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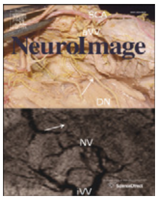

Disambiguating the roles of area V1 and the lateral occipital complex (LOC) in contour integration

Marina Shpaner [a,b,c], Sophie Molholm [a,b,c], Emmajane Forde [a], John J. Foxe [a,b,c,*]

[a] *The Cognitive Neurophysiology Laboratory, Nathan S. Kline Institute for Psychiatric Research, 140 Old Orangeburg Road, Orangeburg, NY 10962, USA*
[b] *The Sheryl and Daniel R. Tishman Cognitive Neurophysiology Laboratory, Children's Evaluation and Rehabilitation Center (CERC), Departments of Pediatrics and Neuroscience, Albert Einstein College of Medicine, Van Etten Building, Wing 1C, 1225 Morris Park Avenue, Bronx, NY 10461, USA*
[c] *The Cognitive Neurophysiology Laboratory, Program in Cognitive Neuroscience, Departments of Psychology & Biology, City College of the City University of New York, 138th Street & Convent Avenue, New York, NY 10031, USA*

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ABSTRACT

Contour integration, the linking of collinear but disconnected visual elements across space, is an essential facet of object and scene perception. Here, we set out to arbitrate between two previously advanced mechanisms of contour integration: serial facilitative interactions between collinear cells in the primary visual cortex (V1) versus pooling of inputs in higher-order visual areas. To this end, we used high-density electrophysiological recordings to assess the spatio-temporal dynamics of brain activity in response to Gabor contours embedded in Gabor noise (so-called "pathfinder displays") versus control stimuli. Special care was taken to elicit and detect early activity stemming from the primary visual cortex, as indexed by the C1 component of the visual evoked potential. Arguing against a purely early V1 account, there was no evidence for contour-related modulations within the C1 timeframe (50–100 ms). Rather, the earliest effects were observed within the timeframe of the N1 component (160–200 ms) and inverse source analysis pointed to principle generators in the lateral occipital complex (LOC) within the ventral visual stream. Source anlaysis also suggested that it was only during this relatively late processing period that contextual effects emerged in hierarchically early visual regions (i.e. V1/V2), consistent with a more distributed process involving recurrent feedback/feedforward interactions between LOC and early visual sensory regions. The distribution of effects uncovered here is consistent with pooling of information in higher order cortical areas as the initial step in contour integration, and that this pooling occurs relatively late in processing rather than during the initial sensory-processing period.

Introduction

Contour integration, the ability to link collinear but disconnected visual information across space, is considered an essential element of object and scene perception. Despite significant progress in our understanding of the physiology of the visual cortex, the precise neural mechanisms of contour integration remain unclear. Two alternative mechanisms have been suggested. The first relies on lateral horizontal connections within the primary visual cortex, which connect cells with similar orientation tuning characteristics across the visual field. These so-called collinear cells, which are sensitive to neighboring regions of visual space, are posited to communicate via long-range horizontal connections resulting in local integration of contour elements (Bauer and Dicke, 1997; Bauer and Heinze, 2002; Gray, 1999; Grossberg and Williamson, 2001; Hess et al., 2003; Kapadia et al., 1995; Kovacs, 1996; Stettler et al., 2002). The second possible mechanism instead involves integration across different levels of the visual hierarchy, with inputs from primary visual cortex converging on cells with larger receptive fields in higher-order regions of visual cortex such as the lateral occipital complex (Hubel and Wiesel, 1962; Spillmann and Werner, 1996). These two mechanisms make a set of clearly dissociable predictions, not only in terms of the cortical regions involved, but also in terms of the timing of contour integration. If the initial integration step occurs locally in V1, one would predict correspondingly early differential neural response modulations originating from neuronal ensembles in the primary visual cortex (Gray, 1999; Hess et al., 2003; Kapadia et al., 1995; Kovacs, 1996; Stettler et al., 2002). Alternatively, if contour integration initially depends on the pooling of inputs in higher order visual areas, the initial contour-specific response should be detected somewhat later in processing and in higher-order extrastriate visual areas (Foxe et al., 2005; Murray et al., 2002).

