(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].

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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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tactile discrimination of grating orientation, an evoked potential is recorded over posterior scalp regions with a latency corresponding to the peak of the TMS interference effect (about 180 ms). The findings indicate that visual cortex is closely involved in tactile discrimination of orientation. To our knowledge, this is the first demonstration that visual cortical processing is necessary for normal tactile perception.

Visual cortex is known to be involved in nonvisual perception in blind humans[4–9]. This has been attributed to neural plasticity resulting from visual deprivation. However, visual processing can also influence certain aspects of normal human tactile perception. For instance, during haptic sorting, instructions to emphasize visual images bias subjects to sort by object properties such as size and shape, whereas without such instructions sorting is based on texture and hardness[2]. Using positron emission tomography (PET), we showed that discrimination of the orientation of a grating on the fingerpad is associated with subjective reports of visual imagery and increased regional cerebral blood flow, relative to that seen during discrimination of grating texture (spacing), in a contralateral region of extrastriate visual cortex near the parieto-occipital fissure[1]. This locus, which is also active during visual discrimination of grating orientation[10] and other tasks requiring spatial mental imagery[11], may be the human homologue of an area in the parieto-occipital fissure of macaques (V6/PO) where a large proportion of neurons are orientation-selective[12]. A functional magnetic resonance imaging (fMRI) study found that visual cortical areas are also active during tactile object recognition, compared with texture discrimination[3]. The recruitment of processing in visual cortex may reflect top-down activation of visual representations to facilitate tactile discrimination of orientation or shape. Alternatively, the observed activity could be merely an epiphenomenon.

One way to distinguish between these two possibilities is to interfere with processing in visual cortex. To do this, we applied TMS over the occipital scalp, a procedure that blocks visual perception by disrupting the function of extrastriate visual cortex[13,14]. In Experiment 1, TMS pulses were delivered to multiple sites over occipital cortex while subjects attempted to discriminate the orientation of a grating on the right index fingerpad (Fig. 1) with their eyes closed. At each site, TMS was applied 10, 180 or 400 ms after the onset of grating presentation. To control for nonspecific effects of the loud noise accompanying TMS, performance was also measured with the magnetic stimulator in air.

Figure 2a shows a clear effect of TMS over occipital cortex at the higher of the two midline sites tested (M4) and contralateral to the hand encountering the grating (L3). Compared with discrimination performance with the stimulator in air, performance at these sites
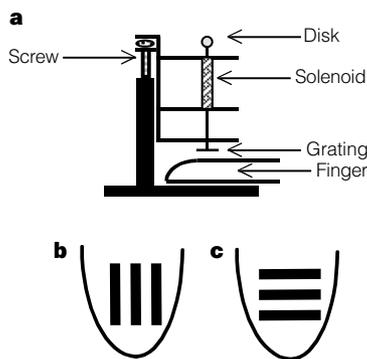
was unaffected by TMS at the 10-ms delay but was markedly impaired at the 180-ms delay. By 400 ms, the effect was slight. In contrast, TMS ipsilateral to the hand feeling the grating (R3) and at the lower midline site (M2) had no effect (Fig. 2a). This spatial restriction, together with the clear time course of the effect, indicates that the impairment of perception was not due to muscle contraction or other nonspecific effects of TMS. Performance was significantly different between the 10-ms and 180-ms delays at the M4 ($t = 11.58$, d.f. $= 10$, $P = 0.00000004$) and L3 ($t = 3.79$, d.f. $= 9$, $P = 0.004$) sites but not at the R3 ($t = 0.25$, d.f. $= 9$, $P = 0.81$) or M2 ($t = 2.14$, d.f. $= 4$, $P = 0.1$) sites.

