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Article

Neural Activities in V1 Create a Bottom-Up Saliency Map

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SUMMARY

The bottom-up contribution to the allocation of exogenous attention is a saliency map, whose neural substrate is hard to identify because of possible contamination by top-down signals. We obviated this possibility using stimuli that observers could not perceive, but that nevertheless, through orientation contrast between foreground and background regions, attracted attention to improve a localized visual discrimination. When orientation contrast increased, so did the degree of attraction, and two physiological measures: the amplitude of the earliest (C1) component of the ERP, which is associated with primary visual cortex, and fMRI BOLD signals in areas V1–V4 (but not the intraparietal sulcus). Significantly, across observers, the degree of attraction correlated with the C1 amplitude and just the V1 BOLD signal. These findings strongly support the proposal that a bottom-up saliency map is created in V1, challenging the dominant view that the saliency map is generated in the parietal cortex.

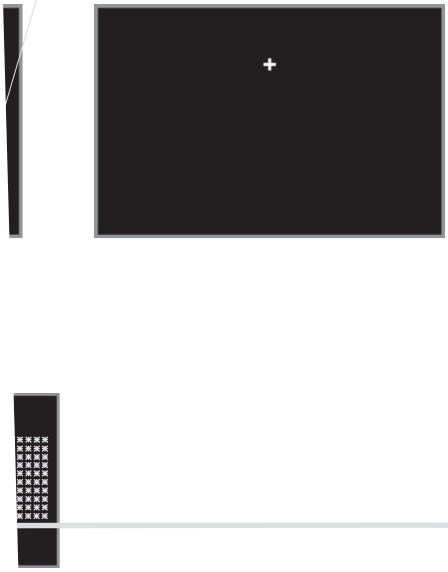
INTRODUCTION

Because neural resources are severely limited, only a very small fraction of visual inputs can reach all the way to perception. One of the main mechanisms of selection involves directing attention to a visual location, either overtly or covertly, without a shift in gaze. Attention may either be directed under voluntary control according to top-down goals, such as when directing gaze to an interesting book, or be attracted automatically by bottom-up stimuli, such as when the sudden appearance of a cat distracts one from reading. Throughout this study, we use the term salience to refer to this bottom-up attraction of exogenous attention. The regions of the brain responsible for top-down selection are well known, and include the frontal eye fields (FEF), dorsomedial prefrontal cortex, and posterior parietal cortex (PPC) (Corbetta and Shulman, 2002; Kastner and Ungerleider, 2000; Serences and Yantis, 2006). However, although bottom-up selection is typically faster and more potent (Jonides, 1981; Nakayama and Mackeben, 1989), there are controversies concerning the brain regions involved.

It is generally thought that the brain constructs a saliency map of visual space, with the activity at a location explicitly reporting the strength of its bottom-up attentional attraction (Koch and Ullman, 1985) so that it can be directly read out to guide attentional shifts before and after combining with top-down control factors. Based on neurophysiological and imaging studies, brain regions proposed to realize this saliency map have included the superior colliculus (Kustov and Robinson, 1996; Fecteau and Munoz, 2006), pulvinar (Shipp, 2004), parietal cortex (Bisley and Goldberg, 2010; Geng and Mangun, 2009; Gottlieb et al., 1998), V4 (Mazer and Gallant, 2003), and FEF (Serences and Yantis, 2007; Thompson and Bichot, 2005). However, neural activities in all these areas are also involved in top-down attentional direction. It is therefore unclear whether the observed neural correlates of saliency are relayed from brain regions upstream along the visual pathway, and whether they are the cause or the consequence of selection. In particular, because salient visual inputs typically enter awareness, it is difficult to determine whether the observed neural activities represent saliency as such, as opposed to being caused by the consequent perception of the selected stimuli.

A dominant view of the saliency map (Itti and Koch, 2001; Koch and Ullman, 1985; Wolfe, 1994) presumes that saliency results from pooling different visual features, being independent of whether the feature distinction making a location salient is in color, orientation, or other features. Hence, previous attempts to find the saliency map have typically concentrated in higher cortical areas, particularly the parietal cortex, whose neurons, unlike those in primary visual cortex (V1), are less selective to specific visual features.

