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Response priming evidence for feedforward processing of snake contours but not of ladder contours and textures

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ABSTRACT

In contour integration, increased difficulty in detection and shape discrimination of a chain of parallel elements (a ladder contour) compared to collinear elements (a snake contour) suggests more extensive processing of ladders than of snakes. In addition, conceptual similarities between ladders and textures – which also involve grouping of parallel elements – raises the question whether ladder and texture processing requires feedback from higher visual areas while snakes are processed in a fast feedforward sweep. We tested this in a response priming paradigm, where participants responded as quickly and accurately as possible to the orientation of a diagonal contour in a Gabor array (target). The diagonal was defined either by a snake, ladder, texture, or a continuous line. The target was preceded with varying stimulus onset asynchrony (SOA) by a prime that was either a snake, ladder, or texture, and was consistent or inconsistent to the response demands of the target. Resulting priming effects clearly distinguished between processing of snakes, ladders, and textures. Effects generally increased with SOA but were stronger for snakes and textures compared to ladders. Importantly, only priming effects for snakes were fully present already in the fastest response times, in accordance with a simple feedforward processing model. We conclude that snakes, ladders, and textures do not share similar processing characteristics, with snakes exhibiting a pronounced processing advantage.

1. Introduction

1.1. General

Organizing a visual scene in coherent perceptual units requires perceptual grouping, that is the combination of elements in meaningful configurations. In contour integration, elements are grouped according to the Gestalt principle of collinearity. In ‘snake’ contours the orientations of contour elements are aligned along a smooth path, while the orientations of background elements are kept random. Alternatively, in ‘ladder’ contours the element orientations are orthogonal to the path of the contour. Finally, in texture segregation, regions differing in texture (e.g., based on orientation discontinuities of texture elements) are segregated from each other and as a result they give rise to a percept of distinct texture regions (Landy, 1996).

1.2. Processing of snakes, ladders, and textures

With respect to snake contours, long-range horizontal connections between neurons in V1 have been proposed as the primary processing stage (for reviews see Hess, Hayes, & Field, 2003; Hess, May, & Dumoulin, 2014; Li, 1998). Intact contour integration of snakes in patients with high level lesions in temporal and parietal areas (Giersch et al., 2000; Vancleef, Wagemans, & Humphreys, 2013) suggests that higher visual areas are not crucial to perceive snake contours. Taken together these observations suggest a predominant feedforward processing of snake contours with a very restricted role of higher visual areas.

With respect to ladder contours, it has been suggested that they are integrated by weak orthogonal horizontal connections (Bosking et al., 1997) or inhibitory transaxional connections (Ledgeway, Hess, & Geisler, 2005) in early visual areas. Furthermore, longer processing time in high level shape encoding of ladders compared to snakes (Vancleef & Wagemans, 2013) suggests a more prominent role for high level visual areas in ladder processing than in snake processing.

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With respect to textures, visual area V4 has been pointed to as a potential area for texture segregation (El-Shamayleh & Movshon, 2011) that receives input from V1 (e.g., Lamme, Van Dijk, & Spekreijse, 1992; Nothdurft, Gallant, & Van Essen, 2000) and sends information to higher level areas LOC (Appelbaum, Ales, & Norcia, 2012) and TEO (Kastner, De Weerd, & Ungerleider, 2000). Also, there is evidence for feedback from these higher level visual areas to lower visual areas (Romani et al., 2003; Scholte et al., 2006). Thus, texture segregation seems to be mediated by a dynamic interplay between visual areas, involving feedback from higher to lower visual areas.

Furthermore, Hess, Hayes, and Field (2003) and Ledgeway, Hess, and Geisler (2005) pointed to a conceptual link between ladder contours and textures: aligned segments in natural images (which correspond to snakes) are primary indicative of object contours, while the parallel segments (which correspond to ladders) are more likely indicators of object regions. Since the region of an object is often filled with a texture, parallel segments (or ladders) correspond to the parallel edges of a texture. On the other hand, ladder contours can imply arrays of collinear terminators like in illusory contours formed by offset gratings and the Ehrenstein illusion (e.g., Seydell-Greenwald & Schmidt, 2012). These observations raise the question whether feedback from higher visual areas is essential not only for processing of textures but also for that of ladder contours.

Taken together, the current evidence points to (1) a processing of snake contours based on horizontal connections in early visual areas, possibly within a fast feedforward sweep, and to (2) a processing of ladder contours and textures with involvement of higher visual areas, possibly relying on feedback from those areas to the primary visual cortex.

