

Preserved local but disrupted contextual figure-ground influences in an individual with abnormal function of intermediate visual areas

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ABSTRACT

Visual perception depends not only on local stimulus features but also on their relationship to the surrounding stimulus context, as evident in both local and contextual influences on figure-ground segmentation. Intermediate visual areas may play a role in such contextual influences, as we tested here by examining LG, a rare case of developmental visual agnosia. LG has no evident abnormality of brain structure and functional neuroimaging showed relatively normal V1 function, but his intermediate visual areas (V2/V3) function abnormally. We found that contextual influences on figure-ground organization were selectively disrupted in LG, while local sources of figure-ground influences were preserved. Effects of object knowledge and familiarity on figure-ground organization were also significantly diminished. Our results suggest that the mechanisms mediating contextual and familiarity influences on figure-ground organization are dissociable from those mediating local influences on figure-ground assignment. The disruption of contextual processing in intermediate visual areas may play a role in the substantial object recognition difficulties experienced by LG.

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1. Introduction

In the normally developed human visual system, visual scenes are effortlessly and rapidly segmented into a structured set of surfaces and objects. Yet it remains far from clear how the visual system achieves such a complex computation. Gestalt psychologists first pointed out that visual perception does not comprise only perception of independent local elements (Wertheimer, 1923). Rather, perception of local elements can depend on their surrounding context (for recent examples see: Anderson, 2003; Gilchrist, 1977; Herzog, 2003; Polat & Sagi, 1993; Rock & Palmer, 1990; Williams, McCoy, & Purves, 1998). There has been substantial interest in studying the mechanisms of such contextual integration (e.g. Albright & Stoner, 2002). A recurring issue is the level of visual processing at which various contextual influences first arise (e.g. Palmer, Brooks, & Nelson, 2003; Palmer & Nelson, 2000; Rock & Brosdale, 1964; Rock, Nijhawan, Palmer, & Tudor, 1992; Schulz & Sanocki, 2003) and its neural underpinnings. Neurophysiological findings shed some light on this. For instance, recent work suggests that perceived brightness (as induced by surrounding

context) may be reflected in the activity of neurons as early as primary visual cortex (e.g. Harris, Schwarzkopf, Song, Bahrami, & Rees, 2011; MacEvoy, Kim, & Paradiso, 1998; Rossi & Paradiso, 1999). Other contextual influences may involve the input of higher-order visual areas with larger receptive fields. For instance, certain Gestalt grouping processes may involve not only horizontal but also feedback connections (e.g. Grossberg, Mingolla, & Ross, 1997; Roelfsema, 2006) from higher areas. This notion is supported by functional imaging and neurophysiological data (e.g. Fang, Kersten, & Murray, 2008; Lee & Nguyen, 2001).

Recent work shows that figure-ground assignment, a well-known topic in Gestalt psychology, can be determined by remote contextual visual information, in addition to the many well-known local figure-ground cues (Brooks & Driver, 2010; Peterson & Salvagio, 2008; Zhang & von Der Heydt, 2010). Figure-ground assignment is an important aspect of visual processing whereby contours are assigned to one or the other adjacent regions to determine relative depth and perceived shape along edges (e.g. Baylis & Driver, 2001; Burge, Peterson, & Palmer, 2005; Driver & Baylis, 1996; Nakayama, Shimojo, & Silverman, 1989). For instance, the visual system could interpret the edge in Fig. 1A as a black object with soft, rounded bumps (on a white background) which may feel nice to touch or, alternatively, as a white object with sharp, spiked points that should be avoided. Such figure-ground assignment ambiguity has often been demonstrated with the

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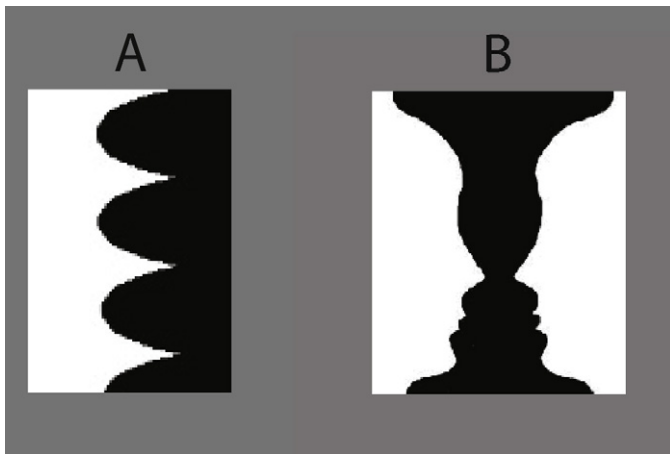


Fig. 1. Examples of how perceived shape depends on figure-ground organization. (A) The shape along the central vertical edge can be perceived as a white object with sharp, spiked points on a black background or a black object with soft, rounded bumps on a white background. Which of these two interpretations is perceived depends on figure-ground organization across the edge. (B) The well-known faces-vase drawing by Rubin demonstrate how the same edges can depict either two profile faces or a central vase depending on the figure-ground organization across the edges.

well-known faces-vase drawing (Fig. 1B) described by Rubin (1921). Figure-ground assignment is influenced by local image factors such as convexity (Kanizsa & Gerbino, 1976; Stevens & Brookes, 1988), edge-region relationships (Palmer & Brooks, 2008), surface curvature information (Palmer & Ghose, 2008), as well as cognitive factors such as previous experience (Peterson & Enns, 2005; Peterson & Gibson, 1994a; Peterson, Harvey, & Weidenbacher, 1991) and attention (Baylis & Driver, 1995; Huang & Pashler, 2009; Vecera, Flevaris, & Filapek, 2004). Neurons in V1 and V2 code the direction of figure-ground assignment across an edge (Fang, Boyaci, & Kersten, 2009; Qiu & von Der Heydt, 2005; Zhou, Friedman, & von Der Heydt, 2000) suggesting that early visual areas can have a strong representation of this important visual property. However, responses of these neurons are notably modulated by contextual information that falls outside the neuron's classical receptive field (Zhang & von Der Heydt, 2010). This suggests a mechanism which must integrate information across the visual field through connections with other neurons perhaps including feedback from higher level neurons with larger receptive fields (Jehee, Lamme, & Roelfsema, 2007; Roelfsema, Lamme, Spekreijse, & Bosch, 2002).

