Cortical responses to invisible objects in the human dorsal and ventral pathways

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The primate visual system is believed to comprise two main pathways: a ventral pathway for conscious perception and a dorsal pathway that can process visual information and guide action without accompanying conscious knowledge. Evidence for this theory has come primarily from studies of neurological patients and animals. Using fMRI, we show here that even though observers are completely unaware of test object images owing to interocular suppression, their dorsal cortical areas demonstrate substantial activity for different types of visual objects, with stronger responses to images of tools than of human faces. This result also suggests that in binocular rivalry, substantial information in the suppressed eye can escape the interocular suppression and reach dorsal cortex.

The theory that the ventral pathway is primarily dedicated to processing object identities and the dorsal pathway is specialized for visually guided actions has received strong support from both animal research[1] as well as neuropsychological studies on patients with localized brain damage[2]. One of the hallmarks of the two-pathway theory is that the function of the dorsal pathway is not dependent on observers' explicit perceptual experience of the visual input. In other words, the dorsal pathway can process the incoming information in a functionally appropriate way even when the observer is not perceptually aware of the visual information. Perhaps the best support for this idea came from the studies on patient DF, who had suffered severe bilateral damage to her occipitotemporal visual area (the 'ventral pathway')[3]. Despite DF's incapability of distinguishing between simple geometric shapes, she was able to use information from objects to guide her hand movements when reaching out and grasping those objects[4]. Similar results have been observed in monkey subjects after bilateral resection of the temporal lobe[5].

Aside from recent behavioral studies that show evidence of a dissociation between conscious perception and visually guided action[6], there is almost no neurophysiological support for the operation of the dorsal pathway in the absence of visual awareness in normal human observers. This is in spite of the enormous amount of functional brain imaging studies in recent years on object-selective properties in normal human observers. These studies show that a host of areas are sensitive to different categories of visually presented objects and scenes, primarily in the ventral pathway[7]. The dorsal pathway also has several object-sensitive areas, including V3A/V7 (ref. 8) and intraparietal sulcus[9–11]. The object-sensitive regions in the dorsal pathway are different from ventral object areas in important functional properties: for example, the dorsal object areas are sensitive to viewpoint change[12] and prefer motion-defined objects[13] and manipulable objects (such as tools)[14].

Consistent with the conventional idea of the ventral pathway's role in supporting conscious perception, neural activity in ventral object areas is correlated with conscious perception in human fMRI (functional magnetic resonance imaging) studies[10,15,16] as well as in monkey single-unit studies[17]. Still, little is known about the role of awareness in the response of the dorsal pathway to objects. In the present study, we examined cortical activity in both the ventral and dorsal regions while observers were presented with pictures of objects. Notably, in some sessions, the object images were rendered invisible through interocular suppression. We found that human dorsal cortical areas responded robustly to object images, especially images of man-made tools, even when they were suppressed and invisible.

RESULTS

Rendering object images invisible

When dissimilar images are presented to corresponding locations in the two eyes, they often compete for perceptual dominance and take turns being visible. One image usually dominates for a fraction of a second to a few seconds while the other is suppressed, and then the perceptual dominance switches. This phenomenon is called binocular rivalry[18,19]. Binocular rivalry provides a useful experimental framework to study the neural correlates of conscious and unconscious visual perception because the stimuli are constantly presented, but perception fluctuates[15,17]. Recently, such an approach has also been adopted in studies of the neural responses to emotional stimuli without awareness[20,21]. The perceptual dominance of one stimulus can be promoted by enhancing its 'strength' (in the form of luminance and contrast, for example) or complexity, or by transient changes or motion[19]. We took advantage of this property of interocular suppression and caused low-contrast, low-luminance object images in the non-dominant eye to be completely suppressed for several minutes by high-contrast, dynamic (10 Hz),

