

Tactile perception recruits functionally related visual areas in the late-blind

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Sponsorship: This work was supported by grants from the MRC and the Volkswagen Foundation, and funding from an Overseas Research Student Award from Universities UK.

Received 26 April 2006; accepted 16 May 2006

When blind people touch Braille characters, blood flow increases in visual areas, leading to speculation that visual circuitry assists tactile discrimination in the blind. We tested this hypothesis in a functional magnetic resonance imaging study designed to reveal activation appropriate to the nature of tactile stimulation. In late-blind individuals, hMT/V5 and fusiform face area activated during visual imagery of moving patterns or faces. When they touched a doll's face, right fusiform face area was again activated.

Equally, hMT/V5 was activated when objects moved over the skin. We saw no difference in hMT/V5 or fusiform face area activity during motion or face perception in the congenitally blind. We conclude that specialized visual areas, once established through visual experience, assist equivalent tactile identification tasks years after the onset of blindness. *NeuroReport* 17:1381–1384
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Keywords: fusiform face area, hMT/V5, human area MT/V5, functional magnetic resonance imaging, blindness, plasticity, imagery

Introduction

In normal humans, much of the temporal and parietal lobes is polysensory, whereas most of the occipital cortex is thought to be exclusively visual in function. Particular aspects of visual stimuli are analyzed in specialized areas [1,2]. Moreover, mental imagination of similar kinds of visual experience can activate these same specialized regions [3,4].

Tactile exploration of textured surfaces activates somatosensory areas in the postcentral gyrus and posterior regions of the parietal cortex and the lateral occipital gyrus [5–10]. Both James *et al.* [8] and Deibert *et al.* [10] found that in sighted individuals who explored objects with their hands, parts of the visual cortex, including the lingual gyrus, fusiform gyri and even the peripheral field representation in the primary visual cortex, were activated. Cross-modal activity is also seen in adjoining areas such as the parieto-occipital cortex, though this might be due to visual imagery evoked by tactile stimulation [11]. Interestingly, movement of a tactile stimulus across an extensive area of the skin has been shown to weakly activate area hMT/V5 in sighted individuals [12,13].

In blind people, blood circulation and glucose utilization in the occipital lobe are generally elevated [14–16]. Several recent reports reveal that when blind people read Braille or explore textured surfaces and objects with their hands, blood flow increases widely in the occipital and temporal cortex – a finding that corroborates earlier evidence from

encephalographic recording [10,17–20]. Early-blind subjects have difficulty in discriminating Braille characters when the occipital pole is inhibited by transcranial magnetic stimulation [21]. Furthermore, Hamilton *et al.* [22] described a congenitally blind woman who developed Braille alexia following a pure occipital stroke.

While these reports reveal that regions of the visual cortex can be activated in blind subjects during nonvisual stimulation, they do not provide compelling evidence that neural circuitry normally used for visual analysis is specifically employed in corresponding tactile tasks in the blind. Indeed, Amedi *et al.* [23] argue that activity in the primary visual cortex of early-blind subjects is related to verbal memory rather than tactile discrimination. Pietrini *et al.* [9] report that tactile discrimination of objects evokes activity in the ventral temporal cortex of blind subjects, and that patterns of response differ for face-masks and man-made objects. Without the knowledge of visual specialization within these activated areas however, they were unable to determine whether the neural machinery for particular visual tasks had been taken over for equivalent tactile tasks.

In the present study, we used functional magnetic resonance imaging to test the hypothesis that the specialized processing capacity of visual areas can be recruited for comparable tactile tasks in the blind. A visual imagery task enabled us to localize specific visual cortical areas in the blind. We employed closely matched experimental tasks to

reveal tactile stimulus-specific activity in three experimental groups: congenitally blind, late-onset blind and sighted subjects.

Methods

Subjects

Three sighted (mean age 25 years, all men), three late-blind (mean age 62 years; mean age at onset of blindness 11 years; all men) and three congenitally blind adults (mean age 21 years; all blind from birth, two women and one man) volunteered and gave informed consent for an experimental protocol approved by a local research ethics committee (Central Office for Research Ethics Committees). All were right-handed and none had any history of neurological disease. The blind subjects had either no or little residual light perception, but certainly no shape perception.

Tasks

Two objects were used as tactile stimuli: a plastic doll's head and a closely matched, unrecognizable 'nonface' object. The doll's head was 20 cm in diameter and accurately represented a female face with skin-like texture. The 'nonface' object, with the same texture and similar features, was made by melting and physically distorting an identical doll's head until it no longer felt like a face. The sighted subjects were not allowed to see either of the objects and were blindfolded during the experiment. All subjects were allowed time to feel both objects before the experiments began. No participant had any difficulty in identifying the doll's head as a face and always perceived the 'nonface' as a meaningless object.

