

# NEURAL MECHANISMS FOR PERCEPTUAL PERMANENCY: AN fMRI STUDY OF THE TUNNEL EFFECT

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## Introduction

Gestalt psychology, founded by Max Wertheimer, is based on the observation that we have a strong tendency to experience the structured whole with individual perceptual components as parts related to it. From phenomenal observations that most perception depends on whole stimulus configuration, Gestalt psychologists consider that this organization is the result of a perceptual organization mechanism operating at a very low level on the stimulus. Wertheimer (1912) performed a series of experiments on stroboscopic movement. One observation from these experiments is what is known as the “tunnel effect”.

When an object moving gradually disappears behind an occluder (the ‘tunnel’) and the object later emerges, we often irresistibly perceive the continuous motion of a single persisting object. This perceptual phenomenon is called ‘the tunnel effect’ (Wertheimer, 1912; Michotte, 1963). One intriguing aspect of the tunnel effect (TE) is the fact that very simple displays give rise to surprisingly high-level percepts: although this phenomenon is perceptual in nature in the sense that it is fairly fast, automatic, irresistible and highly stimulus driven, it yields the impression of phenomenal permanence, which is typically associated with higher-level cognitive processing (Piaget, 1954). Phenomenal permanence refers to the experience that objects persist through space and time although their presence in the visual field may be discontinuous. There are auditory analogues of the TE: if we substitute part of a long tone with white noise, we hear a continuous tone behind the noise that surfaces uninterrupted at the start and the end of the noise (Vicario, 1960). Michotte (1963) showed that the phenomenon of permanence occurs in a large class of perceptual phenomena such as amodal completion, the screen effect (perception of continuity in spite of partial occlusion), the TE, and the stroboscopic effect. This phenomenal categorization suggests that a single perceptual mechanism may be the basis of these phenomena.

This study focuses on to what degree the TE phenomenon reflects modular processing of the human visual system, using fMRI measurement. Recent transcranial magnetic stimulation (TMS) studies have provided evidence to support the role of V1 activity in visual awareness of motion (Pascual-Leone and Walsh, 2001; Silvanto et al., 2005). There is compelling evidence that response properties of V1 neurons can be dynamically modulated by stimulus context (Kapadia et al., 1995; Knierim and van Essen, 1992; Lamme, 1995; Li et al., 2000; Zipster et al., 1996; Lamme and Spekreijse, 2000). The dynamic properties of V1 neurons suggest direct involvement of V1 in analyzing more complex features of the visual environment and in mediating

higher-order cognitive influences. In order to address whether V1 is active during the visual experience of the TE, the fMRI procedure was designed to functionally separate circumscribed retinotopic positions. The fMRI localizer technique was used to identify specific positions in the retinotopic area of V1, where amodal perception of an object took place only on the basis of emerging parts of the 'hidden' object.

## Materials and Methods

### *Subjects*

Sixteen normal subjects (twelve men and four women) took part in this study. All subjects had normal or corrected-to-normal vision.

### *Visual Stimulation*

Visual stimuli were projected on a screen positioned 19 cm in front of the subject's eyes using a color LCD projector (U2-X2000 Plus Vision, Japan; 1024 x 768 pixels, 60 Hz refresh rate) driven by a PC computer (N800w, HP, Japan). The stimulus display inducing the TE stimulus, the control stimulus and localization stimulus are shown in Fig. 1. In the tunnel event, checkered sectors were in motion (112.5deg/sec) and emerged on a spatiotemporally continuous trajectory. The checkered sectors rotated in a clockwise direction. In the control condition, the standing checkered sectors flickered (5Hz) at locations that alternated every 3.2 sec. The control condition was similar to the features of the TE stimulus in terms of temporal frequency and the time over which each point in the visual space was stimulated. A colored point was continuously presented at the center of the stimulus field. In all experimental sessions, the fixation task was designed to maintain central fixation (Somers et al., 1999). Subjects were instructed to continuously fixate on a central point visible throughout the experiment and to press a button when the color of the center point temporarily changed to red. As the timing of the color change was randomized, the subject concentrated on the fixation point.