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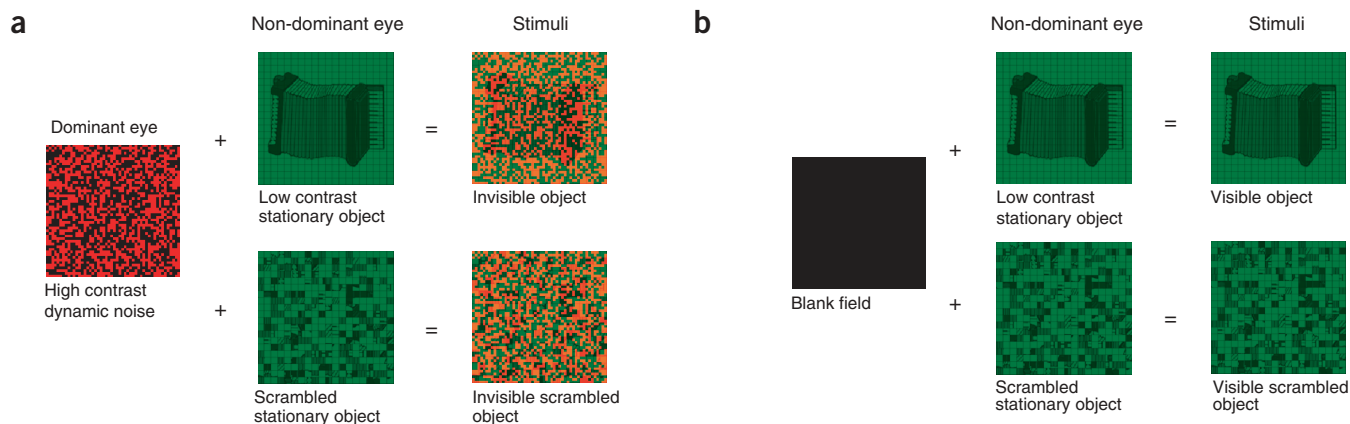
Figure 1 Stimuli and procedure used in experiment 1. (**a**) In the 'invisible' condition, awareness of stationary and low-contrast intact or scrambled objects presented to the non-dominant eye can be completely suppressed by dynamic, high-contrast, random textures presented to the dominant eye. Although the object image in this example may be visible to the reader, observers in our experiment viewed the blended images through a pair of anaglyphic eyeglasses, and the textured noise was dynamic. The 'invisibility' of the suppressed images was validated with objective behavioral experiments. (**b**) In the 'visible' condition, only intact or scrambled objects were presented to the non-dominant eye. (**c**) In both 'invisible' and 'visible' conditions, scrambled and intact object blocks alternated, with 20 s for each. Each block consisted of 50 trials. In each trial, the stimulus was flashed for 200 ms, followed by 300 ms of fixation.

random texture in the dominant eye. This allowed us to measure cortical responses to the invisible object images using fMRI. Activations when the object images were visible were also measured for comparison.

In the fMRI scanner, subjects viewed a composite of red texture and green objects ('invisible' condition, **Fig. 1a**) or green objects alone ('visible' condition, **Fig. 1b**) through red-green anaglyph eyeglasses. The 'invisible' and 'visible' conditions were run in separate scans. In both conditions, scrambled and intact objects were presented in alternating 20-s blocks (**Fig. 1c**) totaling 260 s. In each block, 40 different objects or scrambled objects were presented in rapid succession, with each object on the screen for 200 ms followed by a 300-ms fixation period. The contrast of the object images was adjusted for each individual observer to make sure that the objects were invisible when texture was presented to the other eye but visible when the other eye viewed a blank screen. Subjects were probed after each scan as to whether they saw any objects in the 'noise-on' condition; only two subjects reported seeing a glimpse of an object for a fraction of a second. Data from these two scans (one for each subject) were excluded from further analysis.

Seven of the ten subjects also underwent a 2AFC (two alternative forced choice) discrimination task in separate sessions to check if the suppressed object images were indeed invisible in a criterion-free way. Subjects performed at chance level in determining which of two temporal intervals contained the object images. The results of the 2AFC experiment provided objective support that the suppressed objects were truly invisible (see Methods). For the imaging experiment, the order of the object block and scrambled object block was randomized for each subject but was counterbalanced across subjects. In the 'invisible' condition, subjects were not aware of the order of the object block compared with the scrambled object block. To help subjects maintain their fixation and stay attentive to the visual stimuli, a simple fixation task was used: observers were asked to detect an occasional size change of the fixation point. The same task was performed in both the
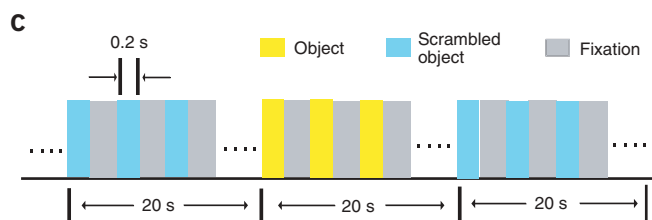
'visible' and 'invisible' conditions. Regions of interest (ROIs) were functionally predefined by a cortical response contrast between intact and scrambled objects that were presented to both eyes. These ROIs responded significantly more strongly to intact objects than to scrambled objects ($P < 0.0001$). The ventral ROIs included lateral occipital cortex (LOC) and part of the anterior fusiform gyrus. The dorsal ROIs mainly consisted of areas V3A and V7 and part of the intraparietal areas (**Fig. 2**; **Supplementary Table 1**).