By contrast, Li (1999, 2002) proposed that V1 (which, notably, projects directly and indirectly to all the previously proposed brain regions for the saliency map [Shipp, 2004]) creates a saliency map via intracortical interactions that are manifest in contextual influences (Allman et al., 1985). According to this theory, the saliency of a location is monotonically related to the highest neural response among all the V1 cells that cover that location with their spatial receptive fields (relative to the V1



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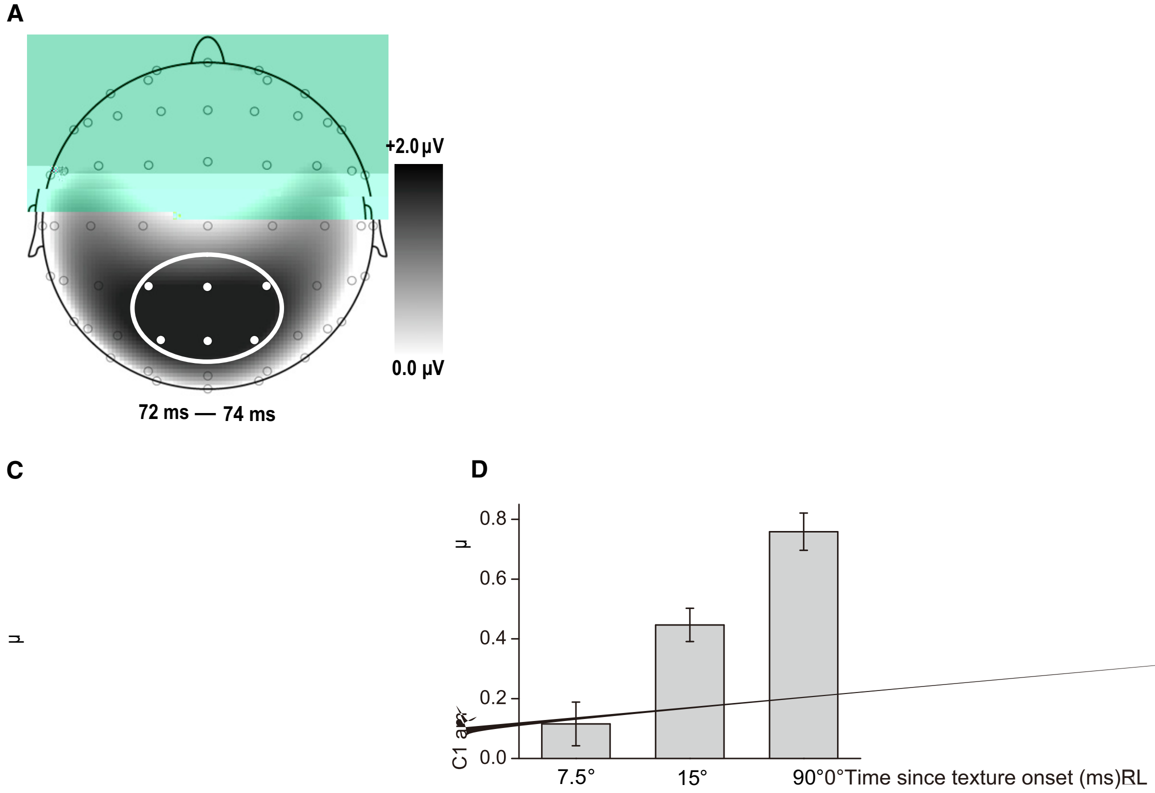
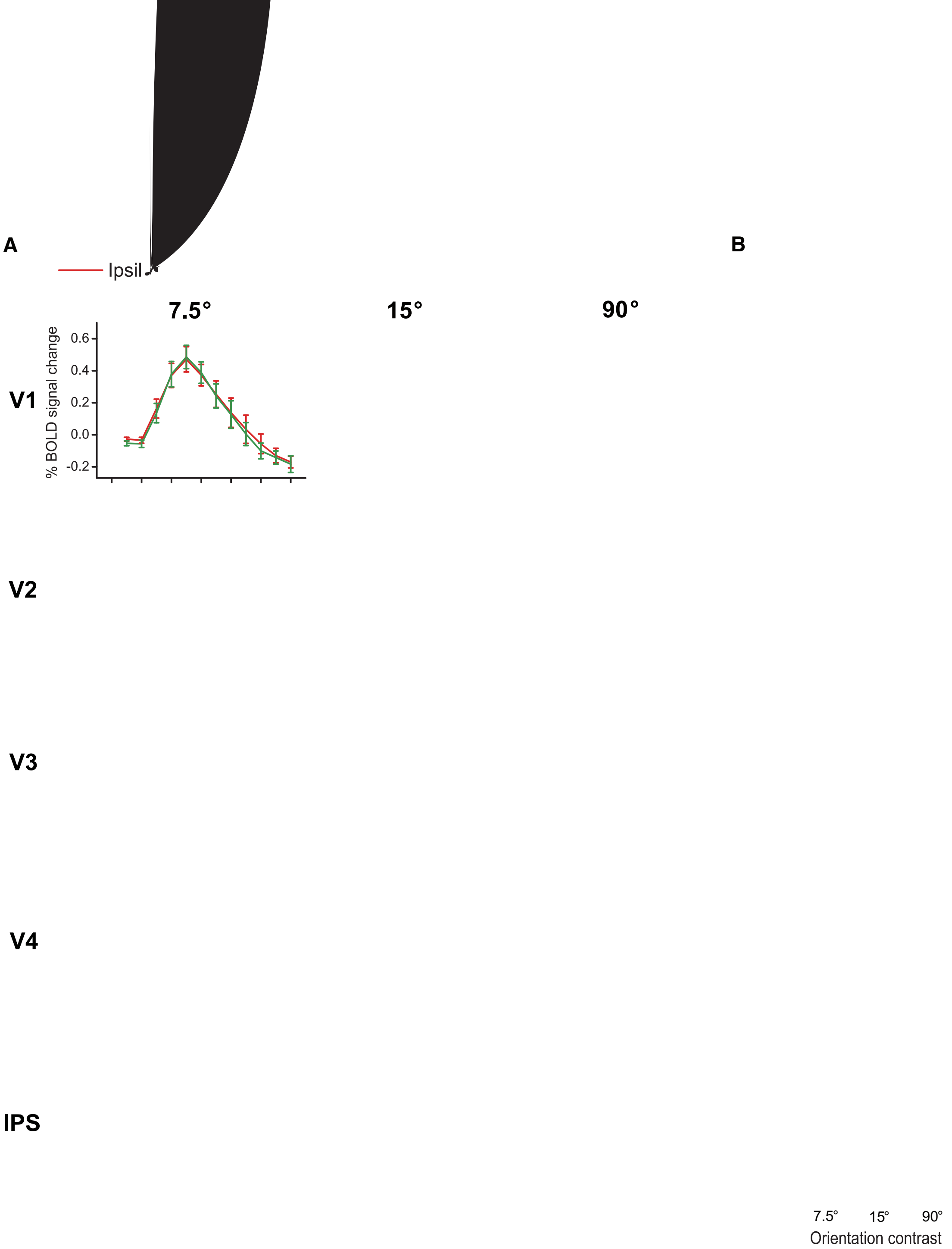


