20 lily bulbs in a field near Breezand in the Netherlands. These mites founded the lab-reared base strain. For selection experiments, starting in January 1995, 132 female deutonymphs (near moulting) were placed individually in vials with five female prey **T**. After one day, matured predators were starved for three days with access to water (no mortality). After putting one female predator, one female and one protonymph of each prey species in each vial, they were observed twice per minute until an attack on prey **R** or **T**. This procedure (feeding for 1 day, starvation for 3 days; choice test) was repeated three times per individual. Predator females that selected three times prey **R** or **T** were mated with their own sons to create isofemale lines, which were fed on **T**. This selection procedure was repeated for four generations, yielding one line preferring **R** (the *R*-line) and one preferring **T** (the *T*-line). As above, *R*-line (148) and *T*-line (140) females were subjected to three prey-choice tests. For each line, ten females were cross-bred with males of the other line. Hybrid females with *R*-line mothers (77) and those with *T*-line mothers (67) were subjected to three prey-choice tests, as above. Ten F_1 hybrid females were then backcrossed with males from each parental line. From offspring of each of the four types of $F_1 \times$ parent backcrosses, ~50 young females were subjected individually to three prey-choice tests. Frequency distributions of prey choices are shown in Fig. 1 (base strain, *R*-line, *T*-line, F_1-hybrids) and Fig. 2 ($F_1 \times$ parent backcrosses). Figure 1 also shows prey-choice frequencies assessed in progeny of females collected in September 1998 (from near the location sampled in 1991).

Estimates of *p*, the probability of choosing prey **R**, were obtained from observed choice distributions of the parental lines according to $p = (3p_{3R} + 2p_{2R} + p_{1R})/3$. Assuming monogenic inheritance without dominance, $p_{R\text{-line}}$ and $p_{T\text{-line}}$ were averaged to predict $p_{RT} = p_{TR}$. The estimates of $p_{R\text{-line}}$, $p_{T\text{-line}}$ and $p_{RT} = p_{TR}$ were used to predict frequency distributions of choices for the four $F_1 \times$ parent backcrosses (for a haplodiploid, a 1:1 ratio of homozygote and heterozygote daughters is expected). Observed frequency distributions of prey choices were tested for goodness of fit to predicted binomial distributions, using a *G*-test with Williams's correction[28] (d.f. $= 4 - 1 - 1 = 2$, when *p* is estimated from the observed distribution under test; d.f. $= 4 - 1 = 3$, when *p* is estimated from an independent distribution) (Table 1).

Population growth on excess food

Predator population size (*N*) was recorded three times each week for 4 weeks under ample prey supply (predator:prey ratio maintained at 1:100) (22 °C, 70% relative humidity). Predators were supplied with either prey **R** alone, **T** alone, or a 1:1 mixture of **R** and **T**, in vials (7 cm diameter, 7 cm high; lid with pinholes covered by mite-proof gauze). All populations were started with a representative sample of 25 individuals including all mobile stages, taken from growing cultures (3–4 weeks old) of either base strain, *R*-line, *T*-line or (*RT* or *TR*) hybrids. Because ln(*N*) increased or decreased linearly over the observation period (*t*), relative population growth rates, $r = \ln(N_t/25)/t$ were calculated per replicate. Each treatment (combination of predator origin and diet) was replicated 4 times (Table 2). Two-way ANOVA was applied with *r* as the dependent variable and with predator populations (base strain, *R*-line, *T*-line and *RT*-, *TR*-hybrids) and prey diets (**R**, **T**, mixture) as factors (Table 3). Post-hoc comparisons were made using the T-method ($\alpha = 0.05$)[28].

