lobe lesions, lesions to the brain stem and basal ganglia, dementia with cortical Lewy bodies and those of the visual impaired and normal elderly all tend to comprise fleeting, complex, natural, *dynamic* forms. Indeed, hallucinations in the visually impaired have been most closely studied in this regard[25]. It appears that the major constraint over extrastriate cortex is the relentless processing demands of sensory input (except in sleep)[26]. If this is disrupted, a 'rogue' processing system may be unleashed. The modularity of the system is thus held in a delicate balance. Upsetting the balance leads this mini-cognitive system to become autonomous and produce 'perception like' phenomena that cannot be overridden.

Conclusion

The work by Kourtzi and Kanwisher[10] plus Senior *et al.*[9] provides a robust demonstration that motion-sensitive cortex is involved in inferring motion. This should provoke a reappraisal of the extrastriate cortex in the perception–cognition continuum. It will undoubtedly shed light on both normal and abnormal perception.

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References

1 Freyd, J. (1983) The mental representation of movement when static stimuli are viewed. *Percept. Psychophys.* 33, 575–581
2 Freyd, J. and Finke, R. (1984) Representational momentum. *J. Exp. Psychol. Learn. Mem. Cognit.* 10, 126–132
3 Freyd, J. (1987) Dynamic mental representations. *Psychol. Rev.* 94, 427–438
4 Ranney, M. (1989) Internally represented forces may be cognitively penetrable: comment on Freyd, Pantzer, and Cheng. *J. Exp. Psychol. Gen.* 118, 399–402
5 Finke, R. and Freyd, J. (1989) Mental extrapolation and cognitive penetrability: reply to Ranney and proposals for evaluative criteria. *J. Exp. Psychol. Gen.* 118, 403–408
6 Reed, C. and Vinson, N. (1996) Conceptual effects on representational momentum. *J. Exp. Psychol. Hum. Percept. Perform.* 22, 839–850
7 Pylyshyn, Z. (1999) Is vision continuous with cognition? The case for cognitive impenetrability of visual perception. *Brain Behav. Sci.* 12, 341–423
8 Fodor, J.A. (1983) *The Modularity of Mind*, MIT Press
9 Senior, C. *et al.* (2000) The functional neuro-anatomy of implicit motion perception or 'representational momentum'. *Curr. Biol.* 10, 16–22
10 Kourtzi, Z. and Kanwisher, N. (2000) Activation in human MT/MST by static images with implied motion. *J. Cogn. Neurosci.* 12, 48–55
11 Watson, J.D.G. *et al.* (1993) Area V5 of the human brain: evidence from a combined study using positron emission tomography and magnetic resonance imaging. *Cereb. Cortex* 3, 79–94
12 McKeefry, D.J. *et al.* (1997) The activity in human areas V1/V2, V3, and V5 during the perception of coherent and incoherent motion. *NeuroImage* 5, 1–12
13 Howard, R. *et al.* (1996) A direct demonstration of functional specialisation within motion-related visual and auditory cortex of the human brain. *Curr. Biol.* 6, 1015–1019
14 Brammer, M. *et al.* (1997) Generic brain activation mapping in functional magnetic resonance imaging: a non-parametric approach. *Magn. Reson. Imaging* 15, 763–770
15 Goebel, R. *et al.* (1988) The constructive nature of vision: direct evidence from functional magnetic resonance imaging studies of apparent motion and motion imagery. *Eur. J. Neurosci.* 10, 1563–1573
16 Tootell, R.B.H. *et al.* (1995) Visual motion aftereffect in human cortical area MT revealed by functional magnetic resonance imaging. *Nature* 375, 139–141
17 Zeki, S. *et al.* (1993) Going beyond the information given: the relation of illusory visual motion to brain activity. *Proc. R. Soc. London Ser. B* 252, 215–222
18 Cohen, M. *et al.* (1996) Changes in cortical activity during mental rotation: a mapping study using functional MRI. *Brain* 119, 89–100
19 Alivisatos, B. and Petrides, M. (1997) Functional activation of the human brain during mental rotation. *Neuropsychologia* 35, 111–118
20 Tagaris, G.A. *et al.* (1996) Quantitative relations between parietal activation and performance in mental rotation. *NeuroReport* 7, 773–776
21 Barnes, J. *et al.* (2000) Cortical activity during rotational and linear transformation. *Neuropsychologia* 38, 1148–1156
22 Ffytche, D.H. *et al.* (1998) The anatomy of conscious vision: an fMRI study of visual hallucinations. *Nat. Neurosci.* 1, 738–742
23 Manford, M. and Andermann, F. (1998) Complex visual hallucinations. *Brain* 121, 1819–1840
24 Ffytche, D.H. and Howard, R.H. (1999) The perceptual consequences of visual loss: 'positive' pathologies of vision. *Brain* 122, 1247–1260
25 Teunisse, R.J. *et al.* (1996) Visual hallucinations in psychologically normal people: Charles Bonnet's syndrome. *Lancet* 347, 794–797
26 Schultz, G. and Melzack, R. (1991) The Charles Bonnet syndrome: 'phantom visual images'. *Perception* 20, 809–825