### *Design of fMRI measurements*

First, a block design paradigm was used to determine the cortical areas dedicated to the perception of the TE, preventing contamination by spreading neural activity. Observers viewed the alternation between the tunnel event and control condition (Fig. 1b). We confirmed that subjects easily perceived the TE for our stimulus display while they performed the fixation task in a preliminary experiment. In the scanning session, after 10-sec adaptation to a uniform field, subjects viewed alternation between the two displays. Each run consisted of six 16-sec tunnel-effect blocks and six 16-sec blocks of the control condition. The sixteen subjects underwent three runs.

Second, the localizer technique was used to determine circumscribed retinotopic areas in V1. After 10-sec adaptation to a uniform field, subjects viewed two alternating localizer stimuli, shown in Fig. 1d. Each run consisted of six 16-sec target blocks and seven 16-sec non-target blocks. The sixteen subjects each underwent two runs.

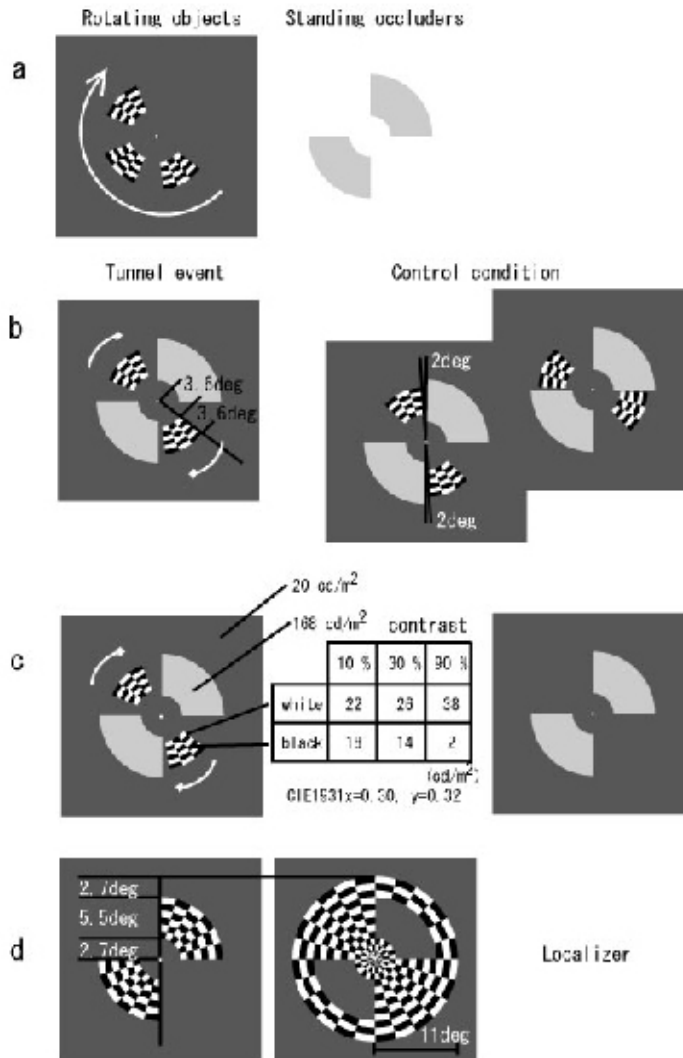


Figure 1. The paradigm and stimuli used in this study.

(a) A display of the TE. Three black-white checkered sectors were in motion (112.5deg/sec), rotating around a fixation point at the center of the field. When the checkered sectors were in contact with one of two standing sectors, they progressively disappeared. After a period of time, the checkered sector reappeared on the opposite side, in motion on a spatiotemporally continuous trajectory at the same speed.

(b) Stimuli used for the block design. The left panel shows a TE display. The right panel shows a display of the control condition, where two checkered sectors flickered at locations adjacent to the standing grey sector.

(c) The stimulus employed for the measurement of the contrast response function. The TE display was alternated by a display consisting of the occluder only.