Mate choice

Female deutonymphs from cultures of *R*-line or *T*-line predators were put in groups of 25 per vial. After sexual maturation (1–2 days) on prey **R** alone, **T** alone or a 1:1 mixture of **R** and **T**, eight females were put in each vial (3 cm diameter, 4 cm high) with eight young *R*-line males, eight young *T*-line males and the same prey as used for conditioning the females. The males, reared invariably on prey **T**, were marked dorsally using water paint. Virgin females were given 0.5 h for mate selection. Vials were inspected once per minute (mating time >5 min). Mate choice per vial was calculated as the percentage of females selecting an own-line male. Each treatment (female origin and diet) was replicated 10 times (Table 4). Two-way ANOVA was applied on ranked data, using the Scheirer–Ray–Hare extension of the Kruskal–Wallis test[28] with the percentage of within-line matings as the dependent variable and predator populations (*R*-line, *T*-line) and diets (**R**, **T**, mixture) as factors (Table 5).

1. Andersson, M. *Sexual Selection* (Princeton Univ. Press, NJ, 1994).
2. Bulmer, M. G. Maintenance of genetic variability by mutation–selection balance. *Genome* **31**, 761–767 (1989).
3. Falconer, D. S. & McKay, R. *Introduction to Quantitative Genetics* 3rd edn (Longman, New York, 1996).
4. Felsenstein, J. Skepticism towards Santa Rosalia, or why there are so few kinds of animals. *Evolution* **35**, 124–138 (1981).
5. Hoekstra, R. F., Bijlsma, R. & Dolman, A. J. Polymorphism from environmental heterogeneity: Models are only robust if the heterozygote is close in fitness to the favoured homozygote in each environment. *Genet. Res.* **45**, 299–314 (1985).
6. Garcia-Dorado, A. The effect of niche preference on polymorphism protection in a heterogeneous environment. *Evolution* **40**, 936–945 (1986).
7. Meeus, T. de, Michalakis, Y., Renaud, F. & Olivieri, I. Polymorphism in heterogeneous environments, evolution of habitat selection and sympatric speciation: soft and hard selection models. *Evol. Ecol.* **7**, 175–198 (1993).
8. Jones, J. S. Can genes choose habitats? *Nature* **286**, 757–758 (1980).
9. Brown, J. L. A theory of mate choice based on heterozygosity *Behav. Ecol.* **8**, 60–65 (1997).
10. Sabelis, M. W. in *Natural Enemies, The Population Biology of Predators, Parasites and Diseases* (ed. Crawley, M. J.) 225–264 (Blackwell Scientific, Oxford, 1992).
11. Lesna, I., Sabelis, M. W. & Conijn, C. G. M. Biological control of the bulk mite, *Rhizoglyphus robini*, by the predatory mite, *Hypoaspis aculeifer*, on lilies: Predator–prey interactions at various spatial scales. *J. Appl. Ecol.* **33**, 369–376 (1996).
12. Lesna, I. Bulb mite biocontrol: evolutionary genetics of prey choice in soil predators. Ph.D. Thesis, Univ. Amsterdam (1998).
13. Witalinski, W. Sperm competition in the Acari. *Exp. Appl. Acarol.* **23**, 455–465 (1999).
14. Maynard Smith, J. Sympatric speciation. *Am. Nat.* **100**, 637–650 (1966).
15. Futuyma, D. J. & Moreno, G. The evolution of ecological specialization. *Annu. Rev. Ecol. Syst.* **19**, 207–233 (1988).
16. Chesson, P. L. in *Community Ecology* (eds Diamond, J. & Case, T. J.) 240–254 (Harper and Row, New York, 1986).
17. Chesson, P. A need for niches? *Trends Ecol. Evol.* **6**, 26–28 (1991).
18. Serradilla, J. M. & Ayala, F. J. Alloprocoptic selection: A mode of natural selection promoting polymorphism. *Proc. Natl Acad. Sci. USA* **80**, 2022–2025 (1983).
19. Gilburn, A. A. & Day, T. H. Evolution of female choice in seaweed flies: Fisherian and good genes mechanisms operate in different populations. *Proc. R. Soc. Lond. B* **255**, 159–165 (1994).
20. Houtman, A. M. & Falls, J. B. Negative assortative mating in the white-throated sparrow: the effect of mate choice and intrasexual competition. *Anim. Behav.* **48**, 377–383 (1994).
21. Lenington, S. The t-complex: a story of genes, behavior, and populations. *Adv. Study Behav.* **20**, 51–86 (1991).
22. Coopersmith, C. B. & Lenington, S. Preferences of female mice for males whose t-haplotype differs from their own. *Anim. Behav.* **40**, 1179–1181 (1990).
23. Lenington, S., Coopersmith, C. B. & Erhart, M. Female preference and variability among t-haplotypes in wild house mice. *Am. Nat.* **144**, 766–784 (1994).
24. Potts, W. K., Manning, C. J. & Wakeland, E. K. The role of infectious disease, inbreeding and mating preferences in maintaining MHC genetic diversity: an experimental test. *Phil. Trans. R. Soc. Lond. B* **346**, 369–378 (1994).
25. Penn, D. J. & Potts, W. K. The evolution of mating preferences and major histocompatibility complex genes. *Am. Nat.* **153**, 145–164 (1999).
26. Penn, D. J. & Potts, W. K. MHC-disassortative mating preferences reversed by cross-fostering. *Proc. R. Soc. Lond. B* **265**, 1299–1306 (1998).
27. Edwards, S. V. & Hedrick, P. W. Evolution and ecology of MHC molecules: from genomics to sexual selection. *Trends Ecol. Evol.* **13**, 305–311 (1998).
28. Sokal, R. R. & Rohlf, F. J. *Biometry* (Freeman, New York, 1995).