The experiment was split into three sessions. Each began with a 2-min rest period used to establish background noise. In the 'face/nonface' protocol, either the doll-face or distorted object, mounted on a wooden rod, was selected in a pseudorandom order, and placed in the participant's right hand for 15 s. During this time, the object was held steady by the experimenter and the participant was asked to explore it actively (i.e. with the whole palm and moving fingers). Participants were instructed to focus on the tactile impression of the object. In order to discourage visual imagery during this task, we instructed that once the object was removed, they had to imagine touching it while making the same exploratory finger movements for a further 15 s. Each stimulus and imagery block was repeated 20 times.

The 'motion/static' protocol was similar in design except participants were told not to move their hand. The distorted object, held on its rod, was lowered on to the palm of the open right hand. The investigator either pressed it steadily into the palm for 15 s, or moved it around vigorously over the surface of the palm. Participants were again instructed to imagine the same sort of tactile stimulation during the 15 s period after the object was removed, before the next presentation.

The third session (for sighted and late-blind participants only) employed visual imagery in an attempt to localize specific visual areas. Participants were instructed in advance that they would be imagining, visually, a sequence of three scenarios, each lasting 12 s. For the first 12 s, they had to imagine looking at a window with its curtains closed and stationary (pattern imagery); then that the curtains were opening and closing (motion imagery); and finally that the curtains were open and a face was looking in through the window (face imagery). The start of each 12 s period was signalled by taps to the participant's knee. After the three

periods, the participant rested during a final 4 s. The entire 40 s procedure was repeated 10 times for each participant.

Imaging

All scannings were performed at the Functional Magnetic Resonance Imaging of the Brain Centre in Oxford, on a 3 T magnetic resonance imaging system (Oxford Magnet Technology, Oxford, UK). A Magnex SGRAD MK III reduced-bore head gradient coil was used with a birdcage radio-frequency head coil. A whole-brain echo-planar imaging sequence (TR=3 s; TE=30 ms; FOV 64 × 64; 24–27 axial 6 × 4 × 3.5 mm³ slices) was used for both experiments. A T1-weighted high-resolution scan (TR=20 ms; TE=4.6 ms; flip angle=12°; FOV 256 × 256; 64 axial 3 × 3 × 3 mm³ slices) was also acquired for all participants and used to register the echo-planar imaging images to standard Talairach space.

The following prestatistics processing was applied on all individual data sets: motion correction using linear image registration; spatial smoothing using a Gaussian filter with a full-width-half-mean of 5 mm and nonlinear high-pass temporal filtering using Gaussian-weighted least-squares straight line fitting. The first five volumes of functional data were deleted, to allow sufficient T1 relaxation and maximal T2 effects. Individual and fixed-effects group analyses were carried out using general linear modelling analysis employed by the Functional Magnetic Resonance Imaging of the Brain Easy Analysis Tool and MEDx (Sensor Systems Inc., Sterling, Virginia, USA). Z-statistic images from the general linear modeling analysis were thresholded using clusters analysis, for clusters with $Z > 2.3$ and $P < 0.05$ for each participant independently and for groups. In view of the small numbers of participants in each group (owing to limited availability of blind subjects with minimal light perception), we accepted a group result only if they also occurred consistently in each individual participant of the group ($P < 0.05$). This standard provides a strict limit on false-positives, but unfortunately limits the statistical power of our study.

For time-series analysis, the fusiform face area (FFA) was defined in sighted and late-onset blind subjects as the region with significant ($P < 0.05$, corrected) activity during visual face imagery, when compared with pattern imagery of the closed curtains, within a horizontal 1 cm² circle centered on previously published Talairach coordinates for FFA in the right fusiform gyrus (40x, -55y, -10z) [2]. Similarly, hMT/V5 was defined as the region of significant activity during visual motion imagery, compared with static pattern imagery, within a horizontal 1 cm² circle centered on previously published Talairach coordinates (-50x, -70y, 0z) [3]. As motion stimuli were presented to the right hand, we concentrated our analysis on the left hMT/V5. In congenitally blind subjects, we monitored activity in the entire circle used to define the two regions. The initial 2 min rest period of each session was used to establish a baseline blood oxygenation level-dependent (BOLD) signal in these selected regions. Event-related BOLD signal changes are expressed as a percent change relative to this baseline. Differences between conditions (e.g. motion versus static) were determined by comparing peak BOLD signal changes following the onset of either the test or the control stimulus using a paired, two-tailed Student's *t*-test.

