

also be regarded as primitive because of their presence in *Psarolepis*. If *Psarolepis* turns out to be a basal osteichthyan, the presence of an intracranial joint and cosmine can no longer serve as defining characters (synapomorphs) for sarcopterygians<sup>16–18</sup>. □

## Methods

**Phylogenetic analysis.** We added *Psarolepis* and three non-osteichthyan taxa (*Acanthodes*, an acanthodian, *Ctenacanthus*, a chondrichthyan, and *Dicksonosteus*, a placoderm) to the 33 taxa in ref. 14. We also added 9 characters to the 140 characters in ref. 14 to reflect the variations found in *Psarolepis* and the three non-osteichthyan outgroups (character 141, large dermal plates; 142, paired pectoral spines; 143, median fin spines; 144, denticulate postbranchial lamina of the cleithrum; 145, wide suborbital ledge; 146, eye stalk or unfinished area for similar structure; 147, ventral and otico-occipital fissures; 148, basiptyergoid articulation; 149, endochondral bone; 0 absent; 1 present). We adopted the same algorithm options as those used in refs 4, 14 (all characters unordered and unweighted) and used the three non-osteichthyan outgroups to root the trees. See Supplementary Information for the expanded matrix and for characters supporting major nodes in Fig. 4a, b. See ref. 14 for the original 140 characters and character states; see ref. 4 for the changed codings for characters 10, 17, 78 and 108.

Sarcopterygii, Dipnoi, Porolepiformes, Actinistia, Onychodontida and Tetrapodomorpha (including Rhizodontida, 'Osteolepiformes', Elpistostegalia and Tetrapoda) remain well supported in both trees. However, *Psarolepis* has changed the distribution and significance of many characters used previously to define osteichthyan groups (see Supplementary Information). In Fig. 4a, Sarcopterygii is defined by ten synapomorphies instead of fourteen as in ref. 14. Osteichthyes has no synapomorphy and is supported only by homoplasies. Actinopterygii is defined by one synapomorphy (character 6) and three reversals (characters 52, 93 and 110). In Fig. 4b, Sarcopterygii is defined by four synapomorphies, and 'Actinopterygii' appears as a paraphyletic group. One synapomorphy (character 7) defines the clade *Minimia* + (*Howqualepis* + *Moythomasia*) and five synapomorphies (characters 46, 63, 69, 98 and 134) define the clade *Polypterus* + (*Psarolepis* + Sarcopterygii). The position of *Polypterus* calls for further study, and the impact of data sampling and character coding on osteichthyan phylogeny deserves more attention.

Received 29 September 1998; accepted 7 January 1999.

1. Janvier, P. *Early Vertebrates* (Oxford Univ. Press, Oxford, 1996).
2. Rosen, D. E., Forey, P. L., Gardiner, B. G. & Patterson, C. Lungfishes, tetrapods, paleontology and plesiomorphy. *Bull. Am. Mus. Nat. Hist.* **167**, 159–276 (1981).
3. Yu, X. A new porolepiform-like fish, *Psarolepis romeri*, gen. et. sp. nov. (Sarcopterygii, Osteichthyes) from the Lower Devonian of Yunnan, China. *J. Vert. Paleontol.* **18**, 261–274 (1998).
4. Zhu, M. & Schultz, H.-P. The oldest sarcopterygian fish. *Lethaia* **30**, 293–304 (1997).
5. Tong-Duzay, T., Ta-Hoa, P., Boucot, A. J., Goujet, D. & Janvier, P. Vertébrés siluriens du Viet-nam central. *C.R. Acad. Sci. Abstr.* **32**, 1023–1030 (1997).
6. Gardiner, B. G. The relationships of the palaeoniscid fishes, a review based on new specimens of *Mimia* and *Moythomasia* from the Upper Devonian of Western Australia. *Bull. Brit. Mus. Nat. Hist.* **37**, 173–428 (1984).
7. Otto, M. Zur systematischen Stellung der Lophosteiden (Obersilur, Pisces inc. sedis). *Paläont. Z.* **65**, 345–350 (1993).
8. Schultze, H.-P. Ausgangform und Entwicklung der rhombischen Schuppen der Osteichthyes (Pisces). *Paläont. Z.* **51**, 152–168 (1977).
9. Janvier, P. On the oldest known teleostome fish *Andreolepis hedei* Gross (Ludlow of Gotland), and the systematic position of the lophosteids. *Eesti NSV Teaduste Akadeemia Toimetised Geol.* **27**, 86–95 (1978).
10. Chang, M. M. in *Early Vertebrates and Related Problems of Evolutionary Biology* (eds Chang, M. M., Liu, Y. H. & Zhang, G. R.) 355–378 (Science Press, Beijing, 1991).
11. Chang, M. M. & Zhu, M. A new Middle Devonian osteolepidid from Qujing, Yunnan. *Mem. Ass. Australas. Palaeontol.* **15**, 183–198 (1993).
12. Jessen, H. L. Lower Devonian Porolepiformes from the Canadian Arctic with special reference to *Powichthys tharsteinsoni* Jessen. *Palaeontogr. Abt. A* **167**, 180–214 (1980).
13. Ahlberg, P. E. A re-examination of sarcopterygian interrelationships, with special reference to the Porolepiformes. *Zool. J. Linn. Soc.* **103**, 241–287 (1991).
14. Cloutier, R. & Ahlberg, P. E. in *Interrelationships of Fishes* (eds Stiassny, M. L., Parenti, L. R. & Johnson, G. D.) 445–480 (Academic, New York, 1996).
15. Swofford, D. L. PAUP: phylogenetic analysis using parsimony, version 3.1.1 (1993).
16. Jarvik, E. Basic structure and evolution of vertebrates. Vol. 2 (Academic, London, 1981).
17. Andrews, S. M. in *Interrelationships of Fishes* (eds Miles, R. S. & Patterson, C.) 137–177 (Academic, London, 1973).
18. Bjerring, H. The 'intercranial joint' vs the 'ventral otic fissure'. *Act. Zool. Stockh.* **59**, 203–214 (1978).

