

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

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 8.40.1443.59wm.013.4p0.1o375).

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) \times Condition (visible/invisible) in the dorsal pathway

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

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,

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