(d) Localizer stimulus. The circumscribed stimulus corresponded to the area of the occluder in the TE display. Three colored checks (black & white, red & green, or blue & yellow) alternated every 2 sec, while the sign of the color contrast was reversed at a rate of 3 Hz.

Third, in order to reveal the stimulus response properties of the neural mechanisms underlying the perception of the TE, we performed parametric fMRI measurements varying stimulus contrast systematically. Contrast response functions were measured using a block design alternating tunnel-event condition and control condition periods, as shown in Fig. 1c. Each run consisted of six 16-sec tunnel-event blocks and seven 16-sec blocks of the control condition. The sixteen subjects underwent two runs.

### *Image acquisition*

Subjects were scanned in a 3 T whole-body MRI scanner (MAGNETOM Trio, Siemens; Erlangen, Germany) with an 8-channel phase-array whole head coil. To minimize head motion, a head restraint system was used. Changes in blood oxygen level-dependent T2\*-weighted MRI signals were measured using echo planar imaging (TR = 2000ms, TE = 30ms, FA = 90 deg; FOV = 192mm, 64 x 64 matrix, 3-mm slices with 3 x 3mm in-plane resolution, 32 axial slices). Thirty-two slices covering the whole brain were acquired. We also performed a high-resolution T1-weighted (IR gradient echo) sequence in order to acquire accurate anatomical information. High-resolution spoiled gradient recalled echo structural images were also acquired at the same locations using the T1-weighted spin echo pulse sequence (TE = 12 ms, TR = 888 ms, FA = 83deg, FOV = 192mm, 256x256 matrix, 3-mm slices with 0.75x0.75 mm in-plane resolution, 32 axial slices) for anatomical registration. In a separate session, high-resolution full-volume structural images were obtained, using fast SPGR imaging (TE = 4.38ms, TR = 2000ms, FA = 8 deg, FOV = 240mm, 256x256 matrix, 1-mm slices with 0.5 x 0.5 mm in-plane resolution). These T1-weighted images provided detailed anatomical information of registration.

### **Data analysis**

#### *ROI analysis and Group analysis*

The fMRI data were analyzed using statistical parametric mapping (SPM2) software (the Wellcome Department of Imaging Neuroscience, London, UK: [www.fil.ion.ucl.ac.uk/spm](http://www.fil.ion.ucl.ac.uk/spm)) running in the MATLAB environment (Mathworks, Inc., Sherborn, MA).

In V1-ROI analysis, after removal of the first 5 scans, all functional images were realigned. High-pass filtering (2x Experimental period = 64sec) removed low-frequency drifts from the signal. Spatial smoothing was not used for V1-ROI analysis. Voxels responding to the occluder stimulus were identified using a general linear model (GLM) contrast of difference between the localizer corresponding to the occluders and the control stimulus covering the rest of the visual field ( $t$  statistics with a threshold of  $P < 0.00001$  (uncorrected)). The V1-ROI was identified as a cluster of activated voxels (more than 20 voxels connected spatially) in the calcarine sulcus of each hemisphere. The statistical model (GLM contrast of difference between the tunnel event and control condition) was then applied using the MarsBar tool (Brett et al., 2002), and the voxels activated ( $p < 0.001$ ; uncorrected) by the display of the tunnel event were extracted.

Group analysis was performed to identify anatomical areas of consistent activation

across subjects. After removal of the first 5 scans, all functional images from different scans within the same session were aligned with each other. Subsequently, they were spatially normalized into standardized neuroanatomical space (EPI.mnc) and smoothed ( $7 \times 7 \times 7$  mm<sup>3</sup> FWHM Gaussian kernel). Using the analytical technique of subtraction for data from the block design experiment, statistical maps were generated for each subject. Differential activations between the tunnel event and the control condition were tested in second-level analysis (random effect design). Activation loci were defined as contiguous regions of voxels surpassing the minimum statistical threshold of  $P < 0.001$  (uncorrected). On the basis of these data, regions of interest, except for V1, were selected. A cluster made up of at least 20 voxels was considered.

