) The colour centre in the cerebral cortex of man *Nature* 340, 386–389

26 Zeki, S. *et al.* (1991) A direct demonstration of functional specialization in human visual cortex *J. Neurosci.* 11, 641–649

27 McCarthy, G. *et al.* (1995) Brain activation associated with visual motion studied by functional magnetic resonance imaging in humans *Hum. Brain Mapp.* 2, 234–243

28 Beauchamp, M.S., Cox, R.W. and DeYoe, E.A. (1997) Graded effects of spatial and featural attention on human area MT and associated motion processing areas *J. Neurophysiol.* 78, 516–520

29 Epstein, R. and Kanwisher, N.K. The parahippocampal place area: a representation of the local visual environment *Nature* (in press)

30 Clarke, S. and Miklossy, J. (1990) Occipital cortex in man: organization of callosal connections, related myelo- and cyto-architecture, and putative boundaries of functional visual areas *J. Comp. Neurol.* 298, 188–214

31 Tootell, R.B.H. and Taylor, J.B. (1995) Anatomical evidence for MT and additional cortical visual areas in humans *Cereb. Cortex* 5, 39–55

32 Von Economo, C. and Koskinas, G.N. (1925) *Die Cytoarchitektonik der Hirnrinde des erwachsenen Menschen,* Springer-Verlag

33 Bailey, P. and Von Bonin, G. (1951) *The Isocortex of Man,* University of Illinois Press

34 Braak, H. (1980) *Architectonics of the Human Telencephalic Cortex,* Springer-Verlag

35 Brodmann, K. (1909) *Vergleichende Lokalisationslehre der Grosshirnrinde in ihren Prinzipien dargestellt auf Grund des Zellenbaues,* Barth, Leipzig

36 Roland, P.E. and Gulyas, B. (1994) Visual imagery and visual representation *Trends Neurosci.* 17, 281–287

37 Roland, P.E. and Gulyas, B. (1995) Visual memory, visual imagery and visual recognition of large field patterns by the human brain: functional anatomy by positron emission tomography *Cereb. Cortex* 5, 79–93

38 D'Esposito, M. *et al.* (1997) A functional MRI study of mental image generation *Neuropsychologia* 35, 725–730

39 Le Bihan, D. *et al.* (1993) Activation of human primary visual cortex during visual recall: a magnetic resonance imaging study *Proc. Natl. Acad. Sci. U. S. A.* 90, 11802–11805

40 Kosslyn, S.M. *et al.* (1995) Topographical representations of mental images in primary visual cortex *Nature* 378, 496–498

41 Farah, M.J. (1985) Psychophysical evidence for a shared representational medium for mental images and percepts *J. Exp. Psychol. Gen.* 114, 91–103

42 Farah, M.J. (1989) Mechanisms of imagery–perception interaction *J. Exp. Psychol. Hum. Percept. Perform.* 15, 203–211

43 Fink, R.A. and Kosslyn, S.M. (1980) Mental imagery acuity in the peripheral visual field *J. Exp. Psychol. Hum. Percept. Perform.* 6, 126–139

44 Wilson, F.A.W., Ó Scalaidhe, S.P. and Goldman-Rakic, P.S. (1993) Dissociation of object and spatial processing domains in primate prefrontal cortex *Science* 260, 1955–1958

45 Desimone, R. *et al.* (1994) Multiple memory systems in the visual cortex, in *The Cognitive and Neural Sciences* (Gazzaniga, M., ed.), pp. 343–364, MIT Press

46 Posner, M.I. and Petersen, S.E. (1990) The attention system of the human brain *Annu. Rev. Neurosci.* 13, 25–42

47 Colby, C.L. (1991) The neuroanatomy and neurophysiology of attention *J. Child Neurol.* 6, 90–118

48 Desimone, R. and Duncan, J. (1995) Neural mechanisms of selective visual attention *Annu. Rev. Neurosci.* 18, 193–222

49 Mangun, G.R. (1995) Neural mechanisms of visual selective attention *Psychophysiology* 32, 4–18

50 Heinze, H.J. *et al.* (1994) Combined spatial and temporal imaging of brain activity during visual selective attention in humans *Nature* 372, 543–546

51 Luck, S.J. *et al.* (1997) Neural mechanism of spatial selective attention in areas V1, V2, and V4 of macaque visual cortex *J. Neurophysiol.* 77, 24–42

52 Fahy, F.L., Riches, I.P. and Brown, M.W. (1993) Neuronal activity related to visual recognition memory: long-term memory and the encoding of recency and familiarity information in the primate anterior and medial inferior and rhinal cortex *Exp. Brain Res.* 96, 457–472

53 Li, L., Miller, E.K. and Desimone, R. (1993) The representation of stimulus familiarity in anterior inferior temporal cortex *J. Neurophysiol.* 69, 1918–1929

54 Miller, E.K., Li, L. and Desimone, R. (1991) A neural mechanism for working and recognition memory in inferior temporal cortex *Science* 254, 1377–1379

55 Riches, I.P., Wilson, F.A. and Brown, M.W. (1991) The effects of visual stimulation and memory on neurons of the hippocampal formation and the neighboring parahippocampal gyrus and inferior temporal cortex of the primate *J. Neurosci.* 11, 1763–1779

56 Begleiter, H., Porjesz, B. and Wang, W. (1993) A neurophysiologic correlate of visual short-term memory in humans *Electroencephalogr. Clin. Neurophysiol.* 87, 46–53

57 Moray, N. (1959) Attention in dichotic listening: affective cues and the influence of instructions *Q. J. Exp. Psychol.* 11, 56–60