fMRI evidence for objects as the units of attentional selection

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Contrasting theories of visual attention emphasize selection by spatial location[1], visual features (such as motion or colour)[2–4] or whole objects[5,6]. Here we used functional magnetic resonance imaging (fMRI) to test key predictions of the object-based theory, which proposes that pre-attentive mechanisms segment the visual array into discrete objects, groups, or surfaces, which serve as targets for visual attention[5–9]. Subjects viewed stimuli consisting of a face transparently superimposed on a house, with one moving and the other stationary. In different conditions, subjects attended to the face, the house or the motion. The magnetic resonance signal from each subject's fusiform face area[10], para-hippocampal place area[11] and area MT/MST[12] provided a measure of the processing of faces, houses and visual motion, respectively. Although all three attributes occupied the same location, attending to one attribute of an object (such as the motion of a moving face) enhanced the neural representation not only of that attribute

but also of the other attribute of the same object (for example, the face), compared with attributes of the other object (for example, the house). These results cannot be explained by models in which attention selects locations or features, and provide physiological evidence that whole objects are selected even when only one visual attribute is relevant.

A central question in current theories of visual attention is whether the units of attention are locations, features, objects, or a combination of these. All of these theories agree that attention entails selection of some associated but irrelevant information, but they make different predictions about which irrelevant information will be automatically selected along with the target. fMRI has advantage over behavioural tests of these predictions[13,14] because it allows the strength of specific neural representations to be measured directly and simultaneously without disrupting the selection task under investigation. Specifically, the magnetic resonance signal from the fusiform face area (FFA), which responds more strongly to faces than to other objects[10], provides a measure of the neural processing of a face stimulus; the signal from the parahippocampal place area (PPA), which responds more strongly to places and houses than to other objects[11], provides a measure of the neural processing of a house stimulus; and the signal from area MT/MST[12] provides a measure of the neural processing of motion.

We asked two questions for which the different models of attention make contrasting predictions. First, is processing enhanced for all visual attributes at the attended location, as predicted only by the space-based theory? Second, does attention to one attribute of an object automatically entail processing of task-irrelevant visual attributes of the same object, as predicted by object-based models?

Each subject was scanned on a General Electric 3T Signa scanner on two runs of a functional localizer that enabled precise and independent identification of the voxels comprising his or her fusiform face area, parahippocampal place area and area MT/MST, as described previously[10–12]. These three sets of voxels served as the regions of interest (ROIs) to be used in the analysis of the data from the main experiments.

In our first experiment, seven subjects were run on 6–8 scans, each consisting of one block of each of the six conditions created by crossing two stimulus types with three attentional conditions. In half the blocks, subjects viewed a series of stationary houses transparently superimposed on faces that oscillated along one of four axes, with a new display presented every 1.4 s (Fig. 1). In the other half of the blocks, the stimulus was identical except that the house was moving and the face was stationary. The subjects' attention was directed to a different stimulus attribute in each block by instructing them to monitor the series of displays for consecutive repetitions of either the face, the house or the direction of motion.