**Supplementary information** is available on Nature's World Wide Web site (<http://www.nature.com>) or as paper copy from the London editorial office of Nature.

**Acknowledgements.** We thank H.-P. Schultze, M. M. Chang and P. E. Ahlberg for useful discussions; W. Harre for the photographs and P. E. Ahlberg, M. I. Coates and M. M. Smith for comments and suggestions. M.Z. acknowledges support from the Alexander von Humboldt Foundation and the Chinese academy of Sciences. X.Y. thanks IVPF for access to specimens and Kean University for support for research and faculty development.

Correspondence and requests for materials should be addressed to M.Z. (e-mail: zhumin@ht.rol.cn.net).

## Influence of motion signals on the perceived position of spatial pattern

Shin'ya Nishida\* & Alan Johnston†

\* Human and Information Science Research Laboratory, NTT Communication Science Laboratories, 3-1, Morinosato-Wakamiya, Atsugi-shi, Kanagawa 243-0198, Japan

† Department of Psychology and Institute of Cognitive Neuroscience, University College London, Gower Street, London WC1E 6BT, UK

After adaptation of the visual system to motion of a pattern in a particular direction, a static pattern appears to move in the opposite direction—the motion aftereffect (MAE)<sup>1,2</sup>. It is thought that the MAE is not accompanied by a shift in perceived spatial position of the pattern being viewed<sup>3,4</sup>, providing psychophysical evidence for a dissociation of the neural processing of motion and position that complements anatomical and physiological evidence of functional specialization in primate and human visual cortex<sup>5–7</sup>. However, here we measure the perceived orientation of a static windmill pattern after adaptation to rotary motion and find a gradual shift in orientation in the direction of the illusory rotation, though at a rate much lower than the apparent rotation speed. The orientation shift, which started to decline within a few seconds, could persist longer than the MAE, and disappeared when the MAE was nulled by physical motion of the windmill pattern. Our results indicate that the representation of the position of spatial pattern is dynamically updated by neurons involved in the analysis of motion.

In the first experiment (see Methods), we investigated whether the MAE is accompanied by corresponding changes in apparent spatial position, and, if so, in what way the position shift changes over time. The results (Fig. 1) showed that after adaptation to a rotating windmill, a test windmill appeared to have rotated in the direction of the MAE. Using vernier tasks, T. Takeuchi (personal communication) and Snowden<sup>8</sup> have found shifts in position after motion adaptation. However, we also found that the shift in perceived orientation, which presumably resulted from local changes in apparent position, gradually increased over the first few seconds. An incremental change began at the test onset rather than at the adaptation offset, a finding reminiscent of the storage effect of the MAE<sup>9</sup>. Over the first two seconds, the orientation shift increased almost linearly; thus, for this interval, we can directly compare the rate of orientation change with the MAE speed. The gain, that is, the slope of the functions in Fig. 1 (0.40 and 0.65 degrees s<sup>-1</sup> for subjects SN and AJ, respectively) divided by the MAE speed measured separately (5.05 and 8.00 degrees s<sup>-1</sup>, respectively), was ~8%. These results show that the shift in orientation is not simply an alternative measure of the MAE and are consistent with the classical view that the perception of motion and that of position change are dissociated<sup>3</sup>. We rejected the idea that the magnitude of the orientation shift might be proportional to MAE strength, because we found that MAE speed did not increase as a function of time over the same interval (data not shown).

