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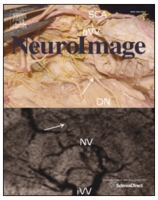

Targets but not flankers are suppressed in crowding as revealed by EEG frequency tagging

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ABSTRACT

Perception of a visual target can strongly deteriorate in the presence of flanking elements (crowding). For example, adding lines next to a vernier makes vernier offset discrimination difficult. Crowding is often considered a bottleneck of low-level vision, determined by the unavoidable limitations of the early visual system. In accordance with this proposal, neural processing of the flankers should be impaired in crowding as much as that of the target. To test this prediction, we used steady-state visually evoked potentials (ssVEPs) to separate target responses from flanker responses. We presented a vernier target either alone or flanked by lines, which had the same color as the vernier or a different color. Crowding by same-color flankers was stronger than by different-color flankers. Mirroring the behavioral results, ssVEP amplitudes corresponding to the target were higher for different-color flankers than for same-color flankers. Flanker related ssVEPs, however, did not depend on crowding strength. It seems that target, but not flanker processing, is susceptible to crowding. In line with previous results, we suggest that crowding is not caused by low-level interferences but is linked to target-flanker grouping instead.

1. Introduction

Human visual acuity is superb. Vernier acuity in the fovea can be as good as 1 arcsec, which is about 30 times smaller than the smallest diameter of a photoreceptor in the retina (hyperacuity, Hering, 1899; Klein and Levi, 1985; Westheimer, 1975; Wülfing, 1882). Hence, it seems that exquisite spatial resolution is important for human survival. Under other circumstances, however, vision is surprisingly poor. For example, performance deteriorates by a factor of 3 when a foveal vernier is flanked by two lines on each side (Malania et al., 2007; Westheimer and Hauske, 1975) and even by a factor of 10 when presented in the periphery (Manassi et al., 2012). This deterioration of performance is known as crowding and is often seen as an unavoidable bottleneck in object recognition (Levi, 2008; Parkes et al., 2001; Pelli et al., 2004; Whitney and Levi, 2011). Hence, the question arises, why does the human brain optimize performance when elements are presented in isolation but not when presented in clutter, which is the standard in everyday situations? Why is exquisite encoding lost?

We have recently argued that the loss of resolution in crowding and many other situations does not reflect a low-level (or any other level) bottleneck of the visual system but is "purposeful and reversible" (Herzog et al., 2014). Whereas superb resolution is desirable in certain situations, it is not when the human brain needs to process wholes rather than parts. For example, we have shown that strong crowding disappears when the flankers *un*group from the target, e.g., by becoming part of a larger whole (Herzog et al., 2015; Malania et al., 2007; Manassi et al., 2012, 2013; Saarela et al., 2009; Sayim et al., 2010).

The grouping hypothesis is supported by a previous EEG study, where we found that flankers, which grouped with the target, caused stronger suppression of the N1 ERP component than flankers that *un*grouped from the target (Chicherov et al., 2014). The P1 component that peaked around 120 ms did not reflect grouping but just the size of the stimuli. Since the N1 peaked around 190 ms, it seems that it takes approximately 70 ms to transform the "raw", retinotopic code into a perceptual code. Our results suggest that crowding occurs in a slow, recurrent process. Using EEG source localization techniques, we found that high-level visual areas reflected crowding better than V1 supporting, again, the idea that crowding is linked to grouping and appearance (Herzog et al., 2015).

The ERP experiments allowed us to estimate the time course and localization of crowding. However, ERPs are not well suited to study interactions among individual elements because all elements are presented simultaneously and ERPs contain responses to both the target and the flankers. Here, to understand how the single elements are processed in crowding situation and to understand better the mechanisms of crowding, we used EEG frequency tagging. In EEG frequency tagging, different elements of a stimulus flicker at different frequencies, thus, evoking EEG responses at different frequencies respectively (e.g., Andersen et al., 2008; Morgan et al., 1996). We can thus analyze neural responses to the target and the flankers separately. We expected that flankers would suppress the vernier according to the strength of target–flanker

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grouping but flankers would not be affected by crowding. This is exactly what we found suggesting that simple (mutual) pooling models are not sufficient to explain crowding.

2. Methods

2.1. Participants

15 paid volunteers joined the experiment. One observer was excluded from the analysis due to a lack of crowding in all conditions. The remaining 14 observers (7 females, aged 21–34 years, mean (SD) = 26.9 (3.9)) had normal or corrected-to-normal visual acuity as measured with the Freiburg Visual Acuity test, i.e., acuity values were above 1.0 in at least one eye (Bach, 1996). All but two of the observers were right-handed as assessed with the Edinburgh inventory (Oldfield, 1971). All observers were naïve to the purpose of the experiment. Participants provided written consent. The experiment was approved by the local ethics committee.

2.2. Apparatus and stimuli

Stimuli were generated using the Psychophysics Toolbox (ver. 3, Brainard, 1997) for Matlab R2011b (Windows OS) and presented on a cathode ray tube (CRT) monitor (resolution 1280 × 1024 pixels, refresh rate 75 Hz). Stimuli were presented on a black background. Observers were seated 150 cm from the monitor in a dimly-lit, electrically isolated room. Observers held one response button in the right and the other one in the left hand. Observers' eye fixation was controlled by an iViewX, SMI eye-tracker.

