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Cue-dependent circuits for illusory contours in humans

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ABSTRACT

Objects' borders are readily perceived despite absent contrast gradients, e.g. due to poor lighting or occlusion. In humans, a visual evoked potential (VEP) correlate of illusory contour (IC) sensitivity, the "IC effect", has been identified with an onset at ~90 ms and generators within bilateral lateral occipital cortices (LOC). The IC effect is observed across a wide range of stimulus parameters, though until now it always involved high-contrast achromatic stimuli. Whether IC perception and its brain mechanisms differ as a function of the type of stimulus cue remains unknown. Resolving such will provide insights on whether there is a unique or multiple solutions to how the brain binds together spatially fractionated information into a cohesive perception. Here, participants discriminated IC from no-contour (NC) control stimuli that were either comprised of low-contrast achromatic stimuli or instead isoluminant chromatic contrast stimuli (presumably biasing processing to the magnocellular and parvocellular pathways, respectively) on separate blocks of trials. Behavioural analyses revealed that ICs were readily perceived independently of the stimulus cue—i.e. when defined by either chromatic or luminance contrast. VEPs were analysed within an electrical neuroimaging framework and revealed a generally similar timing of IC effects across both stimulus contrasts (i.e. at ~90 ms). Additionally, an overall phase shift of the VEP on the order of ~30 ms was consistently observed in response to chromatic vs. luminance contrast independently of the presence/absence of ICs. Critically, topographic differences in the IC effect were observed over the ~110–160 ms period; different configurations of intracranial sources contributed to IC sensitivity as a function of stimulus contrast. Distributed source estimations localized these differences to LOC as well as V1/V2. The present data expand current models by demonstrating the existence of multiple, cue-dependent circuits in the brain for generating perceptions of illusory contours.

Introduction

The visual system can create perceptions of boundaries despite the visual input to the retina being discontinuous or incomplete; resulting from poor lighting, occlusion, or myriad other everyday situations. These perceptions, including ICs, have been the subject of extensive theoretical debate and experimental research across species (Murray and Herrmann, 2013). A commonly-used stimulus was popularized by Kanizsa (1976) and includes an array of circular sectors (pacmen), whose mouths are oriented so to induce ICs or, alternatively, rotated as to prevent such perceptions (hereafter no-contour; NC) (Fig. 1).

Several competing models have been proposed regarding how the brain produces ICs (Murray and Herrmann, 2013). Some propose that low-level areas V1/V2 mediate IC sensitivity in a feed-forward manner (Grosof et al., 1993; Nieder and Wagner, 1999; Redies et al., 1986; von der Heydt et al., 1984). Others propose that lateral occipital cortices (LOC) within the ventral visual pathway (Ungerleider and Mishkin, 1982) mediate it, and that any effects in V1/V2 reflect feedback modulations subsequent to IC sensitivity itself (Lee and Nguyen, 2001; Mendola et al., 1999; Murray et al., 2006, 2004, 2002; Sáry et al., 2008, 2007). Still others propose that the LOC detects salient regions defined by the pacmen inducers, but that IC sensitivity is itself performed within V1/V2 albeit under the control of feedback modulations (from the LOC and elsewhere) (Hochstein and Ahissar, 2002; Stanley and Rubin, 2003; Yoshino et al., 2006).

A VEP correlate of IC sensitivity has been identified – the IC effect – that onsets at ~90 ms post-stimulus (i.e. during the P1/N1 components

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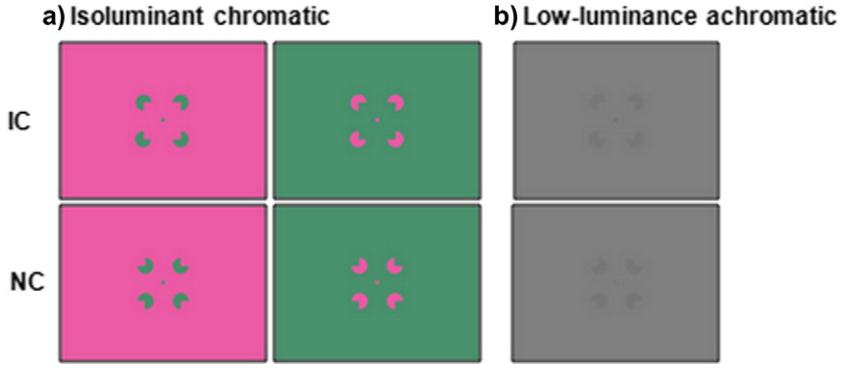

Fig. 1. Illustration of stimulus conditions. **a.** Isoluminant chromatic contrast stimuli either appeared pink on green or vice versa. **b.** Low-luminance achromatic contrast stimuli used pacmen inducers that were slightly darker than the background. Note that the contrast in the figure was modified for ease of visibility. The illusory contour (IC) condition involved inducers whose mouths all faced inward (top row), while the no contour (NC) condition involved inducers whose mouths all faced outward (bottom row). The central fixation point has been enlarged for illustration purposes.