The shift in orientation started to decline a few seconds after the test onset. We measured the shift for a stationary test at repeated intervals for up to 2 min, and compared the decay function with that of the MAE (Fig. 2a) (experiment 2; see Methods). For two subjects the orientation shift decayed more slowly and persisted for longer than the MAE. Significant amounts of orientation shift remained even after the MAE finished. However, for another naïve subject, the decay functions of the orientation shift and the MAE were quite similar.

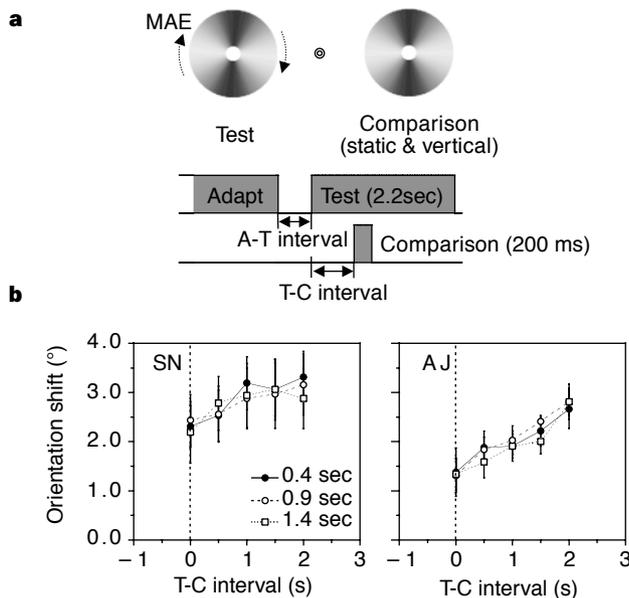
We attribute the orientation shift to an adjustment in the representation of the position of spatial pattern by motion information. Although the adjustment is driven by the motion system, it does not occur through direct linkage to the motion system, because the shift increases at first whereas the MAE always declines, and the shift can last longer than the MAE. We explain this dissociation by suggesting that the motion system induces incremental orientation shifts that are integrated over time within the system that represents spatial pattern, although motion signals can induce a position shift without temporal integration, as the test windmill appeared to be rotated even at test onset. The shift at test onset may be identified with direct effects of motion signals on spatial position. The small slope of the initial increase as well as the subsequent gradual decay can be attributed to the effects of pattern input, which acts to restore the veridical correspondence between the spatial representation and its spatial input. This interpretation implies that the representation of spatial pattern involves a dynamic system with a finite memory that integrates information over time, rather than being simply a reflection of the current spatial input at the eye.

This argument led us to expect that an established spatial representation may be reset in the face of a radical change of the spatial input (for example, presentation of a new stimulus). To test this we repeated experiment 2 (see Methods), this time reversing the phase of the test windmill in the intervals between orientation judgements. If the spatial representation is refreshed at phase

