

## Neural correlates of visual crowding

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### ARTICLE INFO

#### Article history:

Accepted 16 February 2014

Available online 25 February 2014

### ABSTRACT

In visual crowding, target discrimination strongly deteriorates when flanking elements are added. We have recently shown that crowding cannot be explained by simple low-level interactions and that grouping is a key component instead. We presented a vernier flanked by arrays of vertical lines. When the flankers had the same lengths as the vernier, offset discrimination was strongly impaired. When longer flankers were presented, crowding was weaker. We proposed that crowding is strong when the flankers group with the target (equal length flankers). When the target segregates from the flankers, crowding is weaker (long flankers). To understand the neurophysiological mechanisms of grouping in crowding, here, we adapted the above vernier paradigm to a high-density EEG study. The P1 component reflected basic stimulus characteristics (flanker length) but not crowding. Crowding emerged slowly and manifested as a suppression of the N1 component (after 180 ms). Using inverse solutions, we found that the N1 suppression was caused by reduced neural activity in high-level visual areas such as the lateral occipital cortex. Our results suggest that crowding occurs when elements are grouped into wholes, a process reflected by the N1 component.

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### Introduction

Perception of an object is strongly influenced by neighboring elements. For example, a vertical line can appear strongly tilted when flanked by tilted lines (the tilt illusion, Gibson, 1937). Crowding is an example where neighboring elements strongly deteriorate performance (Bouma, 1970; Flom et al., 1963; Levi, 2008; Pelli and Tillman, 2008; Strasburger et al., 1991). For example, a letter that is clearly visible when presented alone cannot be identified when flanked by other letters. The letter itself is visible but its identification is severely impaired.

One influential explanation proposes that crowding occurs by pooling of nearby features. An element is first analyzed by neurons with small receptive fields coding for basic features. The output of these neurons is then fed into neurons with larger receptive fields pooling features of nearby elements. This pooling leads to confusion of features (Greenwood et al., 2009; Pelli et al., 2004; Wilkinson et al., 1997). Other explanations focus on centroids and

lateral inhibition (Levi and Carney, 2009; Westheimer and Hauske, 1975; Wilson, 1986).

We have recently shown that grouping, rather than pooling, plays a key role in both peripheral and foveal crowding (Malania et al., 2007; Manassi et al., 2012; Sayim et al., 2008). For example, we presented a vernier stimulus that comprised two vertical lines which were slightly offset horizontally. Observers were asked to indicate the offset direction (Fig. 1A). When the vernier was flanked by single lines of equal length, performance strongly deteriorated. This is a classical crowding effect. Interestingly, crowding diminished when single long or short flankers were presented and almost disappeared when arrays of short or long flankers were presented. These results cannot be explained with simple pooling models because longer and additional flankers should increase crowding strength, e.g., because more target-irrelevant information is pooled with the relevant target signal. We proposed that grouping determines crowding. Crowding is strong (equal length flankers), when the flankers group with the target. Crowding is weaker, when the target segregates from the flankers (Malania et al., 2007; Manassi et al., 2012; Sayim et al., 2008; see also Livne and Sagi, 2007).