For each of the three ROIs (FFA, PPA and MT/MST) in each subject, we computed the average per cent increase in magnetic resonance signal from the fixation baseline for each of the six experimental conditions. (For raw time course of per cent signal change over the period of the scan for each of the three ROIs, see Supplementary Information.) The averages of these values across subjects are given in Fig. 2. The resulting data set allowed us to confirm two fundamental predictions of object-based theories of attention. First, in each region the change in magnetic resonance signal was greater when subjects attended to the preferred attribute for that cortical region (for example, faces for the FFA) than when they attended to a different attribute of the same display (see comparisons shown in the grey boxes in Fig. 2). This effect was reliable in each of three ROIs tested: FFA ($F(1,6) = 31.9$, $P < 0.001$), PPA ($F(1,6) = 50.7$, $P < 0.0001$), and MT/MST ($F(1,6) = 19.5$, $P < 0.005$). This attentional modulation cannot be accounted for by a purely spatial model of attentional selection, because all of the relevant information occupied the same location.

Second, we tested the central claim of object-based theories: task-irrelevant attributes of an attended object will be selected along with the task-relevant attribute, even when these attributes are independent (as the form and motion attributes were here). This prediction was confirmed for each extrastriate area (see comparisons shown in the black rectangles in Fig. 2). When the subject attended to motion, a higher signal change was observed in the FFA when the faces moved than when the houses moved (with faces stationary) ($F(1,6) = 8.5$, $P < 0.05$). The complementary result was obtained in the PPA: the signal change was greater during the motion task when the house moved than when the face moved ($F(1,6) = 42.5$, $P < 0.001$), even though both faces and houses were present in each condition. Finally, in MT/MST, the signal change was greater when subjects attended to the face or house when they were moving than when they were stationary ($F(1,6) = 16.0$, $P < 0.01$). This effect did not depend on whether subjects were attending to faces or houses ($F(1,6) < 1$, n.s.).

These results cannot be explained by space- or feature-based models of attention alone. Instead they show that, even when the task requires only that subjects select a given visual attribute, both attributes of the attended object are automatically selected.

		Attended attribute			
ROI	Stimulus	Face		House	Motion
FFA	Face moving	2.4	>	1.3	2.0
	House moving	2.2	>	1.3	1.4
PPA	Face moving	0.4	<	1.0	0.3
	House moving	0.4	<	0.9	0.6
MT/MST	Face moving	1.4		0.8	< 1.5
	House moving	1.2		1.0	1.4
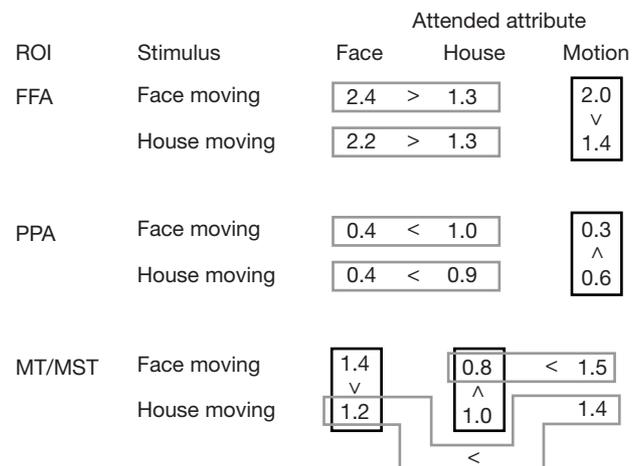
Figure 2 Design and results of Experiment 1. For each condition, the average per cent signal change across subjects is given for each of the three ROIs. The grey boxes show the greater response in each extrastriate ROI to the attended attribute compared with the unattended attribute, which cannot be accounted for by a purely location-based theory of attention. The black boxes show the greater response to the irrelevant attribute of the attended object compared with the unattended attribute of the unattended object, as predicted only by object-based theories of attention (see text for statistics).