Arguments in support of contour computation in the primary visual cortex come from anatomical and physiological studies in animal models, suggesting that V1 is capable of integrating information over a larger extent of the visual field than initially considered. Although

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* Corresponding author at: Albert Einstein College of Medicine, Van Etten Building – Wing 1C, 1225 Morris Park Avenue, Bronx, NY 10461, USA. Fax: +1 718 862 1807.
E-mail address: john.foxe@einsten.yu.edu (J.J. Foxe).

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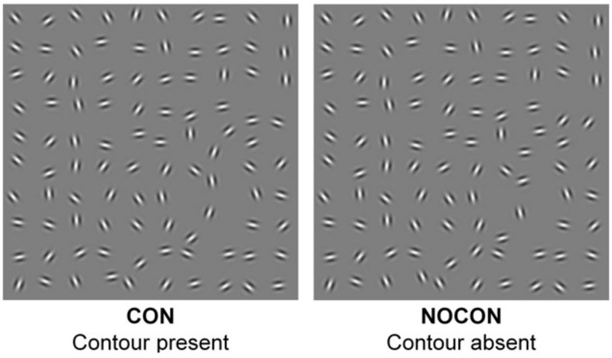
classical receptive fields extend only a fraction of a degree in the fovea (Hubel and Wiesel, 1962), they can be modulated by local horizontal connections responding to visual elements outside the classical receptive field (Allman et al., 1985; Angelucci et al., 2002; Blakemore and Tobin, 1972; Gilbert et al., 1990, 1996; Levitt and Lund, 1997; Nelson and Frost, 1978; Rockland and Lund, 1983; Walker et al., 1999). Neurons of a given orientation selectivity are preferentially connected to other neurons (across orientation columns) with a similar orientation preference and adjacent receptive fields (Hirsch and Gilbert, 1991; Schwarz and Bolz, 1991; Stettler et al., 2002; Ts'o et al., 1986; Weliky et al., 1995). Support for the role of early visual cortex has also been derived from behavioral studies indicating that the physical constraints of contour integration are consistent with the physical organization of hypercolumn within the primary visual cortex. One of the classical psychophysical paradigms explores so-called “association fields” of visual cortex, using “pathfinder displays.” Here, Gabor patches, designed to be well-matched to the tuning properties of cells in V1, are arranged to form continuous contours of about ten-element length while their relative orientation and distance is varied (see Fig. 1) (Field et al., 1993). The term “association field” describes the tendency of neighboring elements to be grouped together within certain constrains (i.e., ≤6 carrier wavelengths (λ) spatial separation and ≤30° orientation difference) (Field et al., 1993; Hess et al., 2003). Together with anatomical considerations (i.e., preferential connectivity between hypercolumns with similar tuning characteristics) (Das and Gilbert, 1995; Gilbert and Wiesel, 1989; Malach et al., 1993; Ts'o et al., 1986), these behavioral tests of “association fields” have been taken to suggest that V1 plays a major role in contour processing (Field et al., 1993; Kovacs, 1996).

The neural underpinnings of contour integration have also been investigated using so-called ‘illusory contour’ (IC) stimuli, a stimulus class specifically constructed to induce perceptions of contours spanning across gaps where the discrete luminance boundaries of real contours are absent. Although earlier intracranial studies in animal models and human neuroimaging studies localized IC processing to V1 and V2 (Bakin et al., 2000; Ffytche and Zeki, 1996; Larsson et al., 1999; Lee and Nguyen, 2001; Peterhans and von der Heydt, 1989; Ramsden et al., 2001; Seghier et al., 2000; von der Heydt and Peterhans, 1989), these studies did not assess the timing of these effects, leaving open the possibility that modulations in V1 and V2 represented feed-back from higher-order visual regions.