Implied motion activates extrastriate motion-processing areas

Response to David and Senior (2000)

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Our fMRI studies[1] showed significantly stronger activations in extrastriate cortical areas MT/MST for still images of human actors, animals and scenes that implied motion than still images that did not imply motion. David and Senior [David, A.S. and Senior, C. (2000) Implicit motion and the brain. *Trends Cognit. Sci.* 4, 293–295][2] suggest that our studies of implied motion suffered from four 'pitfalls', which we here rebut.

First, David and Senior charge cryptically that 'most authorities' locate human V5/MT+ in a location 'rather more posterior and anterior to the area shown by Kourtzi and Kanwisher'. Although it is not clear what the precise concern is here, we localized MT+ using standard techniques that have been used in many studies, and found activations that are consistent with other published loci (e.g. Refs 3–5) including those of Senior *et al.*[6] (compare their Figure 3C with our Figure 1).

Second, David and Senior express concern over the 'lack of precise data on localization' in our paper, apparently referring to the fact that we did not publish Talairach coordinates for our activations. We have happily supplied these coordinates to all researchers who have asked for them (see, for example, Ref. 7), but did not include them in our paper because they were not relevant to the hypothesis we tested. We tested the specific hypothesis that activation in MT+ will be modulated by still images that imply motion, rather than the more general question 'where does the perception of implied motion occur in the brain?'. The best way to test our hypothesis was to identify MT+ using a functional localizer for each subject (as reported in our studies); relying instead on Talairach coordinates would have provided a very poor basis for identifying MT+ because of the well-known anatomical variability across brains. The apparent precision afforded by

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Talairach coordinates is misleading because this coordinate system is based on the necessarily imperfect alignment of physically different brains, and because it specifies *points* in the brain whereas activations generally cover large and irregularly shaped *regions*.

Third, David and Senior comment that 'the lack of a statistical test of coincident activation between the "pure" visual motion versus the implied motion is unfortunate'. If they are referring to a test of the coincidence of motion selectivity and implied-motion selectivity, we accomplished this goal with our finding of a significantly higher response to static images with implied motion than static images without implied motion in areas that respond significantly to stimulus motion. If they are instead referring to a direct statistical comparison of the response to stimulus motion versus that to static images with implied motion, it is not clear what important theoretical question such a test would answer.

Fourth, David and Senior comment that 'the use of such a potent stimulus to induce activity in MT/MST may have maximized the chances of observing overlapping activations'. Maximizing the chance of detecting what you are looking for is generally considered desirable in experimental design provided you minimize confounds. Our test of the response to implied motion did not indiscriminately activate visual areas and David and Senior raise no clear objection to it. Moreover, the MT localizer used in our studies (low contrast moving versus stationary rings) activates MT more selectively than other, higher-contrast stimuli that might also activate regions beyond MT involved in motion processing[8].

Thus, we reject all of the putative pitfalls in our study that David and Senior raise. However, we are in turn concerned about several aspects of the Senior *et al.* study[6].

First, the reliance on a group analysis in the Senior *et al.* study results in substantial blurring of the functional images; this blurring can cause a spurious overlap in brain activations. We avoided this problem by using analyses of regions of interest defined individually for each subject.