Figure 1 Sample stimuli. A sample stimulus from the first experiment is shown on the left. For the second experiment the faces were enlarged to more closely match the region of space occupied by the house in each pair. An example is shown at the right, with the face displaced (in this case, to the right of fixation) as required for the position-repetition detection task. In each stimulus, either the face or the base moved back and forth along one axis.

Furthermore, it would be very difficult to account for these results in terms of smooth-pursuit eye movements; even if subjects ignored our instructions to fixate, any effort to track the moving object would have been ineffective because it reversed direction every 135 ms. Thus, our findings are best explained by object-based theories of attention. However, one remaining possibility is that the blocked design may have encouraged subjects to use the task-irrelevant attribute to aid in selection of the relevant attribute of the same object.

The second experiment precluded this possibility by using an event-related design[15] in which we randomly intermixed trials containing the two stimulus types (moving faces with stationary houses, or moving houses with stationary faces). Four subjects performed a consecutive repetition-detection task in different scans on either the direction of motion of the moving object or the position of the stationary object (which was offset slightly in each stimulus to the left, right, top or bottom of fixation). This design prevented subjects from predicting from trial to trial whether the task-relevant object (the moving or stationary object) would be a face or a house. Thus, attention to the task-irrelevant dimensions could provide no benefit to performance of the required task.

Consistent with previous studies, the evoked response to the stimulus peaked 4–6 s after stimulus onset. We therefore took the average of the three corresponding time points as our measure of response magnitude (Fig. 3). In the motion task, the neural representation of the form (face or house) of the moving object was enhanced, confirming our finding that the processing of the irrelevant attribute of the attended object is increased ($F(1,3) = 143.6$, $P < 0.001$). For the position task, we found the opposite pattern: the representation of the stationary face or house was enhanced relative to the moving stimulus ($F(1,3) = 17.1$, $P < 0.05$). The significant interaction of task × stimulus × cortical area ($F(1,3) = 40.8$, $P < 0.01$) eliminates an account of the data in terms of generally enhanced processing of either moving or stationary stimuli. To ensure that baseline effects were not responsible for any of these results, the same analyses were conducted on the first three time points of the evoked response. No significant effects were found in these analyses (all $P > 0.10$).

Thus, Experiment 2 provides strong support for the key prediction of object-based theories of attention. During a task that requires selection of only one visual attribute, the representation of the other attributes of the same object are automatically enhanced, even if their combination with the target dimension is unpredictable and uninformative. This result rules out any explanation of the data in terms of strategic use of the irrelevant dimension in attentional selection. Furthermore, enhancement of the irrele-

vant attribute occurred even though these attributes (faces and houses) were never task relevant for the subjects in this experiment.

Our data provide, to our knowledge, the first neural evidence that objects serve as the units of attention even when the selection of objects is not required by the task. However, it is unlikely that objects are the only units of attentional selection. The ability to select features and/or feature dimensions is supported by evidence from behavioural[2,4], imaging[3,16,17], single-unit[18] and event-related potential[19] studies. Our finding that the neural response to the task-relevant attribute was stronger than the response to the task-irrelevant attribute of the attended object (Fig. 2) may reflect such a feature-based effect, although it may also reflect the involvement of extrastriate areas in working memory[20] or perceptual decision-making[21].

Spatial locations probably also serve as the units of selection under some circumstances[22]. Several recent fMRI studies have shown attentional modulations of the response to visual stimuli in retinotopic cortex, including area V1[23–25]. However, none of these studies unconfounded object-based selection from location-based selection, because in all such studies each location tested was occupied by a distinct object. Our experiments solve this problem by superimposing two objects in the same location, to preclude location-based selection. Two other studies[16,26] have also shown attentional modulation of objects or textures superimposed in the same location, consistent with object-based attention. However, our study adds a critical new condition enabling us to measure the response to the task-irrelevant attribute of the attended object.

The 'biased-competition' model of attention[27] suggests the following interpretation of our data. The instruction to attend to a particular dimension (such as motion) results in a top-down bias signal[28] which enhances responses in the extrastriate area coding that dimension (such as MT/MST). This increased response to the attended attribute causes an enhancement of the neural response to the other attributes of the same object (for example, the face, represented in the FFA). This enhancement occurs even when the task does not require subjects to determine which object is moving (that is to bind the visual attributes of form and motion).