Results

In all participants, all forms of tactile stimulation cause activation (both contralateral and, to a lesser extent, ipsilateral to the stimulated hand), in the hand region of the somatic sensory cortex, and in the intraparietal sulcus and the cerebellum ($Z > 2.3$, $P < 0.05$, corrected). In agreement with previous results, even in the sighted subjects, tactile stimulation, compared with rest, results in some activity in the inferior temporal cortex [7–10]. In all the blind subjects, however, there is more widespread activation in the occipital and temporal visual cortex, as previously described ($Z > 2.3$, $P < 0.05$, corrected) [18].

The results of visual imagery in our sighted and late-onset blind subjects enabled us to identify areas of extrastriate cortex activated during specific visual perception, for comparison with the results of tactile stimulation. In both sighted and late-blind subjects, motion and face visual imagery, when compared with imagery of a static pattern, significantly increase activity in highly specific locations – hMT/V5 and FFA, respectively (Fig. 1) ($Z > 2.3$, $P < 0.05$, corrected). We used these results to define the voxels of hMT/V5 and FFA in each of our sighted and late-onset blind subjects, and corresponding regions in the congenitally blind subjects as the basis for region of interest analysis in the remaining experiments (see Methods).

In sighted subjects comparison of tactile motion and face stimuli with their matched stationary and nonface controls reveal no significant activation in either extrastriate visual area (Fig. 2) (paired t -test, $P > 0.80$, $P > 0.30$). In our congenitally blind subjects, the tactile motion/static and face/nonface comparison also reveal no significant increases of activity in the region of hMT/V5 or FFA, respectively (paired t -test, $P > 0.60$, $P > 0.15$). In contrast, late-onset blind subjects show significant increases of activity in hMT/V5 and FFA during tactile motion and face stimulation, respectively, when compared with static and nonface stimuli (paired t -test, $P < 0.01$, $P < 0.05$) (Fig. 2). None of the participants, however, show significant activity in hMT/V5 or FFA during motion or face tactile imagery, when compared with imagination of the static and nonface stimuli.

Discussion

The late-onset blind subjects had years of early visual experience, and could remember real visual experiences, but

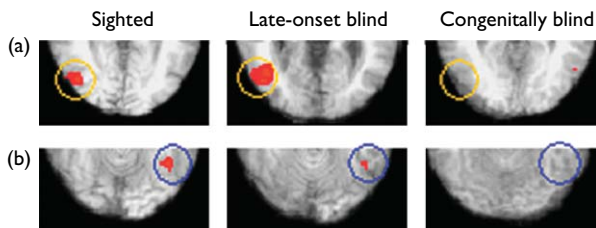


Fig. 1 Visual imagery activates specific extrastriate areas in sighted and late-blind subjects. The panels show horizontal sections of the posterior brain at the levels of area hMT/V5 (a) and fusiform face area (FFA) (b). Orange and blue circles, each 1 cm^2 , are centered on the Talairach coordinates of left hMT/V5 and right FFA. Red areas represent significant voxels of increased activity from group analyses comparing motion and static conditions or face and nonface conditions. Congenitally blind subjects were unable to perform visual imagery and their scans are shown to define respective regions of interest. When sighted and late-onset blind subjects imagined motion and faces, blood oxygenation level-dependent activity increases significantly in left hMT/V5 (a) and in right FFA (b).