1.3. Analyzing processing characteristics of contour integration and texture segregation

The response priming paradigm is suited to investigate temporally early phases of visual processing (Neumann & Klotz, 1994; Vorberg et al., 2003) and can be specifically used to test whether visual processing is in accordance with a simple feedforward model or not (Schmidt et al., 2011; Schmidt, Niehaus, & Nagel, 2006).

In a typical response priming task, participants classify a target stimulus as quickly and accurately as possible. The target is preceded by a prime stimulus that is either mapped to the same response as the target (consistent) or to the alternative response (inconsistent). Typically, in consistent configurations response times are faster and error rates lower compared to inconsistent configurations (response priming effect).

Response priming effects can be analyzed by taking the vantage point of the rapid-chase theory of response priming (Schmidt, Niehaus, & Nagel, 2006; Schmidt et al., 2011). The theory distinguishes between visual *rapid-chase* processing that is in accordance with a feedforward model and visual processing that is not. In rapid-chase processing, prime and target signals elicit feedforward sweeps of neuronal activation that traverse the visuomotor system in strict sequence, without any temporal overlap (Lamme & Roelfsema, 2000; for formal models see Mattler & Palmer, 2012; Schmidt, Weber, & Schmidt, 2013; Vorberg et al., 2003).

Specifically, the response priming paradigm allows to test whether different processes of grouping are in accordance with a feedforward processing model (cf. *base grouping*) or not (*incremental grouping*; Roelfsema, 2006; Roelfsema & Houtkamp, 2011). Here, we use this approach to investigate and compare the processing of snake, ladder, and texture Gabor stimuli (cf. Vancleef & Wagemans, 2013; Vancleef et al., 2013).

In addition, a prime identification task with the same stimulus presentation procedure will inform us about visibility of the primes in consistent and inconsistent trials and confirm earlier findings on detection and discrimination differences between snake and ladder contours (Vancleef & Wagemans, 2013) and between snake contours and textures (Vancleef, Wagemans, & Humphreys, 2013).

The rapid-chase theory makes strong predictions for priming effects in response times. Specifically, priming effects should increase with stimulus onset asynchrony (SOA) between prime and target (Vorberg et al., 2003) and be at least as large in the fastest responses compared to in slower responses (Schmidt & Schmidt, 2014; Seydell-Greenwald & Schmidt, 2012). Based on previous studies, we expected that only priming effects induced by snake contours would be in accordance with a simple feedforward processing model (i.e., would increase with SOA and would be fully present in the fastest responses). Priming effects induced by ladder and texture stimuli, on the other hand, would not be in accordance with a feedforward model as defined by the rapid-chase theory.

2. Experiment

2.1. General

Our experimental paradigm is similar to that used by Seydell-Greenwald and Schmidt (2012) to investigate the processing of illusory contours. Participants were asked to respond as quickly and accurately as possible to the orientation of a diagonal contour with upward or downward slope in an array of Gabor elements (target). The diagonal contour was defined either by a continuous line or emerged from the orientation of Gabor elements (snake, ladder, or texture). The target was preceded at varying SOAs by a snake, ladder, or texture prime that was either consistent or inconsistent with respect to the orientation of the diagonal (Fig. 1, upper panel). By comparing the priming effects induced by the different primes, as well as the effects' time courses, we can test whether primes are processed in accordance with a simple feedforward model of processing. In a subsequent prime identification task, participants were asked to report as accurately as possible the orientation of the diagonal in the prime. By comparing the prime identification performance for the different primes, we can test earlier results on different detection performance for these stimuli when masked (Vancleef & Wagemans, 2013).

2.2. Methods

2.2.1. Participants

Eight right-handed students from the University of Kaiserslautern, Germany (5 female, 3 male, ages 20–24), with normal or corrected vision participated in the experiment for payment of € 6 per hour. Participants were debriefed after the final session and received an explanation of the experiment. All of them gave informed consent in accordance with the Declaration of Helsinki and were treated in accordance with the ethical guidelines of the American Psychological Association.

2.2.2. Apparatus and stimuli

The participants were seated in a dimly lit room in front of a color monitor (1280 × 1024 pixels) with a monitor retrace rate of 85 Hz at a viewing distance of approximately 70 cm.

Stimuli consisted of arrays of small Gabor elements placed on a uniform gray background. The Gabor elements were even-symmetric and constructed by multiplying a cosine luminance grating (spatial frequency of 3.6 cycles per degree) with a circular Gaussian (standard deviation of 2.5 pixels). The elements were placed at quasi