The biased-competition model leaves two crucial questions unanswered. First, how are the correct visual attribute bindings determined in the first place? Feature-integration theory[29] offers a solution, but it relies on location information and so would not be effective for the present case of superimposed objects. Psychophysical and modelling results[30] indicate that, for transparent motion, the solution to the binding problem may require information present only at very early stages of the visual pathway; the same is likely to be true for binding of other independent visual dimensions such as colour and disparity. Second, how do these bindings (once computed) lead visual information represented in one extrastriate neural population (such as MT/MST) to affect the response of a neural population in a remote visual area (such as FFA)? One possibility is that recurrent feedback between each extrastriate area and early stages of the visual pathway is central to the competitive interactions that enable representations of objects to be constructed and to become the units of attention and perceptual awareness. □
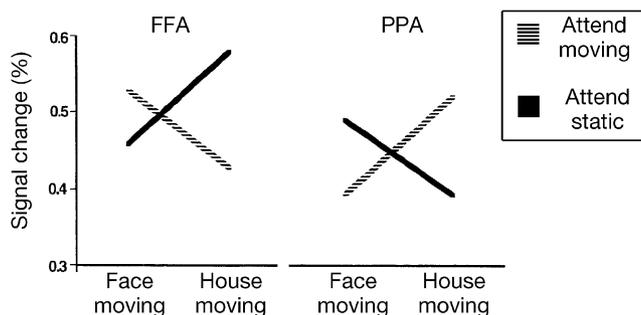
Figure 3 Means of the peak evoked responses from Experiment 2 in the FFA and PPA as a function of task (attend moving or attend static) and stimulus (face moving or house moving). Even though subjects never had to attend to faces or houses in the entire experiment, and could not predict which stimulus would move on a given trial, magnetic resonance responses were greater to the task-irrelevant attribute of the attended object than to the irrelevant attribute of the unattended object, as predicted by object-based theories of attention.

Methods

Subjects and task

Each stimulus was composed by transparently superimposing one of eight greyscale front-view photographs of young white male faces on one of eight greyscale photographs of houses. The stimulus subtended ~10° of visual angle.

In Experiment 1, each trial consisted of a 675-ms stimulus presentation, during which the moving item oscillated (2 cycles) along a straight path on one of four non-cardinal axes. The maximal displacement caused by the motion was less than 10% of the width of the image. The inter-trial interval was 725 ms. Each scan consisted of six 28-s task blocks

(attend face, attend house or attend motion × face moving, house moving) alternating with 10-s blocks in which only a fixation point was present. The initial, middle and final fixation blocks were extended to 30 s to provide a stable baseline measure. The block order was reversed on half of the runs. A cue word ('face', 'house' or 'motion') appearing immediately before each block indicated which task should be performed next. Subjects were instructed to fixate on a central dot that remained present throughout the experiment, and to press a button to indicate a consecutive repetition of the designated attribute. Only stimuli on the task-relevant dimension were repeated, with a probability of 0.125.

The stimuli and task in Experiment 2 were identical to Experiment 1 except as follows. Subjects monitored for consecutive repetitions of either motion direction or position relative to the fixation point in separate scans. Each stimulus presentation lasted 375 ms, with a fixation dot present at all times. On each trial, one item was stationary and was displaced ∼1.0° in one of four directions from the centre. The other item moved along one of the four motion paths, making one excursion out and back to the centre. Each scan contained three trial types, each 2 s long: static house with moving face; static face with moving house; and fixation. Twenty-four trials from each condition were tested in each scan. The presentation sequence was uniquely randomized for each scan. Trials from each condition were preceded equally often by trials from each of the three conditions. Repetitions on each stimulus dimension occurred with probability 0.125, with no correlation across dimensions.