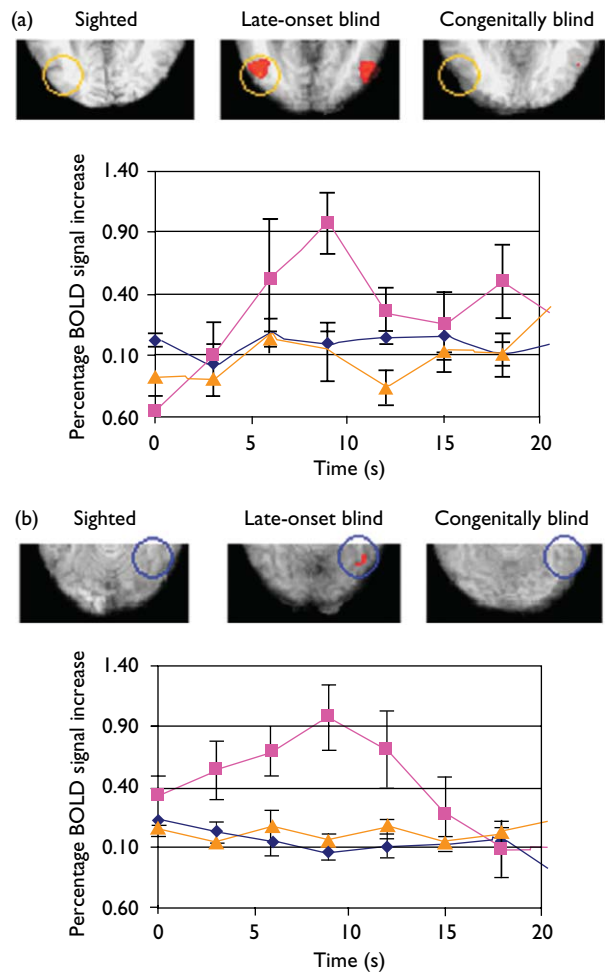


Fig. 2 Tactile discrimination specifically increased extrastriate activity only in late-onset blind subjects. Panels are horizontal sections of the posterior brain from functional magnetic resonance imaging analyses for each group of participants. Red areas represent significant clusters of activity within regions of interest during motion or face stimulation compared with the static or nonface condition, respectively. The graphs below describe average changes in blood oxygenation level-dependent (BOLD) signal intensity during tactile stimulation in the region of interest activated by the corresponding imagery task. BOLD signal change was monitored for each individual separately and then averaged across the sighted (blue diamonds \pm SEM), late-onset blind (pink squares), and congenitally blind subjects (yellow triangles). When participants felt a moving object or actively touched a doll-face (between 0 and 15 s on the abscissa), significant activity occurred bilaterally in hMT/V4 (a) and in right fusiform face area only in late-onset blind subjects (b).

they had all been without vision for at least 20 years. It was, then, a surprise to hear them describe the ease and vividness of their visual imagery and see the strength and spatial precision of their cortical activations (Fig. 1). These results confirm those of De Volder *et al.* [24] and extend it to the imagery of motion and faces. It suggests that visual areas may retain their functional specificity despite decades of blindness.

Our most interesting results came when these participants perceived tactile motion and face stimuli, and these same areas, hMT/V5 and FFA, respectively, were again activated (Fig. 2). The regions in which this activity increased are compact and correspond well with hMT/V5 and FFA defined by the Talairach coordinates from previous studies

as well as by visual imagery in the same participants. In contrast, in sighted subjects and congenitally blind subjects, tactile perception of face and motion stimuli compared with nonface and stationary controls revealed no such localized activity (Fig. 2). This finding is also good evidence that our attempts to discourage visual imagination of the tactile stimuli were successful (see Methods). Further, we questioned the participants closely about their subjective experiences and none of the participants reported imagining the objects visually during the tactile tasks.

It has been suggested that activity in extrastriate areas during tactile tasks represents a shift in modality selectivity of those areas, enabling them to contribute directly to tactile perception rather than visual [5,17]. If that were the case, one might expect these visual areas to be active during tactile imagery. We did not find any significant activity in hMT/V5 or FFA during motion or face tactile imagery, when compared with imagination of the static and nonface stimuli in any of the participants. Our study, however, may not have been powered sufficiently to investigate this.

What we can infer is that when blindness occurs after a period of normal vision, extrastriate areas remain capable of processing specific visual features via imagery. Meanwhile, the neuronal machinery of these areas also becomes engaged during similar forms of tactile stimulation. Some cross-modal process beyond visual imagery is likely to explain this effect. Participants who are becoming blind may initially supplement their rudimentary visual percepts with visual imagery as they manipulate objects, resulting in the coactivation of somatosensory and correlated visual areas. Such conjunctions of activity might gradually strengthen cross-modal connectivity. In fact, a recent study demonstrated that repetitive transcranial magnetic stimulation applied over somatosensory cortex causes greater activity in striate and extrastriate areas in blind individuals than in the sighted [25].

Conclusion

We conclude that in blind persons who have had early visual experience, extrastriate visual areas not only maintain their visual processing capabilities, but engage during tactile stimulation as well. Such cross-modal processing does not appear to require visual imagery, and likely involves direct connectivity between those areas that are directly involved with visual and tactile processing.

Acknowledgements

We thank Paul M. Matthews and Peter Hobden, for their guidance in using the magnetic resonance imaging scanner at the Oxford Centre for Functional Magnetic Resonance Imaging of the Brain. We are especially grateful for the time and energy given by our participants, including blind students from the Royal National College of the Blind in Hereford, UK, who were kindly recruited by Jenny Bradley.

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