### *Surface-based analysis*

To identify the retinotopic areas of the visual cortex, we carried out fMRI scans while subjects viewed phase-encoding stimuli. The retinotopic areas were determined by analyzing data from fMRI scans using phase-encoding stimuli and a standard procedure (DeYoe et al., 1996; Sereno et al., 1995; Engel et al., 1997; Ejima et al., 2003). Activation loci for localizer stimulus and for the TE were determined by the following procedure. **The set of functional MRI scans acquired was spatially realigned and/or normalized to match the individual reconstructed cortical surfaces (Ejima et al., 2003). The linear trend and baseline offset for each voxel time series were first removed.** Activation significance ( $p$ ) values were computed on a voxel-by-voxel basis comparing the Fourier domain amplitude of the voxel time course at the stimulation frequency and average amplitude of the response at other frequencies. All voxels retained by  $F$  statistics limit criterion ( $p = 0.001$ ) displayed some activation consistent with the stimulus.

## **Results**

Table 1 shows the percentage of activated voxels within the occluded-area V1 ROI corresponding to occluders for 16 subjects. The pattern of activation observed for the localizer stimulation, quadrant activation of mid-eccentricities, indicates that subjects generally held central fixation well. We compared the effect of visual stimulation between the tunnel event and the control, and extracted the percent of activated voxels for the TE within the occluded-area ROI for each hemisphere. Despite individual differences, 4.5 % ( $p < 0.001$ ) or 10.0% ( $p < 0.01$ ; )(average across subjects) of the voxels within the occluded area showed significant activation during TE perception. Thus, we may say that V1 is activated corresponding to the amodal perception of a 'hidden' object behind the occluder.

**Table 1 The percent of activated voxels for the TE from V1- occluded-area ROI**

| Subject       | Left-V1-ROI<br>(occluded area)<br>% |         | Right-V1-ROI<br>(occluded area)<br>% |         |
|---------------|-------------------------------------|---------|--------------------------------------|---------|
|               | p<0.01                              | p<0.001 | p<0.01                               | p<0.001 |
| 1             | 1.4                                 | 1.4     | 22.8                                 | 12.7    |
| 2             | 10.3                                | 8.6     | 18.2                                 | 12.1    |
| 3             | 0.0                                 | 0.0     | 3.9                                  | 1.3     |
| 4             | 3.6                                 | 0.0     | 5.3                                  | 3.4     |
| 5             | 14.7                                | 2.9     | 2.3                                  | 0.0     |
| 6             | 24.3                                | 4.3     | 37.0                                 | 21.0    |
| 7             | 1.8                                 | 0.9     | 1.8                                  | 0.9     |
| 8             | 25.0                                | 10.0    | 13.3                                 | 6.6     |
| 9             | 31.6                                | 18.4    | 14.3                                 | 7.1     |
| 10            | 0.0                                 | 0.0     | 23.8                                 | 9.5     |
| 11            | 0.0                                 | 0.0     | 0.0                                  | 0.0     |
| 12            | 4.2                                 | 2.6     | 2.1                                  | 2.1     |
| 13            | 0.0                                 | 0.0     | 7.4                                  | 0.0     |
| 14            | 0.0                                 | 0.0     | 6.0                                  | 0.0     |
| 15            | 10.5                                | 1.9     | 7.4                                  | 1.8     |
| 16            | 3.3                                 | 3.3     | 23.1                                 | 11.4    |
| mean          | 8.2                                 | 3.4     | 11.8                                 | 5.6     |
| grand<br>mean | 10.0 (p<0.01)                       |         | 4.5 (p<0.001)                        |         |

To confirm that activation in the region along the calcarine sulcus was ascribed to the representation of the hidden object, we carried out surface-based analysis. Figure 2 shows brain activities during localizer stimulation (left panels) and TE stimulation (right panels). The regions of the stimulus-related activation were mapped on the reconstructed surface from the right hemisphere for two subjects (at  $p = 0.001$  significance level). For localizer stimulus, confined activation corresponding to the occluder stimulus (located in the third quadrant in the visual field) was observed in V1d. For the TE, activation corresponding to the occluder stimulus area was clearly observed in V1d. Activation in V3v (upper subject) and V3d (lower subject) can be seen. This result suggests that V1 activity may represent the hidden object in TE perception.