58 Reicher, G.M., Snyder, C.R. and Richards, J.T. (1976) Familiarity of background characters in visual scanning *J. Exp. Psychol.* 2, 522–530

59 Shiffrin, R.M. and Schneider, W. (1977) Controlled and automatic human information processing: II. Perceptual learning, automatic attending, and a general theory *Psychol. Rev.* 84, 127–190

60 Desimone, R. and Duncan, J. (1995) Neural mechanisms of selective visual attention *Annu. Rev. Neurosci.* 18, 193–222

61 Ojemann, J.G., Ojemann, G.A. and Lettich, E. (1992) Neuronal activity related to faces and matching in human right nondominant temporal cortex *Brain* 115, 1–13

62 Allison, T. *et al.* (1994) Face recognition in human extrastriate cortex *J. Neurophysiol.* 71, 821–825

63 Haxby, J.V. *et al.* (1994) The functional organization of human extrastriate cortex: a PET–rCBF study of selective attention to faces and locations *J. Neurosci.* 14, 6336–6353

64 Clark, V.P. *et al.* (1996) Functional magnetic resonance imaging of human visual cortex during face matching: a comparison with positron emission tomography *NeuroImage* 4, 1–15

65 Desimone, R. (1991) Face–selective cells in the temporal cortex of monkeys *J. Cogn. Neurosci.* 3, 1–8

66 Perrett, D.I. *et al.* (1992) Organisation and functions of cells responsive

to faces in the temporal cortex *Philos. Trans. R. Soc. London Ser. B* 335, 23–30

67 Damasio, A.R., Tranel, D. and Damasio, H. (1990) Face agnosia and the neural substrates of memory *Annu. Rev. Neurosci.* 13, 89–109

68 De Renzi, E. (1997) Prosopagnosia, in *Behavioral Neurology and Neuropsychology* (Feinberg, T.E. and Farah, M.J., eds), pp. 245–255, McGraw-Hill

69 Puce, A. *et al.* (1995) Face-sensitive regions in human extrastriate cortex studied by functional MRI *J. Neurophysiol.* 74, 1192–1199

70 Puce, A. *et al.* (1996) Differential sensitivity of human visual cortex to faces, letterstrings, and textures: a functional magnetic resonance imaging study *J. Neurosci.* 16, 5205–5215

71 Kanwisher, N., McDermott, J. and Chun, M. (1997) The fusiform face area: a module in human extrastriate cortex specialized for face perception *J. Neurosci.* 11, 4302–4311

72 Gauthier, I. and Tarr, M.J. (1997) Becoming a 'Greeble' expert: exploring mechanisms for face recognition *Vis. Res.* 37, 1673–1682

73 Gauthier, I. *et al.* (1997) Levels of categorization in visual recognition studied using functional magnetic resonance imaging *Curr. Biol.* 7, 645–651

74 Assal, G., Favre, C. and Anderes, J.P. (1984) Nonrecognition of familiar animals by a farmer: zooagnosia or prosopagnosia for animals *Rev. Neurol. (Paris)* 140, 580–584

75 Clarke, S. *et al.* (1997) Face recognition and postero-inferior hemispheric lesions *Neuropsychologia* 35, 1555–1563

76 Buckner, R.L. and Koutstaal, W. (1998) Functional neuroimaging studies of encoding, priming, and explicit memory retrieval *Proc. Natl. Acad. Sci. U. S. A.* 95, 891–898

Connectionism and the problem of multiple instantiation

Jacques Sougné

Multiple instantiation is the ability to handle different instances of the same concept simultaneously. For example, from the following two facts: 'Pepin the Short was the son of Charles Martel' and 'Charlemagne was the son of Pepin the Short', one can infer that Charles Martel was the grandfather of Charlemagne. This inference requires two instantiations of 'Pepin the Short', the first in the role of son, the second in the role of father. For a connectionist model that does not use a working area receiving copies of items from a long-term knowledge base, the problem of multiple instantiation is a particularly thorny one. People are able to deal with multiple instances, unlike most connectionist models, but nonetheless their performance when doing so is reduced. On the other hand, there is no decrease in performance for symbolic models doing multiple instantiation. A good cognitive model should reflect both human competence and human limitations. This review proposes several connectionist solutions to the problem of multiple instantiation and examines their merits.

Multiple instantiation involves the simultaneous use of the same parts of the knowledge base in different ways. Knowing that: 'John is in love with Louise' and that 'Louise is in love with John', one can readily infer that they should be happy. To arrive at this conclusion, one must instantiate the predicate 'is in love with' and the objects 'John' and 'Louise' twice. Precisely how this is done is what certain authors[1,2] call the problem of multiple instantiation or 'the type-token problem[3,4]'. This problem is related to, but not equivalent to the binding problem (Box 1). Even if a connectionist model solves the binding problem, it does not mean that the problem of multiple instantiation is solved. However, solving the problem of multiple instantiation requires the binding problem to be solved.

Symbolic models that load copies of pieces of knowledge into a working area before transforming them have no problem with multiple instantiation. They simply make several copies of the same content from the long-term knowledge base (LTKB) and place them in the working area (Fig. 1A). However, for connectionist models that use the structure of the knowledge base itself as the place where concepts are associated and transformed, and where inferences are drawn, multiple instantiation poses a serious problem (Fig. 1B). How can the same part of the knowledge base be associated with different roles at the same time without making several copies of the knowledge in question? Multiple instantiation also poses significant problems for distributed representations as two closely related concepts will, in principle, share nodes. If both concepts are needed simultaneously, their common parts must be associated with two different entities.

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