Experiment 1: objects versus scrambled objects
We first investigated if there was cortical activity in response to objects that were rendered invisible owing to interocular suppression. For each of the eight subjects, we obtained time course data from those predefined ROIs in both the 'visible' and 'invisible' conditions.
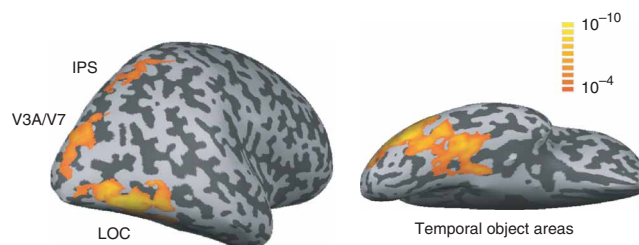

Figure 2 Object-sensitive areas depicted on an inflated brain of a single subject. The statistical map was obtained by contrasting BOLD signals induced from intact and scrambled images of objects. Color bars in the upper right corner show the P values of the contrast between intact versus scrambled objects, with the threshold set at $P = 0.0001$. Identified ROIs consist of V3A/V7, intraparietal sulcus (IPS) in the dorsal pathway and lateral occipital complex (LOC), temporal object areas in the ventral pathway. Activation patterns are consistent within the dorsal and ventral pathway and are collectively reported in the main text. The same right hemisphere is shown in lateral view (left) and in bottom view (right).
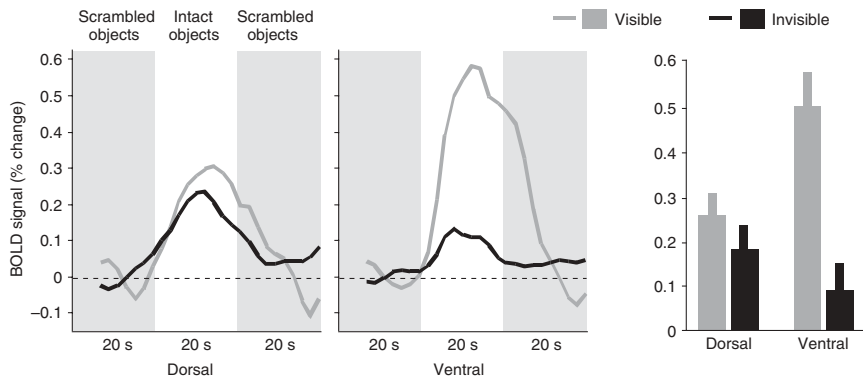
Figure 3 Results from the first experiment showing time courses and the average BOLD signals (percentage change) from dorsal and ventral object sensitive areas in 'visible' (gray curves and bars) and 'invisible' (black curves and bars) conditions. Data (mean ± s.e.m.) were averaged across eight subjects.

Although ventral and dorsal pathways showed different characteristics, ANOVA analysis using ROI and visibility condition as two factors showed that the individual ROIs within each pathway demonstrated similar response patterns. Specifically, two-way ANOVA of ROI (IPS/V3A/V7) × Condition (visible/invisible) in the dorsal pathway showed no main effect of ROI ($F_{1,32} = 0.01$, $P = 0.921$); the difference between visibility conditions was not significant ($F_{1,32} = 2.989$, $P = 0.094$); and there was no interaction between ROI and condition ($F_{1,32} = 0.002$, $P = 0.961$). In the ventral pathway, two-way ANOVA of ROI (LOC/temporal) × Condition (visible/invisible) showed no main effect of ROI ($F_{1,32} = 0.081$, $P = 0.779$); a significant effect of condition ($F_{1,32} = 47.886$, $P < 0.001$); and no interaction between ROI and Condition ($F_{1,32} = 0.059$, $P = 0.81$). Thus, to highlight the difference between the dorsal and ventral pathways, we grouped blood oxygen level–dependent (BOLD) signals from ROIs according to the dorsal and ventral pathways (**Supplementary Fig. 1**).