In contrast, more recent neuroimaging and event-related potential (ERP) studies have emphasized the contributions of generators within higher-order ventral visual stream regions—the so-called Lateral Occipital Complex (LOC) (Altschuler et al., 2012; Fiebelkorn et al., 2010; Foxe et al., 2005; Halgren et al., 2003; Kruggel et al., 2001; Mendola et al., 1999; Murray et al., 2002, 2004, 2006; Ritzl et al., 2003; Shpaner et al., 2009). In these studies, the timing of initial IC processing was explicitly interrogated, and it was shown that initial modulations actually occurred relatively late in processing, and were first observed in the LOC rather than in early visual regions. As such, these studies suggested that previously observed V1/V2 modulations to IC stimuli likely reflected feedback processes.


CON
Contour present

NOCON
Contour absent

Fig. 1. Exemplar pathfinder stimulus arrays. Arrays of ten-by-ten randomly oriented Gabor elements (4 cycles per degree) were constructed with inter-element separation randomly jittered between 1 and 1.5° of visual angle. In the case of contour-present arrangements, 10 of the Gabor elements were oriented within ±30° relative to the neighboring elements with no phase shift. An example is shown in the left hand panel where this arrangement of elements results in the perception of a snaking contour, which can be seen in the lower right corner of the panel. In the right hand panel, orientations of all elements are fully random, and no countour is seen.

Here we used high-density electrophysiology to arbitrate between the thesis that long-range horizontal connections in V1 provide the principle initial substrate of contour integration, and the competing notion that this integration initially relies on pooling of neuronal inputs in higher-level visual cortex (i.e., the LOC). For comparability with the preceding literature, stimuli were modeled on those used in association field studies (Field et al., 1993). We reasoned that if initial contour-related modulations were observed during the earliest phases of sensory processing and were localized to primary visual cortex, this would support the intrinsic horizontal connectivity model. Alternatively, if initial contour-related modulations were found to be localized in higher-order regions of visual cortex, such as the LOC, and were observed during later sensory-perceptual processing phases, this pattern of results would support a model wherein pooling of inputs in visual regions with larger receptive fields represents the initial stage of contour integration.

Materials and methods

Participants

Twenty neurologically normal volunteers participated. Four participants were dropped from the study because they did not cooperate with the task (based on the assessment of the EEG technician and confirmed by very low behavioral accuracy as indicated through calculation of *d′* values), an additional participant was dropped because he could not maintain fixation. The remaining fifteen participants (6 females) were between 22 and 40 years of age (mean age = 28 ± 5). All participants had normal or corrected-to-normal vision and were right-handed, as assessed with the Edinburgh Handedness Inventory (Oldfield, 1971). Participants provided written informed consent, and the Institutional Review Boards of the Nathan Kline Institute for Psychiatric Research and the City College of New York approved all procedures. All procedures conformed to the principles of the Helsinki declaration. Participants received a modest monetary compensation ($10 per hour).

Design and task

Gabor patches of 0.25 carrier wavelength, λ, (i.e., 4 cpd) were used to generate forty different contours embedded in randomly oriented Gabor elements (an algorithm from Field and Hess (Field et al., 1993) was employed using Matlab v. 15). Contours consisted of ten Gabor elements, oriented within ±30° relative to the neighboring elements (a random value, generated from a uniform non-Gaussian distribution, determined the orientation), with no phase shift, presented at 100% Michelson contrast. Arrays of ten by ten elements were constructed. Inter-element separation was jittered between 4 and 6 λ (i.e., 1–1.5° visual angle). Orientation of the elements was not jittered relative to the path. Contours did not close to form full geometric shapes. Forty randomly oriented displays of Gabor patches were also constructed by randomly rotating the orientation of the contour elements. This resulted in identical displays for the contour-present and contour-absent conditions, except for the orientation of the ten aligned contour elements (Fig. 1). Stimulus arrays subtended $10 \times 10°$ of visual angle (with each Gabor occupying 1° of visual angle) and were presented either to the upper left or the lower right quadrant of the screen. Off-center presentation was necessary to evoke the retinotopically generated C1 component