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The influence of orientation and contrast flicker on contour saliency of outlines of everyday objects

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ABSTRACT

One of the most important tasks of the visual system is the extraction of edges and object contours, and the integration of discrete elements to form a coherent global percept. A great deal is known about the spatial properties of contour extraction, but less is known about the dynamics and spatio-temporal aspects. We used Gabor-rendered outlines of real-world objects, where we could manipulate low-level properties, such as element orientation and phase, while incorporating higher-level properties, such as object complexity and identity, to study dynamic relationships in object detection. First we manipulated the time available for integration by changing back and forth between coherent and non-coherent orientations of the contour elements. We then manipulated contrast flicker by reversing the spatial phase of the Gabor elements at various frequencies. We found similar results to earlier studies on contour detection: detection was better for contrast flicker than for orientation flicker, and detection performance was curvature-dependent for orientation flicker but not for contrast flicker. Our results support the existence of at least two temporal frequency channels in the visual system, one low-pass and one band-pass peaking around 10–12 Hz. In addition, we found that object properties, such as identity and complexity, affected detection performance.

1. Introduction

Photoreceptors in the eye receive light from a very small part of the visual scene, and neurons in the primary visual cortex respond to a limited area of retinal stimulation (Hubel & Wiesel, 1968). These very localized signals present a computational challenge for the visual system: it must correctly combine information from different parts of a visual scene to form a coherent representation. The extraction of contours is an important step in these processes, crucial to define edges and borders, for figure-ground segregation, and ultimately the build-up of object representations. Since contours are often not well defined along all of their extent (due to partial occlusion, for example), the visual system also needs to be able to infer their nature from an incomplete representation. It can make use of several cues to construct a coherent percept, for instance, texture gradients, color, depth information, occlusion, and motion. How the brain combines local information into a global structure, how it computes form from these cues, remains an important issue in visual neuroscience.

Others before us have extensively pursued processes involved in contour extraction. Psychophysical studies have shown that elements tend to be grouped if they are nearby (Kubovy, Holcombe, & Wagemans, 1998; Kubovy & Wagemans, 1995) and consistent with a smooth contour (Field, Hayes, & Hess, 1993; Hess & Field, 1999; Ledgeway, Hess, & Geisler, 2005; Watt, Ledgeway, & Dakin, 2008). The percept of a smooth contour has been shown to depend on the orientation of the constituent elements, distance between the elements, the curvature of the contour, and contour length (Field et al., 1993). Alignment of local element orientation with global contour orientation has been shown to modulate perceptual grouping by proximity (Claessens & Wagemans, 2005; see also Claessens & Wagemans, 2008, for a view on the interactions between the different grouping cues). It has also been shown that closed contours are better detected than open ones (Braun, 1999; Kovacs & Julesz, 1993; Tversky, Geisler, & Perry, 2004) and symmetric ones better than asymmetric ones (Machilsen, Pauwels, & Wagemans, 2009). Initially, it was thought that contour integration was greatly impoverished in peripheral vision beyond 10° of visual angle (Hess & Dakin, 1997; Nugent, Keswani, Woods, & Peli, 2003), but later evidence suggests that closed contours in shapes of circles and ellipses can be detected and discriminated up to 35° of visual angle from the fovea (Kuai & Yu, 2006; see also Bleumers, De Graef, Verfaillie, & Wagemans, 2008).

Other studies have shown that a Gabor element is detected at lower contrasts when it is presented with collinear flankers than when it presented on its own (Cass & Alais, 2006a, 2006b; Cass & Spehar, 2005; Freeman, Sagi, & Driver, 2001, 2004; Huang & Hess,

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2008; Polat & Sagi, 1993, 1994; Williams & Hess, 1998). The phenomenon of collinear facilitation is usually considered at contrast threshold for the target Gabor but this does not have to be the case (see Ito & Gilbert, 1999). Although it is not clear to what extent collinear facilitation contributes directly to contour integration, or to what extent these two processes share a common neural network (Li & Gilbert, 2002; Williams & Hess, 1998), it is plausible that the former contributes to the latter in the most challenging conditions, i.e. at low contrast or with short presentation times.