Verniers consisted of two vertical lines, each 84′ (arcmin) long with an 8′ vertical gap. The vernier was presented either alone or flanked by 4 lines on each side. The lines had the same length as the vernier. All lines were 3′ wide and were either red or green (Fig. 1A). Based on previous studies (Kooi et al., 1994; Manassi et al., 2012; Sayim et al., 2008), we expected flankers, which are identical in color to the vernier (same-color flankers), to crowd more strongly than different-color flankers. We presented the stimuli in a two-by-three factorial design with the factors *Vernier Color* (red or green) and *Flankers* (no flankers, same-color flankers, or different-color flankers). The horizontal distance between the flankers as well as between the vernier and the flankers was 35′. The vernier appeared 3.9° to the right of the fixation dot. The vernier flickered on and off at 7.5 Hz (10 monitor refresh cycles per period: 5 on- and 5 off-cycles) and the flankers at 9.375 Hz (8 monitor refresh cycles per period: 4 on- and 4 off-cycles). Red and green flankers or verniers were physically isoluminant (peak luminance during the flicker was 27 cd/m^2).

In each trial, a white fixation dot was presented for 1 s (diameter 8′). Then, the vernier and the flankers (if any) appeared. At stimulus onset, the vernier was always aligned, i.e., there was no offset. Randomly between 100 and 4867 ms, the vernier offset size started to increase and continued so with a constant speed for 500 ms. Then it decreased back to collinear during another 500 ms (total motion duration 1 s). The motion speed (and the vernier offset size) was controlled with an adaptive staircase procedure. After 5.867 s, the stimulus disappeared and observers indicated whether the vernier had changed its offset direction to the right or left by pushing one out of two buttons. The offset motion direction changed randomly from trial to trial. The number of left and right offsets was balanced in each block.

2.3. Procedure

First, we recorded psychophysical data without EEG. Subjects discriminated the vernier offset direction in three blocks of trials. Each block contained 156 trials (26 trials per condition, randomly interleaved). To

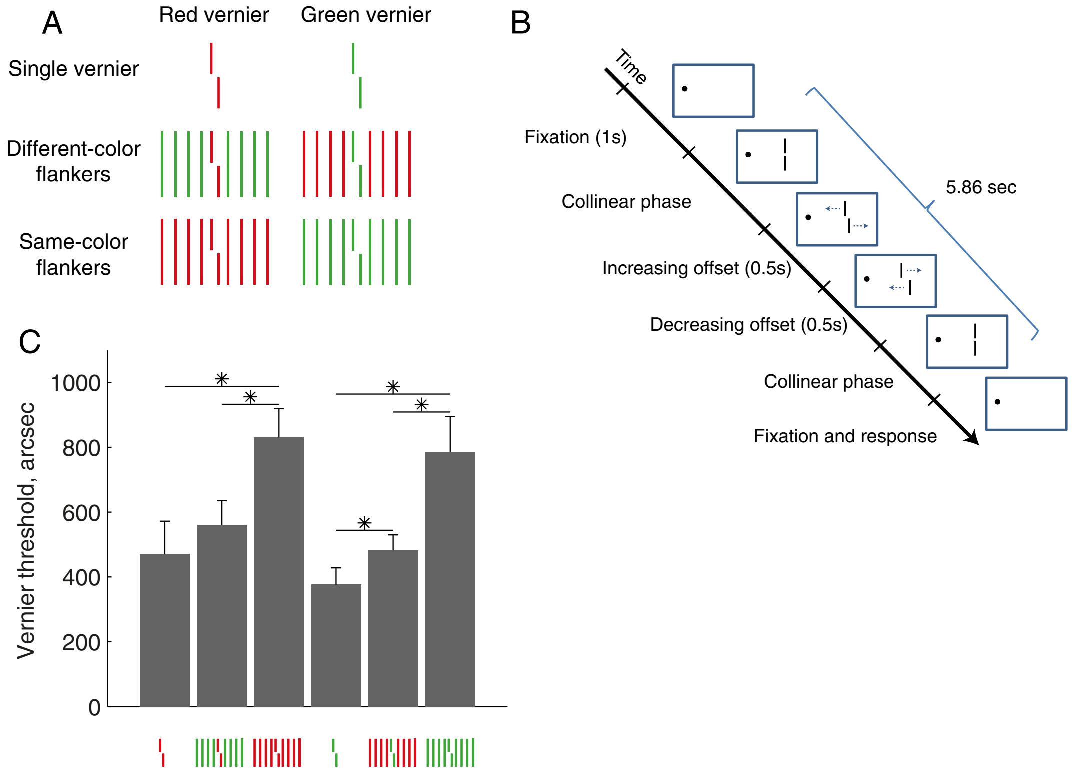

Fig. 1. (A) A vernier comprises two vertical lines with a small horizontal offset (here, a right offset is shown). Either a red or green vernier was presented alone or flanked by either different-color or same-color lines making up a 2 × 3 factorial design. (B) At random times after stimulus onset, the vernier offset started to increase either to the left or right (both lines moved). After reaching the maximum separation, the offset decreased back to the collinear state (here the vernier alone condition is shown). Subjects discriminated the vernier offset direction by pushing either the left or right button after the stimuli had disappeared. The vernier flickered at 7.5 Hz and the flankers at 9.375 Hz. (C) Low vernier thresholds correspond to good performance, large thresholds to weak performance. Flankers strongly deteriorated performance (crowding). Same-color flankers crowded more strongly than different-color flankers.