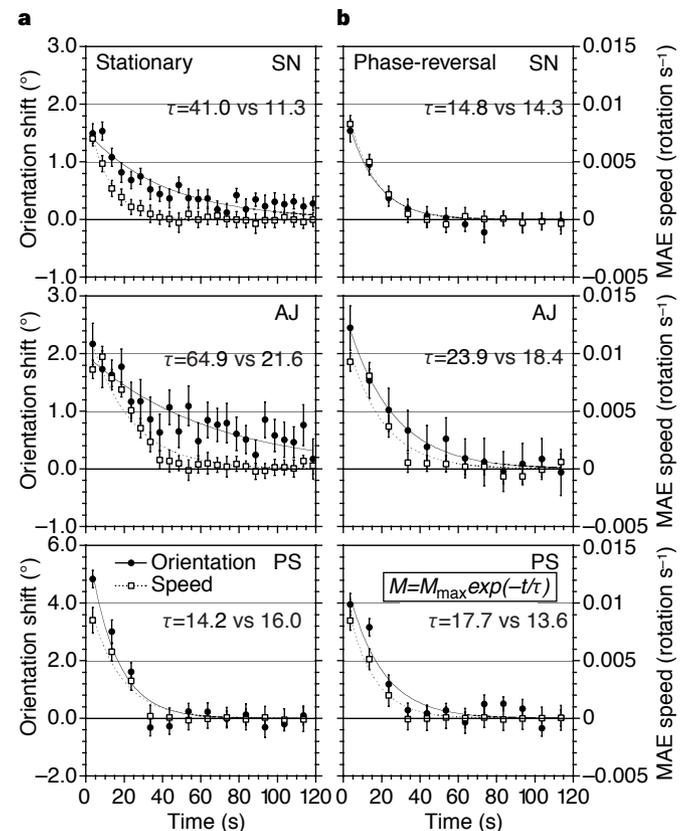
reversals, properties arising from temporal integration should be selectively disrupted whereas direct effects of motion signals on spatial position should remain unchanged. As expected, we found that the orientation shift now declined in step with the MAE for all subjects (Fig. 2b). The phase reversal had no effect for the naïve subject whose position shift decayed rapidly in the initial experiment, which suggests that this subject occasionally refreshed his representation without any change in the test stimulus, perhaps by eye movements or attentional control.

Several studies<sup>10–12</sup> have shown that moving stimuli appear to be spatially displaced in the direction of motion, but the underlying mechanism of this phenomenon remains controversial<sup>13–15</sup>. We measured relative mean orientation for briefly presented pairs of test stimuli that rotated in opposite directions at a range of velocities (experiment 3; see Methods) Perceived orientation was shifted in the direction of rotation by an amount that was roughly proportional to the velocity (Fig. 3). After adaptation, orientation judgements were biased in the direction opposite to that of the adapting stimulus, as before. However, when the test rotation speed was such that it nulled the MAE, the spatial shift disappeared. Thus a moving pattern does not appear to be spatially displaced if it appears static, which suggests a common source for mislocalization effects induced by physical motion and motion adaptation.

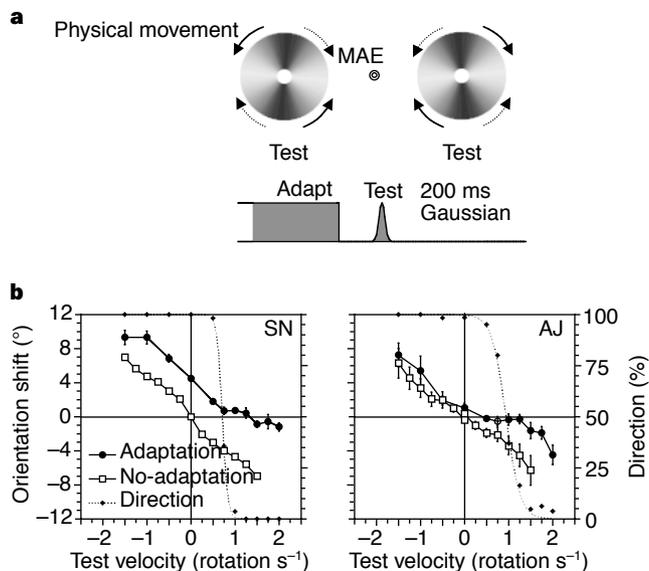
The fact that spatial shifts do occur for physically static but apparently moving test patterns seems to be incompatible with an



**Figure 1** Experiment 1. **a**, The experimental procedure. Top, after adaptation of the visual system to a rotating windmill (not shown), a static test windmill (left) and a comparison windmill (right) on the opposite side of fixation (centre) were presented. The test windmill appeared to have rotated in the direction of the MAE, and the magnitude of the shift gradually increased over time. Bottom, the A-T interval (time between adaptation offset and test onset, and the T-C interval (time between test onset and onset of the comparison stimulus). **b**, Results for subjects SN and AJ. The ordinate shows the amount of rotation in the direction opposite to the MAE required to make the test stimulus appear parallel to the comparison stimulus. The abscissa shows the T-C interval. The symbols indicate variation in the A-T interval. Each point is based on eight measurements (error bar:  $\pm 1$  s.e.m.). Similar results were obtained with another naïve subject (PS).