To test whether the disruption of tactile performance by occipital TMS was specific to discrimination of orientation or represented a more general effect on somatosensory perception, we investigated the effect of occipital TMS on a control task, detection of a suprathreshold electrical stimulus to the fingerpad. Figure 2b shows that performance on this task was unaffected. There were no significant performance differences between the 10-ms and 180-ms delays for TMS at the M4 ($t = -1.83$, d.f. $= 4$, $P = 0.14$), L3 ($t = -1$, d.f. $= 4$, $P = 0.37$) or R3 ($t = -1.29$, d.f. $= 4$, $P = 0.27$) sites. The lack of effect of TMS on this control task may indicate that the effect of TMS is specific to orientation discrimination, rather than being a general suppression of somatosensory processing. However, the control task was slightly easier than the orientation task (performance with the stimulator in air was 94% correct versus 85% correct; Fig. 2b, a) and was also a simple detection task, whereas the main task involved discrimination (of grating orientation). Hence, we conducted another experiment (Experiment 2), in which the control task was discrimination of grating texture (spacing task), the same control task as in our previous PET study[1]. As the locus of activation (orientation minus spacing) in the PET study[1] was superior and lateral to the M4 site, we applied TMS pulses directly over the PET activation locus (L6) in the left hemisphere and the homologous area in the right hemisphere (R6), as well as to M4, using only the 10- and 180-ms delays at these sites in Experiment 2 (as there was little effect at 400 ms in Experiment 1). We also delivered TMS to left primary somatosensory cortex, using a 30-ms delay. Subjects were blindfolded in Experiment 2.

In Experiment 2, TMS at M4 clearly interfered with discrimination of grating orientation at 180 ms but not at 10 ms (Fig. 2c), replicating the effect obtained in Experiment 1. A similar effect was obtained at L6, the PET activation locus, but not at R6, its
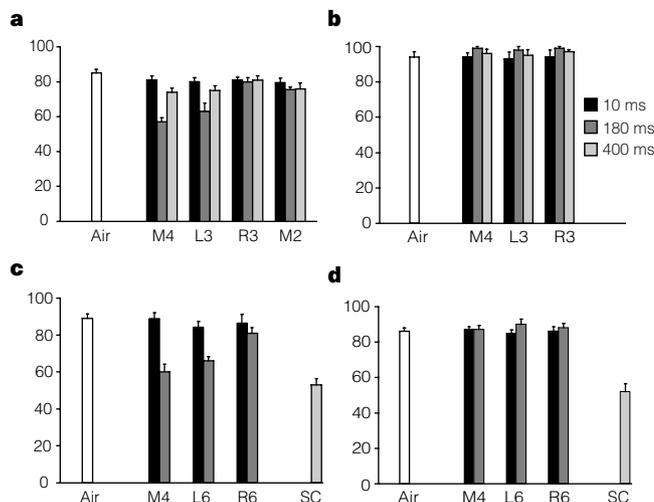

Figure 1 Set up used for grating application. **a**, The screw enabled positioning of the grating just above the fingerpad by a dovetail arrangement. From this position, activation of the solenoid caused downward displacement of the grating by about 3 mm. Rotating the disk changed grating orientation, which was either along (**b**) or across (**c**) the long axis of the finger.

Figure 2 Effect of TMS at the delays indicated. Bar graphs show mean performance (% correct responses) and standard errors. **a**, Experiment 1, orientation task; **b**, Experiment 1, electrical stimulation; **c**, Experiment 2, orientation task; **d**, Experiment 2, spacing task. SC, TMS over somatosensory cortex (30-ms delay). Air, stimulator in air.

homologue in the opposite hemisphere (Fig. 2c). Performance was significantly poorer at the 180-ms delay than at the 10-ms delay at M4 ($t = 6.75$, d.f. $= 5$, $P = 0.001$) and L6 ($t = 4.22$, d.f. $= 5$, $P = 0.008$) but not R6 ($t = 2.22$, d.f. $= 5$, $P = 0.08$). In contrast, occipital TMS had no effect on discrimination performance in the spacing task (Fig. 2d). There were no significant performance differences between the 10- and 180-ms delays at any of the sites (M4: $t = 0$, d.f. $= 5$, $P = 1$; L6, $t = -1.46$, d.f. $= 5$, $P = 0.2$; R6: $t = -0.39$, d.f. $= 5$, $P = 0.71$). Notably, baseline performances with the stimulator in air were almost identical in the orientation (89% correct; Fig. 2c) and spacing (86% correct; Fig. 2d) tasks. Thus, the effect of occipital TMS was specific to the orientation task. Consistent with this, most subjects felt that mental visualization of the grating was helpful in the orientation task but not the spacing task.

