NeuroImage 81 (2013) 73–80

Contents lists available at SciVerse ScienceDirect

NeuroImage

journal homepage: www.elsevier.com/locate/ynimg

Orientation pop-out processing in human visual cortex

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ARTICLE INFO

Article history:
Accepted 6 May 2013
Available online 17 May 2013

Keywords:
Pop-out
Visual attention
Visual cortex
Functional MRI

ABSTRACT

Visual stimuli can "pop out" if they are different to their background. There has been considerable debate as to the role of primary visual cortex (V1) versus higher visual areas (esp. V4) in pop-out processing. Here we parametrically modulated the relative orientation of stimuli and their backgrounds to investigate the neural correlates of pop-out in visual cortex while subjects were performing a demanding fixation task in a scanner. Whole brain and region of interest analyses confirmed a representation of orientation contrast in extrastriate visual cortex (V4), but not in striate visual cortex (V1). Thus, although previous studies have shown that human V1 can be involved in orientation pop-out, our findings demonstrate that there are cases where V1 is "blind" and pop-out detection is restricted to higher visual areas. Pop-out processing is presumably a distributed process across multiple visual regions.

Introduction

A target that differs from distractors in its surround in a single elementary visual feature (such as luminance, color, orientation or motion) can easily be detected. For example a horizontal bar surrounded by many vertical bars perceptually "pops out". This pop-out effect is driven by the *feature contrast* between target and surround. Hence, in our example a vertical bar surrounded by horizontal bars would also pop out, and the pop-out would be stronger the higher the contrast between target and distractors is. The effect is maximal when the feature contrast is high or when the distractors are very similar, i.e. all distractors have exactly the same orientation or color. Under these conditions, visual search for pop-out targets is fast, does not require much attentional resources and is thought to run in parallel for different locations in the visual field, as opposed to serially scanning each location (Treisman and Gelade, 1980).

On a neural level, there has been some debate regarding the neural site of pop-out processing. One theory holds that the origin of the orientation pop-out effect is primary visual cortex (V1) (Kastner et al., 1997; Nothdurft et al., 1999; Zhang et al., 2012). Many studies have reported neural correlates for orientation selectivity in V1 in mammals and humans using a variety of methods including optical imaging (Ts'o et al., 1990), electrophysiological recordings (Hubel and Wiesel, 1962) as well as functional magnetic resonance imaging (fMRI) (Boynton and Finney, 2003; Tootell et al., 1998). Furthermore, the response of neurons in primary visual cortex to a particular stimulus can be modulated by stimuli in the non-classical receptive field. In other words, additional stimuli presented outside the classical receptive field of the respective neuron can influence the processing of the stimulus presented within the neuron's receptive field, for example by means of lateral inhibition (Knierim and van Essen, 1992; Li et al., 2000; Sillito et al., 1995; Zipser et al., 1996). These findings suggest that orientation pop-out could be processed in V1. Furthermore, there are some reports suggesting a direct representation of orientation pop-out in V1 (Kastner et al., 1997; Nothdurft et al., 1999; Zhang et al., 2012).

Other studies challenge this assumption. For example, Hegdé and Fellemann (2003) used a variety of different target–distractor configurations to investigate the response of V1 neurons to pop-out and non-pop-out stimuli. The authors demonstrated that neurons in V1 responded similarly to a target stimulus in their receptive field independent of whether it was embedded in a pop-out or a non-pop-out configuration. These results cast doubt on whether V1 could be the sole neural site for orientation pop-out. In line with this finding, a recent study (Burrows and Moore, 2009) demonstrated that neurons in V4 showed exactly the response profile that would be expected for a region that calculates orientation pop-out. V4 neurons showed increased firing rates only for targets that were surrounded by homogenous distractor sets, which were expected to create a pop-out effect, but not for other configurations of inhomogeneous distractor sets, which were expected to diminish the effect. Schiller and Lee (1991) investigated search performance on different displays after ablation of V4 in monkeys. On the side of the V4 lesion monkeys were severely limited in detecting a dark target between bright distractors and a small target between big distractors compared to the non-lesioned

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http://dx.doi.org/10.1016/j.neuroimage.2013.05.040

side. These results also suggest that V4 has an important role in processing pop-out stimuli and V1 alone is not sufficient to completely encode bottom-up saliency. Taken together, while some but not all studies show pop-out effects in V1, V4 might play a more crucial role for the pop-out calculation.

In the present study we aimed to further investigate the roles of V1, V4 and other potentially important brain areas in the calculation of orientation pop-out using fMRI. Unlike many other studies that treated pop-out as an all-or-nothing property, we experimentally manipulated pop-out parametrically by using different orientation contrasts between stimulus bars and surrounding distractor bars (0°, 30°, 60° and 90° differences) in a visual display. The pop-out effect was also measured behaviorally using reaction times in a separate psychophysical experiment. We then sought for brain regions with a neural response profile similar to the behavioral response profile in the fMRI experiment in which no overt responses were required and no confound with motor responses could occur. Finding such brain regions would strongly speak for a role in calculating the orientation contrast underlying the pop-out effect.