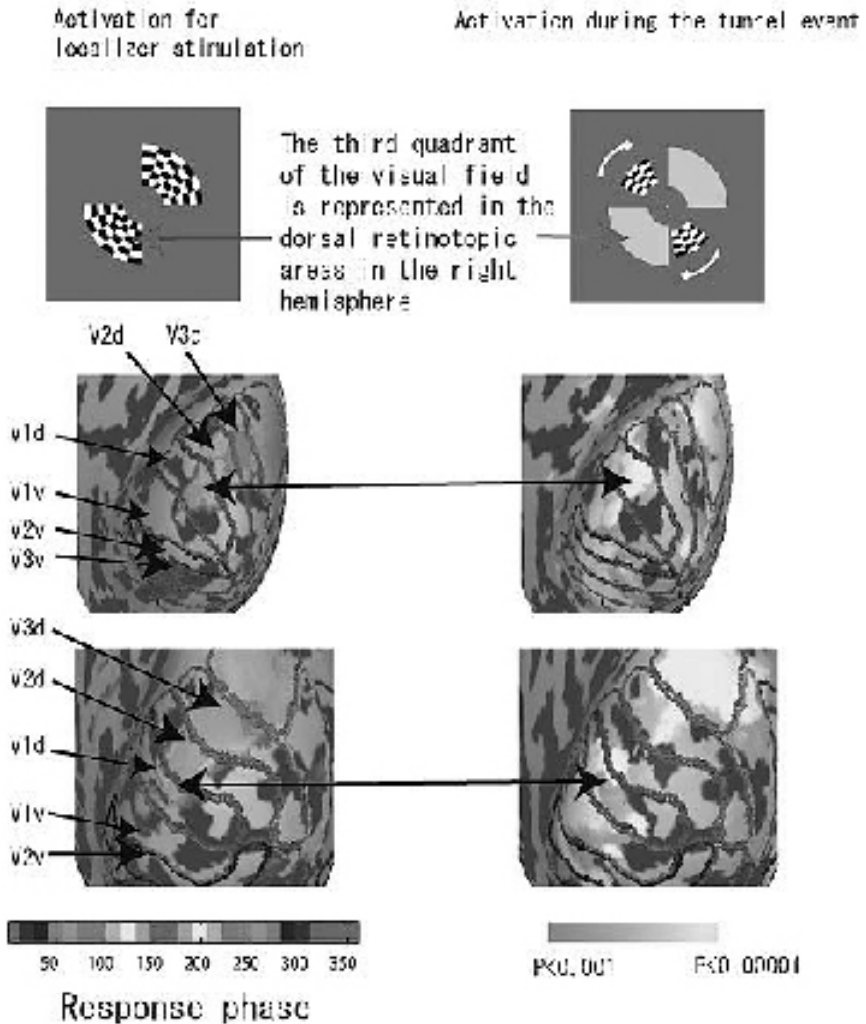


Figure 2. Representative cortical activation patterns in right dorsal V1 evoked by the localizer (left panel) and the tunnel event (right panel). V1d activation during TE perception is observed in the region corresponding to occluder stimulus, indicating the representation of 'hidden sectors' under occlusion (The figure can be seen on <http://www.cis.kit.ac.jp/~gert/2008-GT-YTO.html>).

Although it was difficult to find a direct link to the perception of the TE in higher-order visual areas (lacking a clear retinotopy), we tried to identify cortical areas involved in the visual processing of the kinetic stimulus evoking the TE by computing contrast images between the tunnel event and the control (a random effect design). Figure 3 shows statistical parametric maps. Differentially activated structures ran from the occipital cortex (V1/V2) through the lateral occipital region and the middle temporal areas bilaterally. The other regions differentially activated were the bilateral intra-parietal regions. The activation locus in the middle temporal area is considered