Stimulation over primary somatosensory cortex, however, suppressed discrimination performance to near-chance levels in both orientation and spacing tasks (Fig. 2c, d). The effects were statistically significant: performance was poorer in the TMS condition than with stimulation in air (orientation: $t = 5.55$, d.f. $= 2$, $P = 0.03$; spacing: $t = 20$, d.f. $= 2$, $P = 0.002$). Thus, in contrast to the selective effect of occipital TMS on the orientation task, TMS over somatosensory cortex was nonselective, affecting both orientation and spacing discriminations equally. Subjective reports also differed according to where TMS was applied. At occipital sites where TMS impaired performance on orientation discrimination, subjects reported that they could still feel the grating but were unsure of its orientation. In contrast, with TMS over primary somatosensory cortex, subjects reported interference with perception of the grating itself, often feeling only a sensation of pressure but being unable to distinguish the pattern of the grating.

Figure 3 shows that our results are consistent with the idea that impairment of tactile discrimination of grating orientation by occipital TMS is due to stimulation of the region of parieto-occipital cortex identified b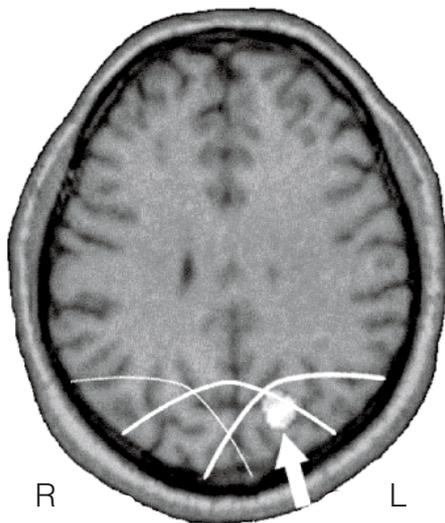y PET[1]. Stimulation at effective sites (M4, L3 and L6) induced electric fields whose calculated magnitudes were consistent with physiological effects at the PET activation locus. In contrast, the fields derived from stimulation at ineffective sites (R6, R3 and M2) failed to enclose the area of PET activation. Although the cerebellum has been implicated in somatosensory discrimination[15], it is unlikely that our results were due to cerebellar stimulation, as there was no effect at the most inferior site (M2), which was the closest site to the cerebellum.

We also studied the distribution and time course of the averaged electrical potential evoked over the scalp in response to stimulation of the fingerpad with the grating. To isolate neural processing that was specific to discrimination of orientation, the potentials evoked when subjects were engaged in this task were compared with those obtained while subjects performed a control task, counting the number of tactile stimuli. This controlled for attentive somatosensory processing. The resulting subtraction potential (Fig. 4) showed a peak at 150–180 ms in contralateral parietal and occipital leads, consistent with the time course of the TMS interference effect.

Together with the subjective reports of visual imagery in this task and the associated parieto-occipital cortical activation noted previously[1], our findings support the proposal that visual processing facilitates normal tactile discrimination of orientation. Visual processing may similarly facilitate tactile object recognition[3]. Perhaps this is related to the fact that we generally rely on the visual system for orientation and shape discrimination. We emphasize that this dependence on the visual system does not apply to all aspects of tactile perception, as shown by the failure of occipital TMS to affect the detectability of an electrical stimulus applied to the fingerpad or discrimination performance on the spacing task. Thus, involvement of visual cortex may be beneficial when macrogeometric features such as orientation and shape are to be discriminated, but not for microgeometric features such as texture. In an earlier study[5], occipital TMS affected the ability of blind but not sighted subjects to identify embossed Roman letters. The lack of effect in the sighted may reflect the dependence of this task, like texture discrimination, on processing of microspatial detail[16]. Alternatively, the different set sizes used for sighted (5-letter sets) and blind subjects (26-letter sets) may underlie the differential effects in these two subject groups, given the intrinsic confusability of certain tactually presented letters[17]—it remains possible that sighted subjects could also show the effect under different experimental conditions. Our findings provide the first demonstration, to our knowledge, that visual cortex is necessary for optimal tactile performance in normally sighted subjects. □