Methods

Psychophysical experiment

Participants

Twelve subjects (seven females, mean age 25.5 years, range 21–31) took part in the psychophysical study and gave written informed consent to the test procedure. The experiment was approved by the local ethics committee and was conducted according to the Declaration of Helsinki. All subjects were right-handed and had normal or corrected to normal visual acuity.

Visual stimuli and experimental procedure

The psychophysical experiment used a background of distractors consisting of a homogenous array of bars with a length of 2.2° (3 rows × 7 columns), all of which had the same orientation of either 0°, 45°, 90° or 135°. On each trial, one bar on either the left or right side, always displayed in the second row and the second column (top left) or sixth column (top right) was rotated counter-clockwise 15°, 30°, 45°, 60°, 75° or 90° relative to the distractor bars. The stimuli were presented on a 17-inch TFT-screen (resolution 1024 × 768, 60 Hz). The visual angle of the full display was $\alpha = 24.5° \times 19.7°$. The stimuli were presented for 500 ms with a fixed inter-stimulus-interval (ISI) of 2.5 s. Subjects had to fixate on a point displayed below the stimulus array in the lower center of the screen and indicated whether the position of the differently oriented bar was left or right by button press with the left and right index fingers respectively. Stimulus presentation and response recording were controlled using MATLAB 7.0 (The MathWorks, Inc.) in combination with the Cogent toolbox (http://www.vislab.ucl.ac.uk/Cogent). The distance between the fixation point and the center of the target bar was always 10.8° (Fig. 1).

Four experimental blocks (each 6 min duration) were conducted. During each block 144 trials (6 target orientations × 4 background orientations × 2 positions (left vs. right) × 3 repetitions) were presented. The aim of the behavioral experiment was to investigate whether the pop-out effect (expressed as faster reaction times for target detection) differed for the different target–distractor combinations. We expected that the reaction times decrease with increasing orientation contrasts.

Functional imaging experiment

Participants

Eleven subjects (6 females, mean age 28.7 years, range 24–34) took part in the neuroimaging study and gave written informed consent to the test procedure. Each subject participated in two scanning sessions on two different days. The experiment was approved by the local ethics committee and was conducted according to the Declaration of Helsinki. All subjects were right-handed and had normal or corrected to normal visual acuity.

Visual stimuli and experimental procedure

The visual display in the experiment consisted of a continuous stream of screens containing oriented bars. Between target displays the screens contained homogenous background stimuli (type A, see

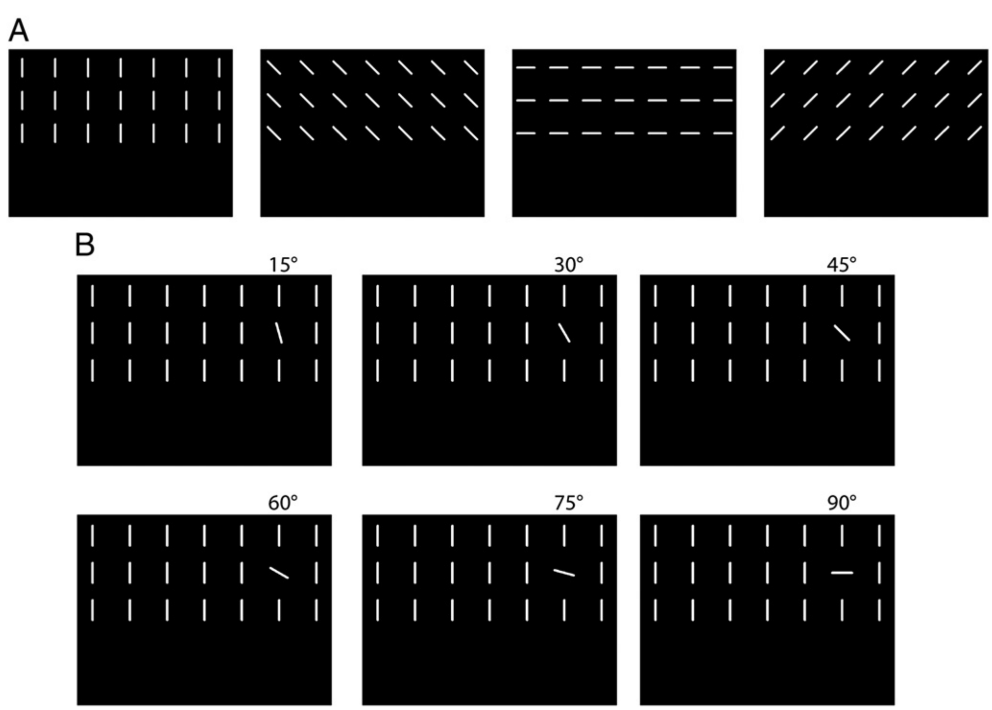

Fig. 1. Stimuli used in the behavioral experiment. A: Four different distractor configurations were used. B: A single bar on the left or right (shown in the example) side was rotated 15°, 30°, 45°, 60°, 75° or 90° counter clockwise to the distractor bars.