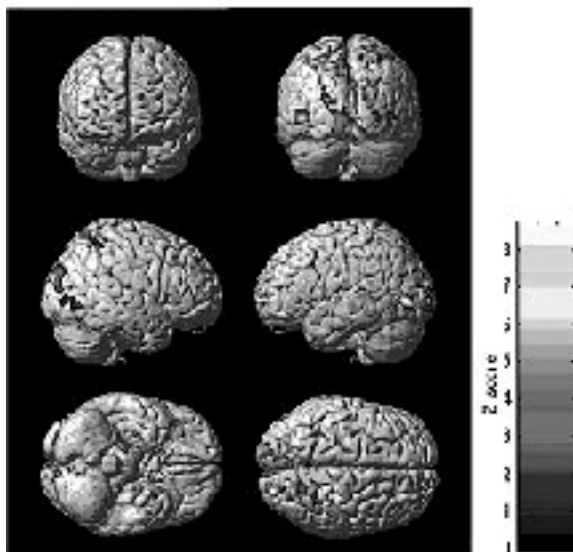


Figure 3. Group (n=16) statistical parametric map indicating voxels for which hemodynamic changes were larger in the TE condition than in the control. The images were put to threshold at  $p < 0.001$  uncorrected for multiple comparison at the voxel level. This contrast revealed significant peaks in V1 along the calcarine sulcus, in the middle temporal region (MT) --Talairach coordinates, x,y,z = -44, -76, 2 and 46, -68, -2) -- in the lateral occipital region (KO) (x,y,z = -20, -94, 16 and 24, -90, 12) and in the intra-parietal region (x,y,z = -20, -70, 56 and 28, -58, 54) (The figure can be seen on <http://www.cis.kit.ac.jp/~gert/2008-GT-YTO.html>).

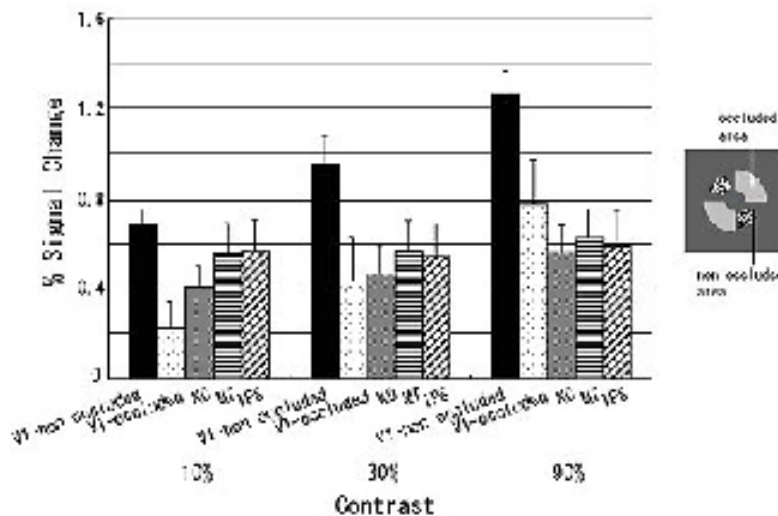


Figure 4. Contrast response functions derived from fMRI measurement. The percent signal change is plotted against the contrast of the checkered sectors. The result shows averaged data from 16 subjects in the areas of non-occluded-area V1, occluded-area V1, MT, KO and the intra-parietal region. SE bars are also shown.



to be MT. The locus in the lateral occipital region was more posterior and medial than MT and close to V3/V3A. This activation area seems to be the kinetic occipital region (KO) (Oostende et al., 1997; Dupont et al., 1997; Tyler et al., 2006). Note here that the activated cortical regions were motion areas along the dorsal visual pathway, no significant differential activation was obtained along the ventral stream.