Methods

Subjects

Figure 3 Activation due to grating orientation (relative to spacing) observed in previous PET study[1] superimposed on an axial, T-1-weighted MRI slice derived from one subject who participated in both the PET study and the present study. Arrow, activation. Talairach coordinates of centre of activation: $x = -20$, $y = -71$, $z = 32$. Isopotential lines of the TMS-induced electric fields corresponding to 90% of the resting motor threshold are also superimposed on the MRI. Brain regions on the concave side of the curves are exposed to electric fields above the threshold of known physiological effects. The heavy curves refer to TMS at the (effective) M4 and L3 sites; the thin curve refers to the (ineffective) R3 site. Similar calculations (data not shown) indicated the compatibility of the effectiveness of TMS at other occipital sites (M2, L6, R6) in the orientation task with the ability to evoke physiological effects at the PET activation locus.
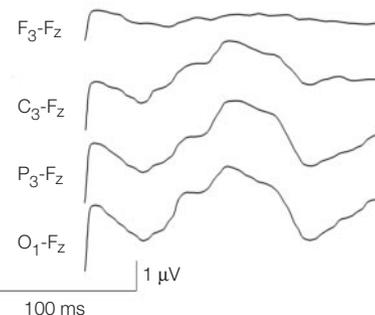

Figure 4 Electrical potential (averaged across subjects) recorded over the scalp during tactile discrimination of grating orientation, relative to counting of tactile stimuli. Arrow, onset of grating contact with fingerpad.

Procedures

Tactile discrimination tasks. Plastic, steel-backed gratings measuring about 20 mm² and with equal groove and ridge widths were manufactured as described[18]. An electromechanical device was used to apply the gratings (for 63-ms duration) to the index fingerpad of the right hand, oriented either along or across the long axis of the finger (Fig. 1). The ability to discriminate orientation increases monotonically as grating groove width (GW) increases up to 3 mm (ref. 19). Subjects were first tested psychophysically on each task. For the orientation task, the discrimination threshold was taken as the GW yielding 75% correct performance[20]. Threshold determinations were based on at least 20 trials for each grating. A grating yielding performance that was above threshold but below ceiling was then selected for each subject. This grating had the maximal GW of 3 mm for most subjects and 2 mm for others. For the spacing task, a similar procedure was followed, resulting in selection of a pair of gratings for each subject (GW 3 mm and 2, 1.5 or 1.2 mm). Gratings were applied in either orientation in the spacing task, at random. Both tasks used two-alternative forced-choices, subjects responding whether the grating was oriented along or across the finger (in the orientation task) or whether the grating grooves/ridges were wide or narrow (in the spacing task). Performance was expressed as the percentage of correct responses.

Electrical stimulation. Electrical stimulation was delivered to the right index fingerpad of five subjects in Experiment 1. A suprathreshold stimulus intensity was chosen for each subject.

TMS. TMS was applied using a Cadwell MES-10 (Cadwell Laboratories) stimulator with a custom high-efficiency iron-core coil that measured 12 cm × 7.5 cm. This coil induces an electric field similar to a figure-of-eight coil, with its maximum directly below the centre[21]. Stimuli were cosine pulses of 200 μs duration, at 150% of the relaxed motor threshold[22]. The inter-stimulus interval was at least 1 s, to avoid seizures. An electronic circuit incorporating a variable delay was used to deliver TMS at particular delays following the onset of the tactile stimulus, registered electrically in the case of gratings with the help of silver gel. On the basis of pilot studies indicating that the peak of the TMS interference effect over occipital cortex occurred at 150–200 ms, the 180-ms delay was chosen as representative of the peak effect. For TMS in air, the coil was held close to but not in contact with the scalp and rotated to direct the magnetic field away from the head.