When the objects were visible (presented to one eye without accompanying random texture in the other eye), the ventral ROIs had very significant activation ($P < 0.0001$; **Fig. 3**). However, when the same objects were suppressed by the dynamic texture from the other eye, the activation in the ventral ROIs decreased markedly to a level that was not much more than the baseline activation from the scrambled objects. In contrast, although the activation level to visible objects in the dorsal ROIs was weaker than that in the ventral ROIs, the dorsal ROIs showed robust activation much higher than in ventral ROIs ($P < 0.01$), when the objects were rendered invisible. The activation levels in the dorsal ROIs showed only a slight reduction from the 'visible' condition to the 'invisible' condition (**Fig. 3**).

Figure 4 Results from the second experiment using images of tools and faces. (**a**) Stimuli (tools and faces) and experimental procedure for experiment 2. Tools and faces were presented in different 20-s blocks interleaved with random texture blocks, as shown at bottom. (**b**) The average percentage change in BOLD signal from the dorsal (top) and ventral (bottom) object-sensitive areas in both the 'visible' and 'invisible' conditions. Data from five subjects (mean ± s.e.m.) are shown for each condition. Both the dorsal and ventral areas responded robustly to visible tools and faces. However, when the images of tools and faces were suppressed by high-contrast dynamic textures, the dorsal response to images of tools remained strong, whereas the dorsal response to invisible images of faces diminished. In the ventral areas, neither invisible tools nor invisible faces evoked appreciable levels of activation.

Experiment 2: tools versus faces

In the first experiment described above, we used diverse categories of objects and demonstrated cortical responses to images of objects in the dorsal pathway even without awareness. One could argue that the differential responses to the objects and scrambled objects reflected differences in image properties (for instance, object images usually contain collinear contours, smooth low spatial frequency regions, etc.) and that the observed dorsal response to the invisible objects might not necessarily mean that object representations are formed. We then asked whether dorsal object-sensitive regions could respond in a category-selective way to objects in the 'invisible' condition. Specifically, in the second experiment, we chose low-contrast face and tool images as object stimuli and low-contrast stationary random textures as baseline stimuli (**Fig. 4a**). As in the first experiment, these images were rendered invisible by pairing them with dynamic random textures presented to the dominant eye. The reason that we selected faces and tools as stimuli is that they have distinct activation patterns across the ventral and dorsal pathways. Cortical face representation has been extensively studied in many different experiments and laboratories[22]. Most of the studies show face-selective regions in the ventral pathway, whereas images of tools strongly activate the human dorsal pathway, especially in the posterior parietal area[14], presumably because the dorsal pathway is important for the preparation of manual control of tools.
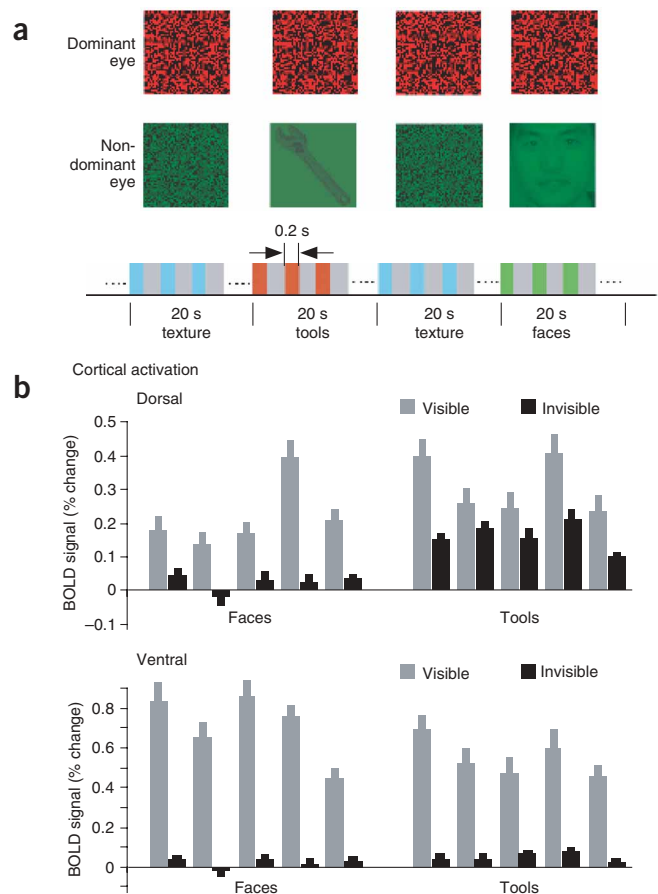
Images of faces and tools were presented to subjects in separate blocks, interleaved with random texture blocks (**Fig. 4a**). Because two-way ANOVA using ROI and visibility as factors again did not show a significant difference between ROIs within each stream, we grouped data into dorsal and ventral streams (**Supplementary Fig. 2**). Data from all five subjects (**Fig. 4b**) clearly and consistently showed that although both dorsal and ventral regions responded robustly to visible images of faces and tools, ventral activation was almost completely abolished when images were suppressed and invisible (**Fig. 4b**, bottom). In contrast, dorsal regions remained responsive to invisible images of tools but not to faces. Two-way ANOVA of the data using object category (face/tool) and awareness condition (visible/invisible) showed that both main effects were significant, in that tool activation was higher than face activation, and activation in the visible condition was higher than that in the invisible condition (object category: $F_{1,20} = 14.045$, $P = 0.002$, tool > face; awareness condition: $F_{1,20} = 30.144$, $P < 0.001$, visible > invisible). However, the interaction between the two factors was not significant ($F_{1,20} = 0.79$, $P = 0.387$). Thus, dorsal cortical areas responded more strongly to tool images than face images when they were visible, and notably, although the subjects could not tell whether the images were faces or tools or even if they were intact, their dorsal cortical neurons still reacted differently to different invisible object images: images of tools induced much stronger BOLD signals in the dorsal ROIs than did images of faces ($P < 0.001$; **Fig. 4b**).

