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ELECTROPHYSIOLOGICAL CORRELATES OF VISUAL BINDING ERRORS AFTER BILATERAL PARIETAL DAMAGE

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Abstract—Illusory conjunctions (e.g. the confusion between the shape of one stimulus with the color of another stimulus) are the most dramatic expression of binding failures in vision. Under brief exposure or when attention is diverted illusory conjunctions may be observed in healthy participants, but they only represent a real-life problem for patients with parietal damage. However, it is unclear whether such failures reflect the impairment of early or late stages of visual processing. Here, we examined the time-course of visual processing using evoked potential measures in a patient with bilateral damage to the posterior parietal cortex presenting prominent binding failures. The patient was asked to identify colored letters that were briefly flashed to the left or right hemifield. When only one item was presented she adequately identified color or shape of left and right letters. In contrast, when presentation was bilateral she either identified the correct right shape-color combination and missed the item in the left hemifield (extinction) or combined incorrectly the right shape with the left color (illusory conjunction). Evoked potential analyses revealed a specific electrophysiological signature of illusory conjunctions, starting ~105 ms after stimulus onset over the right frontal cortex. These findings indicate that binding errors reflect failures of early stages of attentional filtering relying on the integrity of the posterior parietal cortex.

Key words: visual attention, parietal lobe, binding, features, illusory conjunction.

INTRODUCTION

During the initial stages of visual processing at the cortical level information is highly segregated across a multitude of areas specialized for shape, orientation, color or motion (Felleman and Van Essen, 1991; Reynolds and Desimone, 1999). Due to this specialization feature representations are distributed across distinct cortical regions of the visual cortex. Where and when a unified and integrated representation of an object is elaborated by recombining distinct features is referred to as the *binding problem* (von der Malsburg, 1995; Treisman, 1996).

The existence of a binding problem in vision is exemplified by visual search studies. The search for a target characterized by a distinct feature (e.g. a single red letter among green letters) is very fast, effortless and independent of the number of distracters. In contrast, searching for a distinctive combination of features (e.g., a vertical red line among vertical green and horizontal red lines) generally leads to effortful search with response times that increase linearly with increasing numbers of distracters (Treisman and Gelade, 1980; Eckstein, 2011). Many basic stimulus attributes such as color, orientation or shape can be processed preattentively, and often in parallel in early vision (Treisman, 1998). However, unless attention is directed to them they only appear as loose collections of features rather than as coherent visual objects (Wolfe and Bennett, 1997). In contrast, attentive vision has limited capacity, but allows localizing single features and feature combinations. Though under some experimental conditions (in particular if features are rendered salient) the search for feature combinations may be effortless (Wolfe, 1994), many authors agree that the perception of coherent, spatially localized objects requires focal attention, and that capacity limitations lead to binding failures (Treisman, 1998; Cave and Bichot, 1999; Wolfe and Cave, 1999). Thus, at the phenomenological level preattentive vision may signal the presence of redness and curves, while attentive vision may identify a red apple (Billock and Tsou, 2004).

Functional imaging studies have shown that attentive processing of feature combinations strongly activates the superior parietal cortex (Corbetta et al., 1995; Shafritz et al., 2002; Egner et al., 2008). This finding is consistent with experimental studies on rare patients with bilateral parietal damage showing deficits in visual search, localization and binding of different stimulus features (Rafal, 1997; Robertson, 2003). When shown brief displays these patients may erroneously report illusory

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Abbreviation: ERP, event-related potential; EEG, electroencephalogram.

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conjunctions that are, feature combinations that were not present in the display. Illusory conjunctions have been observed for combinations of shape and color, shape and size, or color and motion (Friedman-Hill et al., 1995; Bernstein and Robertson, 1998; Humphreys et al., 2000; Valenza et al., 2004).