Neurophysiological work in V1 and V2 neurons (Sugihara, Qiu, & von der Heydt, 2011) has compared the onset latency of contextually driven figure-ground effects to that of locally-induced figure-ground effects and found that contextual influences are likely to involve feedback from higher-order visual areas. Some computational models (Craft, Schütze, Niebur, & von der Heydt, 2007; Jehee et al., 2007; Kienker, Sejnowski, Hinton, & Schumacher, 1986; Roelfsema et al., 2002; Sajda & Finkel, 1995) also support this notion, while others suggest that figure-ground computations are confined to early visual cortex (e.g. Baek & Sajda, 2005; Nishimura & Sakai, 2004, 2005; Zhao, 2005). At present, it is unclear whether some of the recently established contextual influences on figure-ground assignment (e.g. Brooks & Driver, 2010; Peterson & Salvaggio, 2008) reflect the same mechanism as local figure-ground cues, or whether they may be dissociable.

Here, we sought to address whether local and contextual mechanisms of figure-ground assignment are dissociable by studying a rare case of developmental visual agnosia, case LG (Aviezer, Hassin, & Bentin, 2011; Gilaie-Dotan, Bentin, Harel, Rees, & Saygin, 2011; Gilaie-Dotan, Perry, Bonne, Malach, & Bentin, 2009). LG has no gross structural brain abnormality visible on MRI. Functional MRI

experiments, however, show that while his primary visual cortex is functionally preserved his intermediate visual regions (V2/V3, see Gilaie-Dotan et al., 2009), both ventrally and dorsally, show functional pathology (e.g. are significantly deactivated in response to visual stimulation). Likewise ERP experiments also confirm that components normally associated with processing in intermediate visual cortices are abnormal or absent in LG (Gilaie-Dotan et al., 2009). This rare case, with preserved early visual function but pathological intermediate visual cortical function, provides an opportunity to test whether contextual influences on figure-ground assignment depend on normal functioning of intermediate visual areas, whereas local influences on figure-ground assignment may be computed in earlier visual cortex without feedback from higher level visual areas. If so, then local figure-ground assignment should be preserved in LG, whereas contextual influences should be reduced or eliminated. In addition, since LG also shows object recognition problems, we were further able to test whether top-down object-knowledge nonetheless influences his figure-ground assignment, as in normal individuals (e.g. Peterson & Gibson, 1991, 1994a).

2. Case history

LG was a 24 year old, right-handed male at the time of testing who suffers from developmental visual agnosia. His object and face recognition problems were already apparent from a very young age and he was formally diagnosed at the age of 8 years (Ariel & Sadeh, 1996). As part of a previous study (Gilaie-Dotan et al., 2009), a high-resolution structural MRI scan of his brain was examined by a neuro-radiologist who was unaware of LG's condition. No evidence of structural abnormality was identified. LG functions as a fully independent adult, studies, works and reads, after finishing high school successfully.

A brief overview of the object recognition neuropsychological examination that LG underwent is provided here. More details can be found in an earlier report (Gilaie-Dotan et al., 2009). In the Boston Naming Test, he scored within normal range (45/54, all failures explained by cultural factors) but in the Hooper Visual Organization Test, when objects are presented as a collection of their spatially scattered parts so that their identification requires re-orienting and integrating the parts into a whole, his performance was very weak (12.5/30, categorized as "very high probability of impairment"). While his performance with the minimal feature match, BORB-7 (Riddoch & Humphreys, 1993) was errorless, his ability to recognize overlapping line drawings, BORB-6; (Riddoch & Humphreys, 1993), was deficient. He performed better with simple geometrical shapes and had a noticeable difficulty with letters and more complex line drawings. This difficulty was reflected both by errors (e.g. 11 errors out of 36 superimposed triples of letters) and particularly by extremely long RTs. The ratio between the RTs of overlapping stimuli compared with RTs of isolated stimuli was three times the ratio of the normal mean. He is also severely prosopagnosic as assessed by the Benton Facial Recognition Test (Benton, Sivan, Hamsher, Varney, & Spreen, 1983): 33/54 faces, severely impaired; Warrington's Face/Word Recognition Test (Warrington, 1984), words = 47/50, faces = 37/50; and the Cambridge Face Memory Test (Duchaine & Nakayama, 2006), 34/75, 6 points below the usual congenital prosopagnosia mean.

Testing LG's brain activation patterns to visual stimulation as measured by fMRI (Gilaie-Dotan et al., 2009) revealed that activity in LG's primary visual cortex is apparently normal whereas LG's intermediate visual regions (corresponding to V2 and probably V3/VP) are profoundly deactivated by visual stimulation. This deactivation is independent of the precise nature of the visual stimuli (line drawings, gray scale or color photographs and even

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