7.5°, 15°, and 90° (Figure 3D). C1 amplitude differences asures ANOVA, which



significantly correlated with the C1 amplitude difference for orientation contrasts of 15° ($r = 0.758$, $p = 0.001$) and 90° ($r = 0.798$, $p < 0.001$), but not for the orientation contrast of 7.5° ($r = 0.263$, $p = 0.343$) (Figure 5A) (similar correlations were found using stimuli in the upper visual field; see Figure S4). It was also significantly correlated with the BOLD signal difference in V1 for orientation contrasts of 15° ($r = 0.754$, $p = 0.012$) and 90° ($r = 0.924$, $p < 0.001$), but not for the orientation contrast of 7.5° ($r = 0.260$, $p = 0.468$) (Figure 5B). However, no significant correlation was found between the attentional effect and the BOLD signal difference in the other cortical areas (Figure 5C). Moreover, for the orientation contrast of 90° (but not other contrasts), the correlation coefficient in V1 was (marginally) significantly larger than those in other areas ($p = 0.076$ for V2 and all $p < 0.05$ for V3, V4, and IPS).

Across the seven subjects who participated in both the ERP and fMRI experiments, the C1 amplitude difference was significantly correlated with the BOLD signal difference in V1 for the orientation contrast of 90° ($r = 0.789$, $p = 0.035$), but not 7.5° ($r = 0.111$, $p = 0.814$) and 15° ($r = 0.433$, $p = 0.332$). No significant correlation was found in other areas. These results indicate a close relationship between the attentional effect, V1 activities, and the C1 component.