To address the question of whether the activation of visual areas during perception of the TE changed depending on the image contrast, we obtained the contrast response function for the occluded-area ROI and non-occluded-area ROI in V1, identified by localizer stimulation, and the other activated visual areas shown in Fig. 3. Figure 4 shows the contrast response functions. The percent signal change is shown as a function of contrast of the checkered sector for five visual areas. Increase in stimulus contrast produced a dissociative effect between V1 and higher visual areas. One-way ANOVA for each of the five areas showed that the effect of contrast was significant for non-occluded-area V1 ( $F(2,45) = 28.6; p < 0.001$ ), occluded-area V1 ( $F(2,45) = 10.6; p < 0.001$ ), and KO ( $F(2,45) = 3.32; p < 0.05$ ), whereas it was above significance level slightly for MT ( $F(2,45) = 0.56; p = 0.57$ ) and markedly for the parietal region ( $F(2,45) = 0.16; p = 0.85$ ). The response of the occluded area V1 may be correlated with the amodal perception of a 'hidden' checkered sector, while the response of the non-occluded area V1 may be correlated with the perception of the real object. In both areas, the stimulus produced a linear increase in fMRI signal amplitude with increasing log contrast of the stimulus (10, 30, and 90%). The signal amplitude was much less for the occluded than non-occluded area. In MT, no significant increase was observed across the contrast range tested and this may be ascribed to saturation. The difference in the contrast response function between MT and V1 is consistent with the existing findings that MT activity is saturated at low contrast levels, while V1 activity is increased as a function of log contrast (Tootell et al., 1995; Avidan et al., 2002). In KO, the fMRI amplitude progressively increased with stimulus contrast, although much less than in V1. In the intra-parietal region, the fMRI signal amplitude did not depend on stimulus contrast. This dissociation between contrast response properties of early visual areas and higher-order visual areas provides an important control against non-specific and general arousal effects.

## **Discussion**

Our results demonstrate that V1 activity corresponds to the amodal perception of a 'hidden object', leading to the identification of objects as the same persisting individuals under occlusion. We found that increased stimulus contrast led to a corresponding increase in V1 activity. The role of V1 in perceived contrast and/or brightness remains controversial (Haynes et al., 2004; Cornelissen et al., 2006; Mendola et al., 2006), but the contrast dependence of V1 activity indicates that it may be tightly related to the feature of object contrast in the TE. Thus, we can say that V1 contributes to the representation of hidden objects to allow for high-level cognition of phenomenal permanence in the TE. Our finding of V1 and MT activation during TE perception provides further support for the results of TMS studies that V1 activity is tightly correlated with visual awareness of motion.

It may be argued that the increase of V1 activity during the perception of the TE reflects attention to the occluded areas rather than the representation of a 'hidden object'. There is extensive evidence that the magnitude of brain activity to a visual stimulus in the human striate cortex can be modulated by attention (Somers et al., 1999; Brefczynski and DeYoe, 1999; Martinez et al., 1999; Posner and Gilbert, 1999; Smith et al., 2006). When an object moves in the visual field, it attracts the observer's attention. However, the fact that brain activity in the V1-occluded-area ROI strongly depended on the stimulus contrast suggests that the signals reflected a response to the 'hidden object' itself. Somers and McMains (2005) showed that effects of attention were constant across all contrast levels and that they did not increase with contrast. Our finding of the linear increase of the BOLD signal with increasing contrast of objects in the V1-occluded-area ROI cannot be accounted for by the effects of attention; therefore, it seems unlikely that the increase in activity during the perception of the TE reflects merely an attentional bias.

Another possibility is that the activity increase in the V1-occluded-area ROI during perception of the TE reflects negative BOLD, resulting from "blood stealing" or from decreased neuronal activity. Several fMRI studies have demonstrated that when an observer viewed a flickering checkered pattern in an otherwise uniform grey visual field, the robustly sustained negative BOLD (NBR) was adjacent to the region of activation (positive BOLD, PBR) in V1 (Smith et al., 2004; Shmuel et al., 2002; Shmuel et al., 2006). Our results clearly show that activation increases extend in the non-occluded areas of V1 during perception of the TE (Figs. 2 and 3). This implies that activation (PBR) due to flickering sectors in the non-occluded area adjoining to the occluded area was significantly larger during perception of the TE than during the control condition. Thus, the effect of negative BOLD, if it exists, should serve to rather reduce the activation in the occluded area during perception of the TE than during the control condition. Activity increases during perception of the TE cannot be ascribed to artifacts of the subtraction method resulting from negative BOLD.