DISCUSSION

Results of the first experiment show that the human dorsal pathway can respond to invisible images in the absence of visual awareness. The second experiment shows that the unconscious response in the dorsal pathway can be elicited only from one of the two groups of object images tested. The dorsal regions are strongly activated by images of tools but not by images of faces. The selective nature of the dorsal activation implies that neurons in the dorsal pathway do not uniformly receive all object information. We speculate that the dorsal activation to tools but not to faces may be partially determined by the important role of dorsal cortex in reaching and grasping. Together, results from both experiments support the idea that activation in the dorsal region in the absence of visual awareness of the input images is linked to the functions of the dorsal pathway. Our results provide a potential neural basis for the neuropsychological observation that some patients can act upon objects appropriately without 'seeing' them.

With the rapid presentation of stimuli, it is possible that an apparent motion signal was generated across presentations. Although it remained invisible to the subjects, this possible apparent motion signal would be stronger for tool images than for face images because face images were less variable in position and size than tool images. One might argue then that the dorsal activation in the invisible condition was due to the stronger motion signal rather than to the form of the images (that is, tools versus faces). Although this is a possibility, it is not consistent with a recent neuroimaging study[23] showing that long-range apparent motion activates regions more anterior and inferior to the dorsal ROIs identified in our study. Nonetheless, to test this possibility, we performed a control experiment on two subjects who also participated in the original set of experiments. In the control experiment, we used 1-s inter-stimulus intervals (ISIs) between image presentations, and face images were made much more variable in size, view and position. This new 1-s ISI removed the potential for apparent motion between successive presentations of object images. The faces varied in size (between 2.5 and 3.5°), view (frontal view and various degrees of side views) and position (randomly distributed within a 5 × 5° area, so

that a particular face image could be in one of the four quadrants, and the next face image could be in a completely different quadrant). Under these conditions, the dorsal pathway remained significantly activated to invisible tool images (now without potential apparent motion), whereas the invisible faces images (now variable in size, view and position) still did not generate significant activation in either the ventral or dorsal pathway. This result was consistent across the two subjects tested (**Supplementary Fig. 2**).