Imaging and data analysis

Scanning was done at the MGH NMR Center in Charlestown, Massachusetts, on a 3 Tesla General Electric Signa MR scanner modified by ANMR to perform echo-planar imaging. A gradient echo pulse sequence (TR = 2s for Experiment 1 and localizer scans; TR = 1s for Experiment 2; TE = 30 ms) was employed. Eight near-coronal slices (parallel to the brainstem, 7 mm thick with 3.125×3.125 mm in-plane resolution) were collected with a custom surface coil (built by T. Vaughan) to enhance the signal-to-noise ratio in the posterior brain regions under investigation.

The FFA was defined as the set of all contiguous voxels in the fusiform gyrus that responded more strongly to faces than to houses; the PPA was defined as all contiguous voxels in the parahippocampal region that responded more strongly to houses than to faces; and MT/MST was defined as all contiguous voxels in the occipito-temporo-parietal junction that responded more strongly to moving faces, houses and dots than to stationary ones. For all three analyses we used a threshold of $P < 10^{-4}$ (uncorrected) on a Kolmogorov–Smirnov test.

For Experiment 1, the mean per cent signal change was computed by subject for each condition in each ROI. To compensate for haemodynamic lag or for mixtures of effects at the boundaries of epochs, the first data point of each epoch was assigned to the previous epoch, and the next two data points were omitted from the analysis.

For Experiment 2, the fMRI signal from the FFA and PPA was extracted for each scan separately. Twelve time-points (12 s) of data were averaged by condition, beginning from the onset of each trial. The data were converted to per cent signal change relative to the corresponding timepoint on fixation trials, and mean per cent signal changes were then calculated for each of the four conditions of interest for each subject. The peak of the evoked response (the mean of timepoints 4, 5 and 6) was analysed with ROI (FFA or PPA), task (attend motion or attend position) and stimulus (house moving or face moving) as factors.

In all other respects, the methods used here were as reported[10,11,16].