**Figure 2** Experiment 2. Comparison of the decay function of the orientation shift to that of the MAE when the same test stimulus was continuously presented and when the phase of the test was reversed during interjudgement intervals. **a**, Continuous presentation of test symbols; **b**, reversal of the test phase during interjudgement intervals. The results show that the orientation shift (circles) could persist longer than the MAE (squares) in the former condition (**a**), but not in the latter (**b**). Each point is based on at least eight measurements (error bar:  $\pm 1$  s.e.m.). The smooth curve is the best fitting exponential function,  $M = M_{\max} \exp(-t/\tau)$ . The time constant ( $\tau$ ) of each function is shown; the first number refers to the orientation shift and the second to the MAE.



**Figure 3** Experiment 3. **a**, The experimental procedure. After adaptation to windmills presented on both sides of fixation, two test windmills, rotating at a given speed, were presented within a 200-ms gaussian window. **b**, the orientation shift of the physically rotating windmill as a function of the rotation speed before (squares) and after (circles) motion adaptation is plotted alongside a psychometric function showing judgements of direction measured after adaptation (diamonds). Without adaptation, the average test orientation appeared to be shifted in the direction of real movement (downwards for positive test speeds). After adaptation, perceived orientation was shifted in the aftereffect direction (upward), and the absolute orientation shift almost disappeared when the MAE was nulled by real motion (that is, the test appeared stationary). Each point is based on at least eight measurements. Similar results were obtained with subject PS.

explanation of the mislocalization effect in terms of a possible difference in peripheral-processing time delay between moving and static stimuli<sup>13,14</sup>. Another explanation for mislocalization, that motion sensors may systematically misreport their position towards the sensor's preferred direction<sup>15</sup>, incorrectly predicts that the magnitude of mislocalization should always vary with the activation of the motion sensors (MAE magnitude), whereas we found several examples of dissociation of the magnitude of mislocalization and the MAE magnitude. Finally, motion and position may interact at various levels in the visual system<sup>16,17</sup>. Given that the most precise representation of local spatial information exists in early cortical areas, an intriguing possibility is that our findings may reflect recurrent input from cortical areas V5/MT to V1 (ref. 18) or V2 (ref. 19). □

**Methods**

Stimuli were presented on a Manitrn monitor (P31 phosphor, 60 Hz refresh) under control of an IBM compatible PC with a VSG2/3 board. Viewing was binocular from 93 cm. Windmills subtended 4° in diameter with a 40-min hole at the centre and were presented 4° left or right of a fixation bullseye. Each windmill had a sinusoidal luminance modulation of 2 cycles per rotation at 80% contrast on a 6.5 cd m<sup>-2</sup> background.

**Experiment 1.** After a 3-min adaptation to a windmill moving at 3 rotations s<sup>-1</sup> (6 Hz), a static test windmill was presented for 2.2 s at the same location, and a comparison windmill was presented for 0.2 s on the opposite side of the fixation, both with sharp onset and offset. Subsequent test presentations were always preceded by an 8-s re-adaptation period. Subjects judged whether the dark region of the test windmill was rotated in the clockwise or anti-clockwise direction relative to a comparison windmill in which the dark region was always vertical. The use of a relative judgement allowed us to discount any influence of eye movements. The shift was estimated using a standard staircase program that adjusted the test orientation until at least four reversals of direction had

occurred. The time of onset of the comparison stimulus (T-C interval) and the time between offset of the adaptation and onset of the test (A-T interval) was varied between trials. To equate the state of adaptation, the staircase sequences, for each stimulus condition, were intermingled within a single block, with each staircase waiting at the *n*th reversal point until all the other staircases reached that point. The adaptation direction and position were changed between blocks.

**Experiment 2.** In the first experiment 2, the temporal decay of the magnitude of the position shift was measured by the method of adjustment. The test stimulus was presented for 2 min after 1 min of adaptation to a rotating windmill and a 1-s blank interval. During the test presentation, a comparison windmill was presented on the opposite side of fixation for 4 s every 10 s. The subject had to adjust the orientation of the comparison to match it with the test. The perceived orientation was estimated from the settings during the last 1 s of every 4-s matching period. The test orientation as well as the initial comparison orientation for each matching period were randomly jittered within ±2.5° of the vertical. There was at least a 1-min interval between blocks. The direction and position of the adaptation stimulus were changed between blocks. To halve the sampling interval, the first matching period started at the onset of the test in half of the blocks, and 5 s later in the other half. When repeating experiment 2, we used the same procedure as before, except that, although the test stimulus was always vertical (with a small jitter) during the matching period, its orientation switched to the horizontal 0.5 s after a match was recorded, and then returned to the vertical 0.5 s before the next matching period. The first matching period always started at test onset.