In Experiment 1, 11 subjects were tested with TMS applied at the M4 (occipital midline, 4 cm above the inion), L3 and R3 sites (both 3 cm above and 4 cm lateral to the inion on the left and right, respectively), except for one subject who dropped out after testing at M4 at the 10- and 180-ms delays. TMS was applied at the M2 site (2 cm above the inion in the midline) in 5 of the 11 subjects. Six subjects (including three who had taken part in Experiment 1) were tested with occipital TMS in Experiment 2, at L6, R6 (both 6 cm above and 2 cm lateral to the inion on the left and right, respectively) and M4. For stimulation over primary somatosensory cortex, the site over the left hemisphere from which a motor response in the right thumb and/or index finger could just be evoked was located. The coil was then moved posteriorly until the motor response just disappeared, and this site was chosen as the somatosensory cortical site. In two out of three subjects, this localization was aided by reports of somatic sensations in the hand—warmth in one subject and numbness in another. As the early peak (presumably from primary somatosensory cortex) in the evoked potential response to stimulation with the grating occurred at 30–50 ms (data not shown), a delay of 30 ms was chosen for TMS at this site. Owing to the discomfort resulting from stimulation at this site (due to muscle contraction), only a single delay was used and only three subjects were tested. The stimulus intensity at this site had to be reduced to the motor threshold for two subjects as they could not tolerate stimulation at higher intensities. Trials were presented in interleaved blocks of 10 with a minimum of 20 trials at each delay and location.

To determine the relationship between the sites at which effects of occipital TMS were obtained and the previously reported PET activation locus[1], we used the averaged resting motor threshold[22] in our subjects to scale the TMS-induced electric fields in a model head[13,23]. The approximate boundaries for physiological effects of TMS (taken as 90% of the resting motor threshold[24]) at selected sites are displayed in Fig. 3.

Statistical testing. Paired t-tests (two-tailed: $\alpha = 0.05$) were used to assess the statistical significance of differences between conditions.

Evoked potentials. Evoked potential recordings were carried out in five subjects in response to tactile stimulation of the right index fingerpad with a grating, as described above. The evoked potentials were averaged with band-pass filters of 0.1–200 Hz. In one session, the active scalp electrodes were positioned on the left side of the head over frontal (F_3), central (C_3), parietal (P_3) and occipital (O_1) sites. In another session, recordings were made with the active scalp electrodes in the corresponding positions on the right. A midline frontal electrode (F_z) was used as the reference. In each session, two runs of 100–120 trials were performed for each condition (discrimination of grating orientation and counting stimuli). The two conditions alternated with each other and the order was counterbalanced across subjects. To ensure that the posterior location of the observed peak in Fig. 4 was not an artefact of the frontal reference electrode used, evoked potentials were also recorded in two subjects using a linked earlobe reference electrode. The potential thus obtained (data not shown) was similar in scalp distribution and time course to that in Fig. 4.

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Primate spinal interneurons show pre-movement instructed delay activity

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Preparatory changes in neural activity before the execution of a movement have been documented in tasks that involve an instructed delay period (an interval between a transient instruction cue and a subsequently triggered movement). Such preparatory activity occurs in many motor centres in the brain, including the primary motor cortex[1–6], premotor cortex[7–9], supplementary motor area[6,10,11] and basal ganglia[6,12,13]. Activity during the instructed delay period reflects movement planning, as it correlates with parameters of the cue and the subsequent movement (such as direction and extent[5,6,9]), although it occurs well before muscle activity. How such delay-period activity shapes the ensu-