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 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.

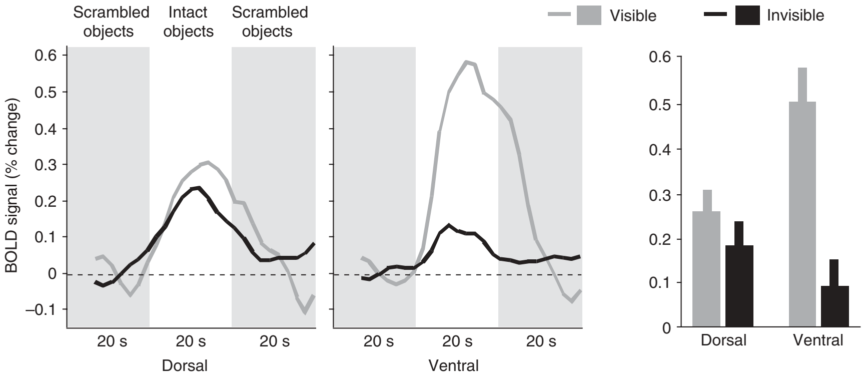


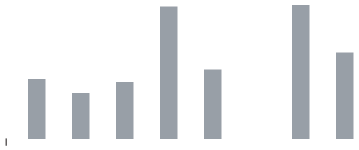
Figure 3 Results from the first experiment showing time courses and the average BOLD signals (percentage change) from dorsal and ventral object sensitive areas in 'visible' (gray curves and bars) and 'invisible' (black curves and bars) conditions. Data (mean ± s.e.m.) were averaged across eight subjects.

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**).

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 tha(to)-280.8(thu)19.6(s 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

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