In addition to showing that the human dorsal cortex can process visual information without awareness, we demonstrate that although object images are blocked at the site of interocular competition (generally considered to be V1), this blocked information somehow reaches the dorsal pathway. The current data do not define an exact pathway by which invisible information reaches the dorsal region, but there are two possibilities for how the meaningful object information could escape the interocular suppression and activate the dorsal cortical regions. First, the object information could travel through subcortical pathways (for example, superior colliculus and Pulvinar) and bypass V1 to reach the dorsal regions. Alternatively, part of the information from the suppressed eye might escape the interocular suppression and therefore be transmitted through V1 to the dorsal region. In both cases, the information from the suppressed eye could be represented 'unconsciously' at the input levels of V1, and neither situation is inconsistent with recent neuroimaging studies showing BOLD signal suppression in V1 during binocular rivalry[24–26].

The first hypothesis suggests that the information reaching V1 stops there owing to interocular suppression and that the dorsal pathway instead receives information from subcortical projection. This idea is consistent with the subcortical pathway interpretation of the observations of preserved action in the absence of awareness in some patients[2], and it is also consistent with the dominant view of the phenomenon of blindsight[27]. Indeed, a recent anatomical study showed that there is a direct projection in the macaque monkey from the lateral geniculate nucleus (LGN) to the motion-selective middle temporal area (MT or V5), which belongs to the dorsal pathway[28].

The second hypothesis states that interocular suppression does not completely block cortical information from the suppressed eye and that some information can still 'leak through'. Under this hypothesis, interocular suppression may result in attenuation rather than blocking of the signal (this distinction may be similar to the difference between Treisman's attenuation model and Broadbent's filtering model of selective attention). With regard to the difference between the dorsal and ventral pathways, there is evidence suggesting a differential susceptibility of the magnocellular and parvocellular pathways to interocular suppression. Specifically, information processed in the parvocellular pathway might be more susceptible to interocular suppression, and information processed in the magnocellular pathway might be less so[29]. The object information that reaches the dorsal regions could be processed primarily by the magnocellular pathway, and processing along the parvocellularly biased ventral pathway could be blocked by the interocular suppression. This hypothesis is consistent with the finding that the magnocellular pathway projects more heavily to the dorsal route than to the ventral route[30] and that the activity of many MT neurons is dictated by retinal stimulus rather than perception[31]. One possible prediction based on this hypothesis is that the suppressed information should be able to reach MT. As the current study focused on unconscious object representation, the ROIs were localized on the basis of sensitivity to objects (object versus scrambled object), thus excluding MT. We also contrast tool activation to face activation in the invisible condition using a simple t-test. This analysis shows stronger activation to tools than to faces in the dorsal regions

similar to the dorsal ROIs defined in our study; however, no region near the anatomically defined MT is more active to invisible tools than faces. Furthermore, in the two subjects for whom we have MT localized from other studies, we do not see significant activation differences between the invisible tools and invisible faces or between invisible objects and invisible scrambled objects. We do not find this surprising, as (i) MT is not known for representing objects, and (ii) there was strong dynamic noise coming from one eye regardless of the other eye's input (tool, face or scrambled images), and the dynamic noise was most likely driving the MT activity, which was not significantly different across conditions. Nevertheless, the above discussions of pathways are speculative, and further experiments are needed to clarify the exact pathway for the suppressed object information to reach dorsal regions.

To summarize, this fMRI study provides strong support that in normal human observers, dorsal cortical areas can form representations for selected types of visual objects (for example, images of man-made tools) in the absence of observers' conscious knowledge of the visual input. This result also suggests that in binocular rivalry, substantial information in the suppressed eye can escape the interocular suppression and reach dorsal cortex, possibly through direct subcortical projections or through the magnocellular pathway, which is believed to be less susceptible to interocular suppression.

METHODS

Participants. Eight (four men) and five (three men) healthy subjects participated the first and second experiments, respectively. Two male subjects participated in both. All subjects are right-handed and ranged in age from 22 to 39. They had normal or corrected-to-normal vision and gave written, informed consent in accordance with procedures and protocols approved by the human subjects review committee of the University of Minnesota.

Localizer and rivalry experiments. For retinotopic mapping, subjects viewed two types of retinotopic mapping stimuli[32,33]. The first were counter-phase (8 Hz) checkerboard wedges of 12° located at the horizontal and vertical meridians. These served to map boundaries between visual areas. The second were foveal (2° in diameter) and peripheral (9°) counter-phase (8 Hz) annuli that served to map the retinotopic extent of each area. Two retinotopic mapping scans were performed: one that alternated the horizontal and vertical meridian stimuli and one that alternated the foveal and peripheral ring stimuli. In both scans, stimuli were presented in 20-s blocks with seven alternations between conditions. For object-sensitive area localization, subjects viewed alternating 20-s blocks of scrambled and intact objects. The scrambled objects were made by segmenting the object images into a 20 × 20 square grid and randomly rearranging the grid elements. Each scrambled/intact object extended ~10 × 10° and was presented for 1 s.