DISCUSSION

We assume that the absence of awareness to an exogenous cue (and indeed the whole texture stimuli) maximally reduced various top-down influences, even if it did not completely abolish them. These influences include those arising from feature perception, object recognition, and subjects' intentions (Jiang et al., 2006). By contrast with most previous studies on visual saliency, this enabled us to observe a relatively pure saliency signal. This is particularly important because temporally sluggish fMRI signa [redacted] typically reflect neural activities resulting from both botto [redacted] and top-down processes, even in the early visual cortic [redacted] (Fang et al., 2008; Harrison and Tong, 2009; Ress a [redacted], 2003). We could then investigate whether the a [redacted] ree saliency signal would be observed in IPS and/ [redacted] visual areas. Human IPS (and its monkey analog [redacted] ated with both top-down and bottom-up attentio [redacted] site at which correlates of saliency have been obse [redacted] y and Goldberg, 2010; Geng and Mangun, 2009; G [redacted] al., 1998). We found that the BOLD response to this [redacted] ue in V1–V4, but not in IPS, increased with the att [redacted] deing effect. Indeed, this resembled the saliency [redacted] s cue that was the output of a V1 saliency model ([redacted] 002). The cue-evoked C1 amplitude, believed to r [redacted] 1's sensory responses (Clark et al., One should note that according to the V1 saliency hypothesis, saliency of a visual location is determined by its highest evoked V1 response relative to those evoked by other locations. In other words, saliency is determined by the relative rather than absolute levels of V1 responses. This perspective is necessary to understand why V1 responses to a non-salient conjunctive search target in an inhomogeneous background (e.g., a red-vertical bar among many green-vertical and red-horizontal bars) is not necessarily lower than those to a salient pop-out target against a homogeneous background (e.g., a red-vertical bar among red-horizontal bars, Hegdé and Felleman, 2003). As explained in the analysis above, due to the intracortical iso-orientation suppression, and iso-feature (e.g., iso-color) suppression in general (Li, 1999), the V1 population responses to a homogeneous background are quite low, and lower than those to a less homogeneous background, such as the background for the conjunction target. Therefore, the unique feature target can be more salient than the unique conjunctive target even when the former evokes a lower V1 response, provided that the population responses to the homogeneous background of the unique feature target are sufficiently lower still. The dependence of saliency on the relative rather than the absolute levels of neural responses means that one has to look at the population responses, rather than a single neuron response, to assess saliency in a scene (Hegdé and Felleman, 2003). Alternatively, one may compare the relative saliency of two items from their evoked V1 responses only when they share the same or comparable background stimuli. The latter is the case in our cueing stimuli, in which different pop-out foregrounds share the same homogeneous background texture.

Our data suggest that the neural correlates of saliency observed in intermediate and higher cortical areas, such as V4 or the parietal cortex, may be relayed from V1 rather than created within these areas. Parietal regions are known to integrate bottom-up and top-down attentional guidance (Bisley and Goldberg, 2010). Meanwhile, consistent with the idea that saliency is computed outside V4, V4 lesions impair the selection of the non-salient but not the salient objects in the scene (Schiller and Lee, 1991), and modulations in V4 responses to salient locations are eliminated when monkey prepares a goal related saccade elsewhere (Burrows and Moore, 2009). Similarly, lesions of the frontal eye field disrupt visual pursuit (Lynch, 1987) but barely affect input-driven saccades to salient locations (Schiller et al., 1987). Because neural correlates of saliency in these areas are generally evoked by highly visible inputs, and because the saliency signal was absent in IPS in our data which generated saliency using invisible stimuli, it remains unclear whether saliency is only relayed to parietal regions when the visual input responsible is perceptually visible.

Note that we distinguish a cortical area (V1) creating the saliency map from those that read out or inherit the saliency values from earlier regions along the visual pathway. Hence, for example, superior colliculus and parietal cortex, both receiving inputs from V1 directly or indirectly, may be viewed as areas reading out the saliency values to execute attentional shifts or to combine with top-down factors (note that retinal drives to SC do not lead to visual evoked saccades) (Schiller, 1998). Meanwhile, retina and LGN cannot be viewed as saliency maps. Of course, saliency values can be computed from their population responses (as indeed in the proposal that this happens via V1 intracortical mechanisms). However, the responses in these regions lack the significant context dependence required for saliency (e.g., that a vertical bar is salient in a background of horizontal, but not vertical, bars).

