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A temporo-spatial analysis of the neural correlates of extrinsic perceptual grouping in vision

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ABSTRACT

Principles of perceptual grouping can be divided into *intrinsic grouping cues*, which are based on built-in properties of the grouped elements (e.g., their shape, position, colour, etc.) like most of the classical Gestalt laws, and *extrinsic grouping principles,* based on relations between the discrete elements and other external stimuli that induce them to group (e.g., common region, connectedness). Several studies have explored the neural correlates of intrinsic grouping factors but, to our knowledge, no previous study has studied the neural correlates of extrinsic principles. The present study aimed to shed light on this issue by exploiting the high temporal resolution of event-related potentials (ERPs) and recent advances in source localization. Specifically, grouping by common region was compared with two comparison conditions, an intrinsic grouping (luminance similarity) and a uniform stimulus condition, in a perceptual discrimination task. We reported three main neural effects associated with grouping by common region. First, a posterior N210 component with a neural origin in the left extrastriate cortex was related to perceptual analysis of extrinsic elements inducing grouping and the formation of a visual group. Second, an enhanced posterior P280, which presumably reflects higher confidence decisions during response selection. Finally, a P550 originated in the right superior parietal cortex that seems to be associated with top-down suppression activity connected with the termination of the processing of the current trial. Overall, our results suggest that common region cues belong to the category of long latency grouping principles that mainly involve activity in extrastriate cortices.

1. Introduction

The world we perceive consists of objects and their interrelations coherently arranged in scenes. The human visual system arranges the retinal mosaic into structured images by means of internal processes of organization (Palmer, 1999). The study of perceptual organization was developed by Gestalt psychologists one century ago (see Wagemans et al. (2012) for a review). According to Wertheimer (1923), organization is basically composed of grouping and segregation processes. The classical Gestalt principles describe the stimulus factors that determine the visual grouping of discrete elements, including proximity, similarity, common fate, good continuation and closure (Wertheimer, 1923). In the last two decades, other principles of grouping have been proposed, such as common region (Palmer, 1992), element connectedness (Palmer and Rock, 1994a, 1994b), synchrony (Alais et al., 1998; Lee and Blake, 1999), regularity (van den Berg et al., 2011) and induced grouping (Vickery, 2008).

Most relevant to the present study, Palmer (1992, 1999) introduced a distinction between *intrinsic grouping principles,* which are based on built-in properties of the grouped elements (e.g., their shape, position, colour, etc.) like most of the classical Gestalt principles, and a new set of *extrinsic grouping principles* based on relations between the elements and other external elements that induce them to group. For example, identical elements equally spaced in a display tend to be grouped together when they are located within the same spatial region (i.e., grouping by common region proposed by Palmer (1992)) or when they are connected by lines (i.e., grouping by connectedness proposed by Palmer and Rock (1994a, 1994b)). The main goal of the present study was to

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examine the neural correlates of common region, a representative sample of the extrinsic grouping principles.

During the last century, there has been important progress in research on perceptual grouping in the context of vision science, mainly concerning the development of quantitative laws and measures of strength of classical grouping factors (for an extensive review on these issues, see Wagemans et al. (2012)). More recently, several studies have been devoted to examining the temporal course and neural substrates of intrinsic perceptual grouping (see Sasaki, 2007). In contrast, the study of extrinsic grouping principles has received less attention. The results of several behavioural studies have suggested that they could constitute a different kind of principle, which operate differently from intrinsic principles (Palmer, 1992; Palmer and Beck, 2007).

The evidence from behavioural studies devoted to intrinsic principles suggests that different subtypes of grouping could have a different temporal course: grouping by proximity can be processed faster or earlier than grouping by similarity (Ben-Av and Sagi, 1995; Han and Humphreys, 1999; Han et al., 1999a, 1999b); grouping by proximity is faster than grouping by good continuation (Kurylo, 1997); and grouping forming simple shapes (i.e., elements grouped by common lightness into columns or rods or into a shape that does not require segregation from other elements) is faster than grouping forming complex shapes (i.e., elements grouped by common lightness into a shape that requires segregation from other elements; Kimchi and Razpurker-Apfeld, 2004; Razpurker-Apfeld and Kimchi, 2007).