In the TE, phenomenal permanence can be obtained by a simple display but there is a precise condition: slight manipulation of the display concerning the spatiotemporal continuity of trajectory can cause the perception of permanence to disappear. The TE occurs even when pre- and post-occlusion views have distinct visual features, so long as the perceived trajectory is spatiotemporally consistent. This property resembles that of the perceptual reconstruction of path-guided apparent motion, in which observers perceive a circularly moving object when several stimuli are flashed successively. Merchant et al. (2005) found that populations of area 7a macaque neurons could accurately reconstruct the circular trajectory of real moving stimuli, showing a strong correlation between neurophysiological and psychophysical responses to path-guided apparent motion. This finding, together with our finding that intra-parietal cortical regions are significantly activated during TE perception, suggests that the posterior parietal cortex is part of a higher-level system that is directly involved in the dynamic representation of complex motion in motion kinematics. Our finding that visual areas along the dorsal, but not ventral, stream were differentially activated during TE perception indicates a clear separation of motion processing from shape processing in the human visual cortex. Visual processing in the dorsal stream may

be linked to cognition of phenomenal permanence, while visual processing in the ventral stream may be linked to cognition of object categories.

There is cumulative evidence that the modulatory influence of stimuli placed outside the receptive field of V1 neurons constitutes a powerful force in the primary visual cortex (Kapadia et al., 1995; Knierim and van Essen, 1992; Lamme, 1995; Li et al., 2000; Zipster et al., 1996; Lamme and Spekreijse, 2000). Representation in the V1 is precise in the space domain because the receptive fields are small and arranged in retinotopic coordinates. The proposed hypothesis is that higher-order inference that relies on information with spatial precision and fine details necessarily engages early visual areas (Lee, 2003). It is also suggested that center-surround modulation in the spatial-temporal domain in V1 could play a role in the facilitation or extrapolation of continuous trajectories (Series et al., 2003). Note that contextual modulation typically evolves only after the initial transient response. One possible interpretation of our data is that delayed feedback, manifesting itself in contextual modulation, would permit V1 access to perceptual interpretations of the visual scene such as object or surface representations of the distal world, ascribed previously only to higher-order cortical areas. V1 seems to provide the highest resolution map for spatial localization of a “hidden” object.

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### **Summary**

In natural scenes, the visual system requires a task that identifies moving objects as the same persisting individuals over space and time under various occlusions. This fMRI study explores how the visual system manages this task using a new variant of the ‘tunnel effect’. We identified the activation of the striate cortex (V1) corresponding to the amodal perception of a ‘hidden’ object, which showed stimulus contrast dependency. We also found that visual areas along the dorsal stream, from V1 through the middle temporal (MT) and lateral occipital (KO) regions to the intra-parietal regions, were activated for kinetic stimulus of the tunnel effect. V1 could function as a ‘master map’ to integrate motion information across multiple areas of MT, KO, and the intraparietal region.

**Keywords:** tunnel effect; amodal completion; V1; visual cortex; fMRI; motion.

### **Zusammenfassung**

Im Alltag häufig auftretende Verdeckungen stellen das Sehsystem vor die Aufgabe, die dahinter bewegten Objekte über Raum- und Zeitlücken hinweg als gleichbleibend zu erfassen. Mittels funktioneller Magnetresonanztomographie (fMRT; bildgebendes Verfahren, das

aktivierte Hirnstrukturen beim Menschen mit hoher räumlicher Auflösung erfasst) wurde erkundet, wie das Sehsystem diese Aufgabe löst. Mit einer neuen Variante des „Tunnel-Effekts“ als Reizmuster gelang es, Aktivierungsmuster in der primären Sehrinde (V1) zu identifizieren, die der amodalen Wahrnehmung eines verdeckten Objekts entsprachen. Tunnel-Effekt spezifische Aktivierung zeigte sich auch in weiteren Hirnarealen entlang der dorsalen Sehbahn: mediotemporal (MT), okzipital (KO), intraparietale Bereiche. Eine die Bewegungsinformationen dieser Hirnareale integrierende Ortsbestimmung erfolgt vermutlich in V1.

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