of the VEP) and is localised to the bilateral LOC (Murray et al., 2002). This IC effect has been observed across various manipulations of low-level stimulus features inducing ICs, including contrast polarity, eccentricity, types of inducers, and modal/amodal completion (Murray and Herrmann, 2013). However, a major shortcoming of *all* prior neurophysiologic studies of IC sensitivity in animals and humans is that the employed stimuli were invariably high in contrast (black and white, in fact). The extent to which the spatio-temporal brain dynamics of the IC sensitivity are cue-dependent and impacted by stimulus features, such as luminance and chromaticity, remains unknown. Resolving the role of these stimulus features in IC sensitivity would provide much-needed insights into potentially differing contributions of magnocellular versus parvocellular subdivisions of the visual system to IC sensitivity (Ejima and Takahashi, 1988; Gregory, 1977; Li and Guo, 1995; Soriano et al., 1996) as well as potentially reconcile the discrepant findings and the resultant models of IC sensitivity.

It has been suggested that mechanisms based on luminance and those based on chromaticity might both contribute to IC sensitivity, with the two mechanisms operating concurrently (Takahashi et al., 1992; see also Ferrera et al. (1992) for evidence of parvocellular and magnocellular convergence in macaque area V4). At present, direct neurophysiologic support for this proposal is largely lacking. Indirect supporting evidence has been provided by the results demonstrating that ICs can be induced with both static and moving inducers (e.g., Seghier et al., 2000) as well as with inducers that oscillate (Masuda et al., 2015). Such data would suggest that both dorsal and ventral visual pathways (which are thought to receive a preponderance of magnocellular and parvocellular inputs, respectively) likely contribute to IC sensitivity processes. In line with this suggestion, parietal sources have been identified as contributing to the IC effect (cf. Figure 6a in Murray et al., 2002; reviewed in Murray and Herrmann, 2013). However, parietal structures do not appear to forcibly be requisite for IC perception. Studies of brain-lesioned patients have shown that IC perception critically depends on the integrity of the LOC, but persists despite damage to parietal cortices (cf. Figure 5 in Vuilleumier et al., 2001). Similarly, studies of patients with schizophrenia would indicate that the IC effect triggered by high-contrast achromatic stimuli is indistinguishable from that recorded from healthy controls, despite severely impaired P1 component responses in the former group (Foxe et al., 2005; Knebel et al., 2011). More generally, evidence is accumulating to support the idea of impaired magnocellular system function in schizophrenia (Butler et al., 2007; Javitt, 2009). One implication for IC sensitivity is that this process might operate largely independently of the magnocellular and/or dorsal pathway, relying instead on the integrity of the parvocellular system and the ventral stream structures. However, and because extant studies have used high-contrast achromatic stimuli, it is not clear if IC processes operate in a cue-invariant manner. Data from recordings within lower-level visual cortices (V1/V2) in animals would suggest that orientation and contour sensitivity may operate in a largely cue-invariant manner (e.g. (Song and Baker, 2007; Gharat and Baker, 2012)).

In light of such, we reasoned that cue-invariant IC effects would be consistent with IC processing being mediated in a (largely) feed-forward manner by regions such as V1/V2. By contrast, cue-dependent IC effects would instead support LOC-centred models of IC processing. The current study thus determined whether the IC effect is limited to the specific type of stimulus contrast used to elicit it; the evidence for such limitation would undermine the emerging consensus on the (uniform) brain underpinnings of IC sensitivity. By analysing VEPs within an electrical neuroimaging framework, we differentiated effects arising due to changes in the brain response timing, strength, and topography (Michel and Murray, 2012; Murray et al., 2008). If differences were found merely in the strength of responses of a statistically indistinguishable network across the two IC contrasts, this would suggest that a single, uniform brain network/mechanism mediates IC sensitivity. If, instead, early differences in the topography and underlying sources were found between the two types of contrast, such a result – depending on how strong/early were the differences observed – could suggest a 1) certain flexibility within the already identified network or, alternatively, 2) separate and distinct brain circuits activated by different types of stimulus contrast. The latter would necessitate revision of the emerging consensus about the brain mechanisms giving rise to IC sensitivity.

Material and methods

Participants

Analyses presented in this study are based on data from 12 participants (4 male, all right-handed; aged 23–33 years, mean 25.8 years). All were post-graduate university students at the time of testing. No subject had history of or current neurological or psychiatric illness. All participants had normal or corrected-to normal vision and no problems with colour vision or colour-blindness were reported. The integrity of colour vision was based on participants' self-reports according to their prior experiences with the Ishihara colour test (Ishihara, 1972), as routinely performed in Swiss primary schools as well as in military recruiting centres. Data from an additional 8 subjects were excluded due to either excessive muscle and/or alpha frequency EEG artefacts ($N = 7$) or technical issues with behavioural response recording during data acquisition ($N = 1$).

Stimuli and task

Stimuli were comprised of a set of 4 circular Kanizsa-type (Kanizsa, 1976) 'pacmen' inducers that were arranged to either form an illusory contour or not (IC and NC conditions, respectively) (Fig. 1). Each inducer subtended 1.26° in diameter of visual angle at a distance of