ERP studies also showed differences in the temporal course of the neural correlates underlying intrinsic grouping principles. Grouping by proximity was associated with a positive component over occipital electrodes that peaked between 100 and 120 ms after sensory stimulation. Similarly, contour integration by collinearity emerges from 130 ms after stimulus onset, as evidenced by the results from Machilsen et al. (2011). In contrast, grouping by similarity (in shape or colour) was linked to a negativity over occipito-temporal scalp regions occurring much later, around 300 ms (Han, 2004; Han and Humphreys, 2007; Han et al., 2001, 2002, 2005a; Mao et al., 2004). However, the claim that grouping by proximity produces shorter latencies in ERP studies than grouping by similarity has been questioned by some authors (Kubovy and van den Berg, 2008; Nikolaev et al., 2008), given that the subjective strength of grouping by proximity and similarity was not equated, or even measured, in the studies quoted above. Thus, controlling for grouping strength seems to be a crucial aspect to consider in future research in order to obtain more conclusive results. Another relevant result observed in several ERP studies is related to the asymmetric hemispheric distribution of the intrinsic grouping factors. Han et al. (2001, 2002) found a greater role for the right hemisphere in proximity but a greater left lateralization in similarity. An explanation has been proposed in terms of spatial filtering of visual images and the relative dominance of the left and right hemispheres in the processing of high and low spatial frequencies, respectively (Beck et al., 1987; Ginsburg, 1986). According to this view, similarity grouping would require applying a high-pass filter, mainly mediated by the left hemisphere, in order to detect the visual cues needed for clustering the local elements (colour, shape, size, etc.). In contrast, proximity grouping can be usually solved by an analysis of low spatial frequencies, which is associated with activity in the right hemisphere (but see Han et al. (2001, Experiment 2)).

Neuroimaging studies also showed a different neural substrate for grouping by proximity and by similarity, suggesting that the primary visual cortex (V1) may be involved in grouping by proximity but not in grouping by similarity, which seems to depend on activation of higher visual areas (Han, 2004; Han et al., 2005b). Similarly, Altmann et al. (2003) found that Gabor patches grouped by collinearity generated greater activity in V1 than ungrouped Gabor patches. Finally, Wu et al. (2005) found that collinearity and proximity could share a common neural substrate in the primary visual cortex (see Sasaki (2007) for a review). In contrast, grouping by shape similarity has been associated with activation of higher areas such as the middle occipital and temporal cortices (Han et al., 2005a, 2005b). Also, activation within a shape-selective region, the lateral occipital complex (LOC), has been observed when participants had to respond to global shapes independently of the low-level visual cues (see Grill-Spector et al. (2001) for a review). In particular, perception of an object formed by grouping by motion (Fang et al., 2008; Ferber et al., 2003) or generating global shapes through grouping by collinearity (Altmann et al., 2003) seem to increase activation within this area.

A key question concerns to the spatiotemporal characteristics of perceptual organization mechanisms in early and higher visual areas in the human brain (Kourtzi and Huberle, 2005). Especially, the role of feedback loops from higher areas to lower sensory regions is largely unknown. Animal studies have provided support for the presence of recurrent mechanisms mediating top-down effects in the integration of local elements into a global configuration (see Roelfsema (2006) for a review). In humans, however, the study of feedforward and feedback processes with only non-invasive methods is more challenging (de-Wit and Schwarzkopf, 2014; Kourtzi and Huberle, 2005). Notably, a recent study including a simultaneous EEG–fMRI recording have provided precise evidence for the existence of a feedback loop from LOC to low-level retinotopic areas such as V1 during the processing of contour integration (Mijovic et al., 2014). Other studies have explored the top-down modulation of grouping associated with attention. Measuring fMRI and ERP activity, Han et al. (2005a, 2005b) found that the calcarine cortex was involved in grouping by proximity but not in grouping by shape similarity. In addition, they reported that the relevance for the task of stimulus arrays, as well as its locus, inside or outside of the attended area, modulated neural substrates of perceptual grouping. Activity in the calcarine cortex decreased when the elements fell outside of the attended area or when its relevance for the tasks was low. Finally, recording ERPs from two patients with fronto-parietal lesions and eight controls, Han and Humphreys (2007) found that the visuo-attentional fronto-parietal network (Corbetta, 1998; Corbetta and Shulman, 2002; Gazzaley and Nobre, 2012) was involved in the top-down modulation both of early and late intrinsic grouping processes. Interestingly, their results suggested that the activity of the fronto-parietal cortex was associated with enhanced initial sensory processes but, in contrast, inhibited neural activity in the visual cortex at a later stage. In a similar direction, the fMRI study of Seymour et al. (2008) revealed that the processing of different Gestalt grouping cues (i.e. proximity and shape similarity) involved the activation of the inferior parietal cortex, suggesting a top-down reentrant modulation over the visual areas.

In sum, the previous literature on intrinsic grouping suggests that different types of grouping principles have divergent temporal courses and different neural origins. From an integrative perspective, prior results could be grouped into two categories: (1) a short latency grouping involving the activity of the striate cortex and linked to Gestalt principles such as proximity or collinearity and (2) a long latency grouping that involves activation in the extrastriate and occipito-temporal areas associated with similarity grouping (see Sasaki (2007) for a similar account). In the first case, an early representation of spatial clustering of local elements based on their proximity or a detection of collinearity by linking responses of V1-cells aligned across space (but with similar orientation tuning) may be mainly supported by the striate cortex. In contrast, similarity grouping entails processing of more complex visual features (e.g., colour, shape, luminance, size, etc.) acting as