Our findings can be viewed as identifying V1 as the neural substrate of the early component of attentional selection. There has been over half a century of debate about the extent to which exogenous attentional selection occurs early or late, i.e., before or after visual inputs is perceptually identified (see Yantis and Johnston [1990] for a review). In principle, both top-down and bottom-up selection could occur at early or late stages. Most evidence discriminating early versus late selection has come from behavioral studies, whereas physiological evidence from ERP and single unit recordings has mainly implicated the extra-striate cortices in early selection (Luck et al., 1994; Moran and Desimone, 1985). V1 neurons are tuned only to primitive features rather than complex objects, and they respond even to stimulus features that are invisible to awareness. Thus, identifying V1 as the neural substrate of saliency confirms that selection can occur before input identification and awareness. Locating bottom-up selection in V1 invites us to re-evaluate the brain network for attention control.

EXPERIMENTAL PROCEDURES

Subjects

A total of 22 human subjects (7 male, 20–35 years old) were involved in the study. All of them participated in the psychophysical experiment. Sixteen and ten of them participated in the ERP and fMRI experiments, respectively. One subject in the ERP experiment was excluded because of frequent eye blinks. All subjects were naive to the purpose of the study except for two subjects (two of the authors). They were right-handed, reported normal or corrected to normal vision, and had no known neurological or visual disorders. They gave written, informed consent in accordance, and our procedures and protocols were approved by the human subjects review committee of Peking University.

Stimuli

Each texture stimulus (Figure 1A) had a regular Manhattan grid of 15 × 29 low-luminance bars (3.4 cd/m^2), presented in the lower visual field on a dark screen (1.6 cd/m^2). Each bar was a rectangle of 0.075° × 0.75° in visual angle. The center-to-center distance between the bars was 1.13°. All bars were identically oriented except for a foreground region of 2 × 2 bars with another orientation in either the lower left or the lower right quadrant. The foreground region was centered at 7.2° eccentricity. The orientation of the background bars was randomly chosen from 0° to 180°. There were five possible orientation contrasts between the foreground bars and the background bars: 0°, 7.5°, 15°, 30°, and 90°. The mask stimulus (Figure 1B) had the same grid as the texture stimuli. Each mask element contained 12 intersecting high-luminance bars (120 cd/m^2) oriented from 0° to 165° at every 15° interval. The bars in the mask had the same size and shape as those in the texture stimuli.

Psychophysical Experiment

Visual stimuli were displayed on an IIYAMA color graphic monitor (model: HM204DT; refresh rate: 60 Hz; resolution: 1024 × 768; size: 22 inches) at a viewing distance of 57 cm. Subjects' head position was stabilized using a chin rest. A white fixation cross was always present at the center of the monitor.

Each trial began with the fixation. A texture stimulus was presented for 50 ms, followed by a 100 ms mask and another 50 ms fixation interval. The foreground region in the texture stimulus could serve as a cue to attract spatial attention. Then a two-dot probe was presented for 50 ms at randomly either the foreground region (valid cue condition) or its contralateral counterpart (invalid cue condition) (Figure 1C) with equal probability. Subjects were asked to press one of two buttons to indicate whether the upper dot was to the left or a foreground region (i.e., 2 × 2 bars) like in our experiments. The model mechanisms include (1), direct inputs to V1 neurons from each bar according to the classical receptive fields, and (2), interactions between V1 neurons by the intracortical connections implementing contextual influences (such as surround suppression) of the surround to the neural responses. At each grid location, the maximum response from all pyramidal model neurons was obtained. This maximum was averaged over all simulation time steps within 50 ms (simulated by five membrane time constant of the model neurons). The saliency of each grid location is the *Z*-score of this maximum obtained as follows: take the difference between this maximum and the average of the maximums over all grid locations and then divide it by the standard deviation of all the maximums (Li, 1999). Saliency in the foreground region is the maximum of the *Z*-scores over the 4 × 4 bar region centered on the foreground region. The result for each orientation contrast (7.5°, 15°, 30°, and 90°) as plotted in Figure 2 was obtained by averaging the foreground region saliency from 24 simulations for 24 different background bar orientations evenly distributed between 0° and 180°. The saliency of the foreground region should be directly related to the strength of its attentional attraction (i.e., its cueing effect).

SUPPLEMENTAL INFORMATION

Supplemental Information includes four figures and can be found with this article online at doi:10.1016/j.neuron.2011.10.035.

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