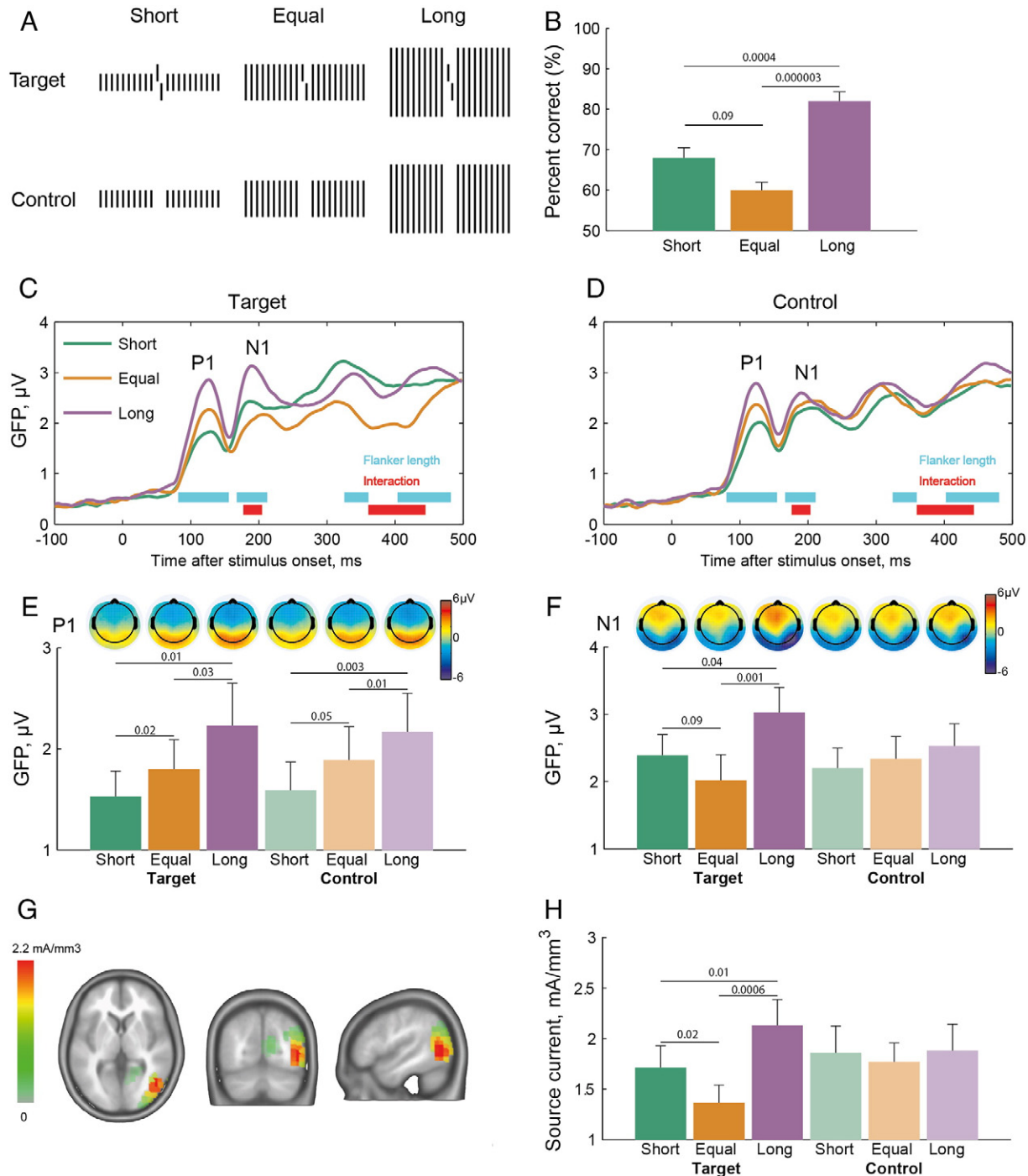
Whereas there is a vast amount of studies on crowding, there are only a few human neuroimaging studies (Anderson et al., 2012; Bi et al., 2009; Fang and He, 2008; Freeman et al., 2011; Millin et al., 2013) and almost nothing is known about the time course of crowding (but see early EEG studies on vernier acuity (Steinman et al., 1985; Zak

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and Berkley, 1986)). To understand the neurophysiological mechanisms of crowding and contextual modulation in general, we adapted the above vernier paradigm to a high-density EEG study and found that

crowding is reflected in late but not early visual processing, indicating that crowding occurs during higher-level visual processing when elements are grouped into wholes.



**Fig. 1.** Experiment 1a: foveal presentation. (A–B) In the *target conditions*, observers indicated whether the vernier was offset to the left or right (an offset to the right is shown here). In the *control conditions*, observers pushed randomly any button they wished. Performance in the target conditions was best when the vernier was flanked by long flankers, intermediate for short, and worst for equal length flankers. (C–D) Global field power (GFP). The P1 components in both the target (C) and control (D) conditions reflect flanker length. The N1 component reflects performance level in the target conditions. In the control conditions, this is not the case. The horizontal turquoise bars under the GFP curves indicate time periods of a significant main effect of Flanker length, the red bars — of significant interaction effects (see Supplementary Fig. 1 for the time course of the p-values). The main effect of Target/Control was not significant. (E) Amplitudes of the P1 component averaged over the time window 80–156 ms. Average topographical maps for each condition are shown above the bar plots. (F) Amplitudes of the N1 component averaged over the time window 176–202 ms. (G) Inverse solutions for the target conditions (LAURA inverse solution technique). A one-way ANOVA with the factor Flanker length was conducted in the source space in the N1 time window. Significant sources were attributed to two areas, one in the lateral occipital cortex (with parietal and temporal overlap) and a smaller area on the medial surface (precuneus), in the right hemisphere. The color scale shows current density differences between the long flanker condition and the equal length flanker condition indicating which sources contribute most strongly to the scalp differences (Talairach coordinates of the maximum: 48, –66, 1 mm). (H) Current densities averaged over all significant source points. As with N1 amplitudes, current densities were highest in the long condition, intermediate in the short, and lowest in the equal length condition. In the control conditions, current densities in the same source points were not significantly different. Error bars show the standard errors of mean. P-values for two-tailed paired t-tests are shown above the bar plots.

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