Second, Senior *et al.* did not attempt to control for attentional confounds that might be expected to result from the fact that the images with implied motion are more interesting than the stills without implied motion. Indeed, the activations observed in the regions posterior to MT+ in the Senior *et al.* study might be better explained by such attentional confounds than in terms of the semantic processing of implied-motion images postulated by David and Senior[2]. Our study minimized these problems by including a task (repetition detection) that requires attention to all stimuli.

Third, David and Senior argue that the 400–600 ms reaction times found in their behavioral test of implied motion are 'rather fast to allow for much cognitive elaboration', and therefore activation of MT is more likely to reflect processes that occur within the visual system itself (rather than as a result of feedback from higher areas). However, research in cognitive psychology has provided ample evidence of high-level cognitive processes that are unlikely to be computed within the visual system but that can nonetheless be carried out in less than half a second (e.g. Refs 9,10). So the fast reaction times in the behavioral implied-motion task do not speak to the question of whether it is MT+ itself, or a 'higher' area, that extracts the information about implied motion. An answer to this question will require the use of a technique with higher temporal resolution than fMRI.

It is encouraging that despite the methodological differences in the two studies, largely similar results were obtained. These findings converge on the important conclusion that high-level perceptual inferences can substantially influence activity in extrastriate cortex.

References

1 Kourtzi, Z. and Kanwisher, N. (2000) Activation of human MT/MST by static images with implied motion. *J. Cogn. Neurosci.* 12, 48–55
2 David, A.S. and Senior, C. (2000) Implicit motion and the brain. *Trends Cognit. Sci.* 4, 293–295
3 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
4 Watson, J.D.G. *et al.* (1993) Area V5 of the human brain: evidence from a combined study using positron emission tomography and magnetic resonance imaging. *Cereb. Cortex* 3, 79–94
5 Zeki, S. *et al.* (1991) A direct discrimination of functional specialization in human visual cortex. *J. Neurosci.* 11, 641–649
6 Senior, C. *et al.* (2000) The functional neuroanatomy of implicit-motion perception or 'representational momentum'. *Curr. Biol.* 10, 16–22
7 Allison T. *et al.* (2000) Social perception from visual cues: role of the STS region. *Trends Cognit. Sci.* 4, 265–277
8 Tootell, R.B.H. *et al.* (1997) Functional analysis of V3A and related areas in human visual cortex. *J. Neurosci.* 15, 7060–7078
9 Kutas, M. and Hillyard, S.A. (1980) Reading senseless sentences: brain potentials reflect semantic incongruity. *Science* 207, 203–205
10 Rayner, K., ed. (1983) *Eye Movements in Reading : Perceptual and Language Processes*, Academic Press

Meetings

Essential ingredients of imaging

The *f*MRI Experience II , 11–12 May 2000, Weston Education Centre, Kings College Hospital, Denmark Hill, London, UK.

Functional magnetic resonance imaging (fMRI) is rapidly becoming the technique of choice for many investigators in the clinical and cognitive neurosciences. The growing demand for this technology spurred the initiative to organize a meeting that would bring together some of the foremost practitioners of fMRI to share their knowledge and experience to a wide audience of students and established researchers. The timing of this meeting at the outset of a new millennium was also an opportune moment to review the contribution of fMRI to our understanding of human brain function and to speculate on its potential capabilities in the future.

The 'fMRI Experience II' was the first forum to bring together experts in functional neuroimaging from four centres of excellence in the UK; the Institute of Psychiatry (IOP), King's College London; the Functional Imaging Laboratory (FIL) at the Wellcome Department of Cognitive Neurology, University College London; the Centre for Functional Imaging of the Brain (FMRIB) at the University of Oxford; and the Brain Imaging Unit at the University of Cambridge. The meeting evolved from two smaller workshops held at Oxford and the IOP last year. The first day consisted of teaching sessions in which experts described basic principles and state-of-the-art developments in fMRI. On the second day, graduate students gave oral presentations on a diverse range of topics from innovative neurocognitive studies to sophisticated advances in signal processing and data-analytic techniques. This was a valuable component of the meeting as it afforded a rare opportunity for PhD students to make oral presentations and to obtain helpful feedback on their research from an audience of peers and imaging specialists.

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