**Experiment 3.** After adaptation to windmills presented on both sides of fixation, two test windmills, rotating at a given speed, were presented within a 200-ms gaussian temporal window (s.d. = 35.4 ms, peaking at 1.5 s after the adaptation offset). The two windmills were always mirror-image symmetric with respect to a virtual central vertical line. Subjects compared the average orientation of the two test stimuli. We used a staircase method to estimate the perceptually parallel angle, adjusting orientation according to the subject's response. To find the motion null point, we also asked the subject to judge the direction of perceived motion. If, on occasion, the test stimulus appeared to move first in the MAE direction and then in the other direction, subjects were instructed to choose the dominant direction. In each block, staircases for each test velocity were intermingled. A similar procedure was used for the no-adaptation condition, except that a uniform field was presented for 3 s between trials and the judgement of rotation direction was not required.

Received 9 September; accepted 12 December 1998.

1. Wohlgenuth, A. On the aftereffect of seen movement. *Br. J. Psychol. Monogr. Suppl.* **1**, 1–117 (1911).
2. Mather, G., Verstraten, F. A. J. & Anstis, S. M. *The Motion Aftereffect: A Modern Perspective* (MIT Press, Cambridge, Massachusetts, 1998).
3. Gregory, R. L. *Eye and Brain* (McGraw-Hill, New York, 1966).
4. Nakayama, K. Biological image motion processing: a review. *Vision Res.* **25**, 625–660 (1985).
5. Zeki, S. M. Functional organization of a visual area in the posterior bank of the superior temporal sulcus of the rhesus monkey. *J. Physiol. (Lond.)* **236**, 549–573 (1974).
6. Zihl, J., VonCramon, D. & Mai, N. Selective disturbance of movement vision after bilateral brain damage. *Brain* **106**, 313–340 (1983).
7. Livingstone, M. S. & Hubel, D. H. Psychophysical evidence for separate channels for the perception of form, color, movement, and depth. *J. Neurosci.* **7**, 3416–3466 (1987).
8. Snowden, R. J. Perceived spatial position is altered by motion adaptation. *Perception* **27** (Suppl.), 49–50 (1998).
9. Spigel, I. M. The effects of differential post exposure illumination on the decay of a movement aftereffect. *J. Psychol.* **50**, 209–210 (1960).
10. Ramachandran, V. S. & Anstis, S. M. Illusory displacement of equiluminous kinetic edges. *Perception* **19**, 611–616 (1990).
11. De Valois, R. L. & De Valois, K. K. Vernier acuity with stationary moving Gabors. *Vision Res.* **31**, 1619–1626 (1991).
12. Nijhawan, R. Motion extrapolation in catching. *Nature* **370**, 256–267 (1994).
13. Baldo, M. V. C. & Klein, S. A. Extrapolation or attentional shift. *Nature* **378**, 565–566 (1995).
14. Khurana, B. & Nijhawan, R. Extrapolation or attentional shift: reply. *Nature* **378**, 566 (1995).
15. Anstis, S. M. & Remachandran, V. S. in *The Artful Eye* (eds Gregory, R., Harris, J., Heard, P. & Rose, D.) 232–248 (Oxford Univ. Press, Oxford, 1995).
16. Merigan, W. H. & Maunsell, J. H. R. How parallel are the primate visual pathways? *Annu. Rev. Neurosci.* **16**, 369–402 (1993).
17. Zeki, S. *A Vision of the Brain* (Blackwell, Oxford, 1993).
18. Shipp, S. & Zeki, S. The organisation of connections between areas V1 and V5 in the macaque monkey visual cortex. *Eur. J. Neurosci.* **1**, 309–332 (1989).
19. Shipp, S. & Zeki, S. The organisation of connections between areas V2 and V5 in the macaque monkey visual cortex. *Eur. J. Neurosci.* **1**, 333–354 (1989).

**Acknowledgements.** S.N. was a visiting fellow at the Institute of Cognitive Neuroscience, UCL. We thank S. Naito and K. Ishii, NTT Communication Science Laboratories for their support. A.J. is supported by a grant from the EPSRC/BBSRC Mathematical Modelling Initiative.

Correspondence and requests for materials should be addressed to A.J. (e-mail: a.johnston@ucl.ac.uk).