Though under very brief presentation conditions and especially in peripheral vision illusory conjunctions may be provoked in healthy observers (Treisman and Schmidt, 1982; Billock and Tsou, 2004), they only represent a real-life problem in patients with parietal damage (Cohen and Rafal, 1991; Friedman-Hill et al., 1995). The binding deficit in these patients is secondary to a severe impairment of explicit spatial localization (Cinel and Humphreys, 2006), and was therefore hypothesized to reflect the failure of a late stage of visual processing (Robertson et al., 1997). This proposal is in agreement with the feature integration theory, which states that single features are separately processed in parallel in preattentive feature maps and then integrated at a later stage where the spatial positions of distinct features become available (Treisman and Gelade, 1980; Treisman, 1998). In addition, early versions of feature integration theory proposed that spatial attention is necessary for feature binding and acts as 'glue', binding features that are within its spotlight into a coherent object (Quinlan, 2003). Support for two-stage models such as feature integration theory has mainly come from visual search studies, and in particular from the observation that search for a target characterized by a single salient feature is fast and largely independent of the number of distracters while search for a feature conjunction is slow and effortful (Treisman and Gormican, 1988; Quinlan, 2003). However, this experimental finding contrasts with the relative ease and velocity with which healthy observers perceive complex feature combinations characterizing everyday objects. In addition, visual search for a single feature may be rendered difficult and effortful when the target is only slightly distinct from the distracters, while under some conditions feature combinations may be detected in the absence of focused attention (Duncan and Humphreys, 1989; Holcombe and Cavanagh, 2001; Wolfe and Horowitz, 2004). In addition, though a role of attentional limitation by brief exposures, crowding or diverted attention has been considered as crucial for the occurrence of illusory conjunctions (Wolfe and Cave, 1999), some studies obtained feature integration errors with long durations and without diverting attention (Prinzmetal et al., 1995). Thus, behavioral studies do not make it clear whether illusory conjunctions result from the failure of early or late perceptual processes. A possible alternative is to study electrophysiological correlates of visual binding errors by measuring event-related potentials (ERPs). However, while there is a tradition of studying visual search performance with ERP methods (Luck et al., 1993; Luck and Hillyard, 1994; Leonards et al., 2003; Hickey et al., 2009; Eimer and Kiss, 2010), these studies focused on attentional mechanisms implicated in serial or parallel search rather than on the attentional failures leading to visual binding errors.

Here, we studied a rare patient with bilateral damage to the posterior parietal cortex exhibiting prominent binding errors when shown simple displays containing colored letters. We took advantage of the excellent temporal resolution of ERP measures to investigate whether binding in our patient depended on early (preattentive) feature combination processes, or whether a later process requiring focused attention is necessary. We found that illusory conjunctions were associated with a specific electrophysiological signature starting ~105 ms following stimulus presentation, indicating that visual binding relies on early selection processes.

EXPERIMENTAL PROCEDURES

Participant

EB, a right-handed 74-year-old woman, suffered from two consecutive strokes that left her with a combination of symptoms characteristic of Bálint's syndrome: inability to perceive more than one object at a time (simultanagnosia), optic ataxia and ocular apraxia (Bálint, 1909; Rafal, 1997; Ptak and Müri, 2013). High-resolution structural MRI performed three years following the second stroke revealed chronic necrotic changes affecting mainly the supramarginal and postcentral gyrus of the right hemisphere and the angular, supramarginal and superior occipital gyrus of the left hemisphere (Fig. 1A).

At the time of this study the patient had recovered from ocular apraxia and optic ataxia up to a point allowing her to gain independence in some daily activities, but continued to show severe deficits of spatial attention. Her visual fields were preserved on confrontation testing, and she could identify simple shapes, colors, or everyday objects, but frequently made visual errors suggesting that she failed to explore an object in its entirety (e.g., she would confound a match with a crayon). Visual extinction was complete on confrontation testing, mostly affecting the left side. Table 1 shows results of neuropsychological testing of

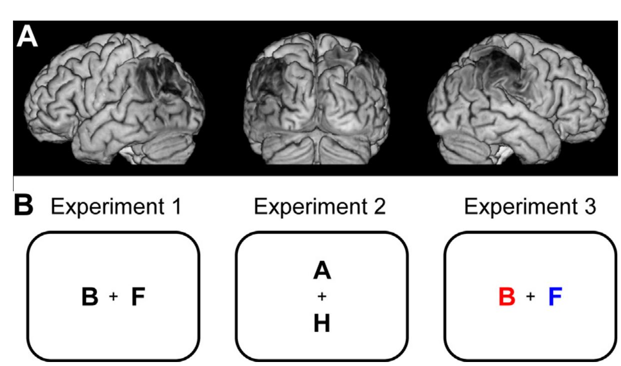

Fig. 1. (A) Left, posterior and right view of EB's brain showing bilateral parietal damage, while the occipital cortex appears preserved. (B) Examples of double simultaneous displays presented in the three experiments. Note that letters are not shown in the original scale and that in reality all stimuli were either white or colored and shown on black background.