In the first rivalry experiment, subjects viewed alternating 20-s blocks, totaling 260 s, of scrambled and intact objects in both 'visible' and 'invisible' conditions. Scrambled and intact object images were the same as those used in the object area localizer, but with low contrast, low luminance and smaller size (~5 × 5°). The temporal frequency of the dynamic texture was 10 Hz, and each pixel making up the texture were approximately 0.1 × 0.1°. Each temporal block consisted of 40 trials. In each trial, the stimulus was flashed for 200 ms, followed by 300 ms of fixation. In the second experiment, tool, face and texture blocks replaced scrambled and intact object blocks. In both experiments and conditions, subjects were asked to detect an occasional (about every 8 s) ninefold size change of the fixation point. Functional scans in the 'visible' and 'invisible' conditions were run 2–3 and 4–6 times, respectively. After each functional scan in the 'invisible' condition, subjects were asked to report if they perceived any shape or object. If they did, data from this scan were discarded. In our experiments, object images were suppressed by dynamic textures very well. Only two subjects reported seeing a glimpse (<1 s) of a vague shape, although they could not name it. Data from these two scans were excluded from further analysis.

Because the interpretation of the study depends critically on the suppressed images being truly invisible, we also tested the invisibility of the suppressed

images in a more objective 2AFC experiment. Seven out of the ten subjects who participated in the fMRI experiments also participated in the behavioral 2AFC experiment in the scanner in separate sessions. The experimental situation (contrast, luminance, viewing angle, etc.) was exactly the same as in the functional imaging experiments. Intact object images and scrambled controls used in the 'invisible' condition of imaging experiments were presented in two successive temporal intervals (200 ms each, with a 300-ms blank gap between them). The intact object could be presented in the first or the second interval. Observers pressed one of two buttons (2AFC) to indicate whether the object was presented first or second. Each observer performed 500 trials. The percentage correct was 0.4963 ± 0.006582 (mean ± s.e.m., $n = 7$), which is not significantly different from chance ($t_6 = 0.564$, $P = 0.593$). Although it is reassuring that the observers performed at chance level in the 2AFC task, we thought it was also informative to know their subjective perception during the behavioral experiment. Thus, we also asked them to press a third key if they felt that they saw an object in any trial. In total of 3,500 (500×7) trials, there were only three trials (one trial from one observer and two trials from another observer) in which observers claimed that they detected objects, although they could not name them.

fMRI data acquisition. In the scanner, the stimuli were back-projected by means of a video projector onto a translucent screen placed inside the scanner bore. Subjects viewed the stimuli through a mirror situated above their eyes. Structural and functional MRI data were collected using a Siemens 3-T Magnetom TRIO scanner with an eight-channel phase array surface coil. BOLD signals were measured with an EPI (echo-planar imaging) sequence (TE: 30 ms, TR: 2000 ms, FOV: 22×22 cm^2, matrix: 64×64, flip angle: 75°, slice thickness: 5.0 mm, number of slices: 20, slice orientation: axial) when subjects were performing the experimental tasks. The scans for retinotopic mapping were run in a different session in the same scanner.

Data analysis. The imaging data were processed using BrainVoyager (Brain Innovation). The anatomical volumes were transformed into a brain space that was common for all subjects[34] and then inflated. Functional volumes for each subject underwent preprocessing, including three-dimensional motion correction, slice scan time correction, linear trend removal and temporal frequency filtering between 3 and 60 cycles per scan. Correlation analysis was performed on the localizer data to define object-sensitive areas ($P < 0.0001$, uncorrected). The spatial position of V3A/V7 was further confirmed by retinotopic mapping.

The first 12 s of BOLD signals in each scan were discarded to minimize transient magnetic saturation effects. The remaining data were grouped according to different pathways and experiment conditions. The percentage signal change was calculated using average signals between 8 and 20 s in each block, leaving out the first 7 s, as the signal usually took 6–7 s to rise to the full magnitude in each block.

Note: Supplementary information is available on the Nature Neuroscience website.

COMPETING INTERESTS STATEMENT
The authors declare that they have no competing financial interests.

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