1. Posner, M. I. Orienting of attention. *Q. J. Exp. Psychol.* **32,** 3–25 (1980).
2. Treisman, A. M. Strategies and models of selective attention. *Psychol. Rev.* **76,** 282–299 (1969).
3. Corbetta, M. *et al.* Attentional modulation of neural processing of shape, color, and velocity in humans. *Science* **248,** 1556–1559 (1990).
4. Wolfe, J. M., Cave, K. R. & Franzel, S. L. Guided search: an alternative to the feature integration model for visual search. *J. Exp. Psychol. Hum. Percept. Perf.* **15,** 419–433 (1989).
5. Duncan, J. Selective attention and the organization of visual information. *J. Exp. Psychol. Gen.* **113,** 501–517 (1984).
6. He, Z. J. & Nakayama, K. Visual attention to surfaces in three-dimensional space. *Proc. Natl Acad. Sci. USA* **24,** 11155–11159 (1995).
7. Vandenberghe, R. *et al.* Attention to one or two features in left or right visual field: a positron emission tomography study. *J. Neurosci.* **17,** 3739–3750 (1997).
8. Roelfsema, P. R., Lamme, V. A. & Spekreijse, H. Object-based attention in the primary visual cortex of the macaque monkey. *Nature* **395,** 376–381 (1998).
9. Driver, J., Baylis, G. C., Goodrich, S. J. & Rafal, R. D. Axis-based neglect of visual shapes. *Neuropsychologia* **32,** 1353–1365 (1994).
10. Kanwisher, N., McDermott, J. & Chun, M. The fusiform face area: A module in human extrastriate cortex specialized for the perception of faces. *J. Neurosci.* **17,** 4302–4311 (1997).
11. Epstein, R. & Kanwisher, N. A cortical representation of the local visual environment. *Nature* **392,** 598–601 (1998).
12. Tootell, R. B. *et al.* Functional analysis of human MT and related visual cortical areas using magnetic resonance imaging. *J. Neurosci.* **15,** 3215–3230 (1995).
13. Eriksen, B. A. & Eriksen, C. W. Effects of noise letters upon the identification of target letters in a nonsearch task. *Percept. Psychophys.* **16,** 143–149 (1974).
14. Driver, J. & Baylis, G. C. Movement and visual attention: The spotlight metaphor breaks down. *J. Exp. Psychol. Hum. Percept. Perf.* **15,** 448–456 (1989).
15. Rosen, B. R., Buckner, R. L. & Dale, A. M. Event-related functional MRI: Past, present, and future. *Proc. Natl Acad. Sci. USA* **95,** 773–780 (1998).
16. O'Craven, K. M., Rosen, B. R., Kwong, K. K., Treisman, A. & Savoy, R. L. Voluntary attention modulates fMRI activity in human MT-MST *Neuron* **18,** 591–598 (1997).
17. Beauchamp, M. S., Cox, R. W. & DeYoe, E. A. Graded effects of spatial and featural attention on human area MT and associated motion processing areas. *J. Neurophys.* **78,** 516–520 (1997).
18. Treue, S. & Trujillo, J. C. M. Feature-based attention influences motion processing in macaque visual cortex. *Nature* **399,** 575–579 (1999).
19. Hillyard, S. A. & Munte, T. F. Selective attention to color and location: An analysis with event-related brain potentials. *Percept. Psychophys.* **36,** 185–198 (1984).
20. Courtney, S. M., Ungerleider, L. G., Keil, K. & Haxby, J. V. Transient and sustained activity in a distributed neural system for human working memory. *Nature* **386,** 608–611 (1997).
21. Salzman, C. D. & Newsome, W. T. Neural mechanisms for forming a perceptual decision. *Science* **264,** 231–237 (1994).
22. Mangun, G. & Hillyard, S. A. Allocation of visual attention to spatial location: Tradeoff functions for event related brain potentials and detection performance. *Percept. Psychophys.* **47,** 532–550 (1990).
23. Brefczynski, J. A. & DeYoe, E. A. A physiological correlate of the 'spotlight' of visual attention. *Nature Neurosci.* **4,** 370–374 (1999).
24. Somers, D. C., Dale, A. M., Seiffert, A. E. & Tootell, R. B. Functional MRI reveals spatially specific attentional modulation in human primary visual cortex. *Proc. Natl Acad. Sci. USA* **96,** 1663–1668 (1999).
25. Gandhi, S. P., Heeger, D. J. & Boynton, G. M. Spatial attention affects brain activity in human primary visual cortex. *Proc. Natl Acad. Sci. USA* **96,** 3314–3319 (1999).
26. Valdes-Sosa, M., Bobes, M., Rodriguez, V. & Pinilla, T. Switching attention without shifting the spotlight: Object-based attentional modulation of brain potentials. *J. Cogn. Neurosci.* **10,** 137–151 (1998).
27. Desimone, R. & Duncan, J. Neural mechanisms of selective visual attention. *Annu. Rev. Neurosci.* **18,** 193–222 (1995).
28. Kastner, S., Pinsk, M. A., De Weerd, P., Desimone, R. & Ungerleider, L. G. Mechanisms of directed attention in the human extrastriate cortex as revealed by functional MRI. *Neuron* **22,** 751–761 (1999).
29. Treisman, A. M. & Gelade, G. A feature-integration theory of attention. *Cogn. Psychol.* **12,** 97–136 (1980).
30. Qian, N., Andersen, R. A. & Adelson, E. H. Transparent motion perception as detection of unbalanced motion signals. I. Psychophysics. *J. Neurosci.* **14,** 7357–7566 (1994).

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Involvement of visual cortex in tactile discrimination of orientation

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The primary sense modalities (vision, touch and so on) are generally thought of as distinct. However, visual imagery is implicated in the normal tactile perception of some object properties, such as orientation[1], shape and size[2]. Furthermore, certain tactile tasks, such as discrimination of grating orientation[1] and object recognition[3], are associated with activity in areas of visual cortex. Here we show that disrupting function of the occipital cortex using focal transcranial magnetic stimulation (TMS) interferes with the tactile discrimination of grating orientation. The specificity of this effect is illustrated by its time course and spatial restriction over the scalp, and by the failure of occipital TMS to affect either detection of an electrical stimulus applied to the fingerpad or tactile discrimination of grating texture. In contrast, TMS over the somatosensory cortex blocked discrimination of grating texture as well as orientation. We also report that, during

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