Several suggestions to explain contour extraction in terms of neural mechanisms have been made. These include local, single-channel filters (i.e., end-stopped cells; Yu & Levi, 1997), lateral long-range connections in V1 (Angelucci & Bullier, 2003; Kapadia, Ito, Gilbert, & Westheimer, 1995), and higher level, informationally and attentionally driven processes (Freeman, Driver, Sagi, & Zhaoping, 2003; Freeman et al., 2001, 2004). A great deal is known about the spatial properties of these interactions (see above), but the data do not allow differentiation of the suggested underlying neural mechanisms. In an attempt to clarify some of these issues, focus has turned to the dynamics and spatio-temporal aspects of contour extraction (Cass & Alais, 2006a, 2006b; Hess, Beaudot, & Mullen, 2001; Huang & Hess, 2008) and form perception (Aspell, Wattam-Bell, & Braddick, 2006). In a study where they modulated the orientation of contour elements, from aligned with the contour to a random orientation and back again, Hess et al. (2001) found that performance decreased with increasing temporal frequency and that contour linking was temporally modulated between 1 Hz and 12 Hz, depending mostly on contour curvature. Temporal resolution of orientation modulation was 6–12 Hz for straight contours and 1–2 Hz for curved ones (curvature of 30°). They also modulated element contrast (contrast reversal) in a separate experiment and also found a performance decrease with temporal frequency, but with a much higher resolution of 10–30 Hz for contour detection. Change in contrast polarity along the contour decreased asymptotic performance, but did not affect the critical frequency for contrast modulation. They consequently suggested that this higher temporal resolution might represent the initial feedforward input of element detection, and that contour detection was the result of slower intra- and extra-cortical feedback processes (Hess et al., 2001). Collinear facilitation showed fast, but sustained, dynamics, negating the possibility of slow, long-range horizontal connections as the sole source of collinear facilitation (Huang & Hess, 2008). Both Cass and Alais (2006a, 2006b) and Huang and Hess (2008) seem to suggest that these phenomena could be explained by two separate mechanisms: a rapid signal to initiate facilitation across large retinal distances, and a slower, more sustained response responsible for the local-level detail.

The mechanisms used to extract global structure from a local pattern are less well understood. Early visual cortex (V1, V2) is tuned to edge orientation, spatial frequency, and position. The computational complexity increases in later stages of the visual hierarchy, where V4 encodes for more complex object features such as circular forms, concentric, radial, and hyperbolic gratings (Gallant, Braun, & VanEssen, 1993; Gallant, Connor, Raksit, Lewis, & VanEssen, 1996) and complex curved shapes sensitive to the location of convex curvature extrema (Pasupathy & Connor, 2001, 2002). Further processing occurs in the lateral occipital complex (LOC), an area deemed important for the recognition of shapes (Grill-Spector, Kourtzi, & Kanwisher, 2001; Kourtzi & Kanwisher, 2000; Kourtzi, Tolias, Altmann, Augath, & Logothetis, 2003). LOC reacts favorably to whole shapes in relation to scrambled shapes or random contours, and fMRI studies have shown a correlation between how well an object can be recognized and LOC activity (more recognizable shapes give a higher signal intensity) (Grill-Spector et al., 2001; Kourtzi & Kanwisher, 2000; Kourtzi et al., 2003). Moreover, a study by Altmann, Deubelius, and Kourtzi (2004) has shown that LOC activity is modulated by form saliency.

The stimuli that have been used in most of the above studies relating to contour and form detection have been relatively simplistic in nature, consisting of geometric figures (squares, circles, polygons) or parametric contours (radial frequency patterns) with little, if any, biological significance. We have developed a set of stimuli where we use Gabor-rendered outlines of real-world objects. This enables us to manipulate low-level properties that can be used in models of human contour and object perception, while incorporating also higher-level object properties such as complexity and identity (see also Nygård, Van Looy, & Wagemans, 2009). The goal of the current study is to test temporal aspects of their perception, and compare results with the current literature on contour and form detection, both spatially and temporally. We will address the two-way linkage between grouping and detection and use these stimuli to generalize the earlier findings obtained with simpler, parametrically controlled stimuli to more complex, natural shapes. We expect that objects containing smooth contours fulfilling a "good continuation" criterion will be better detected than those containing more jagged contours. Furthermore, we predict that objects containing straighter segments will be better detected at higher temporal frequencies than objects containing more curved segments. We wish to verify that contour detection dynamics work in a similar way for open contours and object contours, thus leading the way to more intricate studies involving higher-level aspects of object perception. We suggest that stimuli derived from real-world objects are likely to induce some extra processing in the highest levels in the visual hierarchy, where contact is made with representations of existing objects and associations with other items in semantic memory become available. Hence, we wish to investigate to what extent object complexity and identity influences object detection in our experimental conditions. Although it is not the ambition of the present study, we hope that eventually our stimuli can shed light on the topics of the ongoing discussion regarding underlying neural mechanisms of object perception, enabling a clarification of some of the feedforward, recurrent, and feedback mechanisms that underlie these processes.

2. Experiment 1

We asked subjects to detect object outlines, defined by aligned Gabor elements on the object's contour, embedded in a noisy background. The Gabor elements changed orientation from aligned to random, and back (thus flickering back and forth between two orientations), at varying frequencies. The objective was to see if, and how, orientation flicker frequency affected object detection, address the linkage between contour integration and detection, and to see if there was an influence of object characteristics like complexity and identity on detection.

2.1. Subjects

Subjects ($N = 6$) were four males and two females, aged 22–36, with normal or corrected-to-normal vision. One subject is the first author; the remaining subjects were naïve regarding the purpose and the details of the experiment.

2.2. Stimuli

The stimuli consisted of Gabor elements that were placed and oriented such that they gave rise to the percept of an object embedded in a background (Fig. 1A). The objects were contour versions of 20 items from the Snodgrass and Vanderwart (1980) set of line drawings, which we had first converted into silhouettes and