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The effort to close the gap: Tracking the development of illusory contour processing from childhood to adulthood with high-density electrical mapping

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ABSTRACT

The adult human visual system can efficiently fill-in missing object boundaries when low-level information from the retina is incomplete, but little is known about how these processes develop across childhood. A decade of visual-evoked potential (VEP) studies has produced a theoretical model identifying distinct phases of contour completion in adults. The first, termed a perceptual phase, occurs from approximately 100–200 ms and is associated with automatic boundary completion. The second is termed a conceptual phase occurring between 230 and 400 ms. The latter has been associated with the analysis of ambiguous objects which seem to require more effort to complete. The electrophysiological markers of these phases have both been localized to the lateral occipital complex, a cluster of ventral visual stream brain regions associated with object-processing. We presented Kanizsa-type illusory contour stimuli, often used for exploring contour completion processes, to neurotypical persons ages 6–31 ($N = 63$), while parametrically varying the spatial extent of these induced contours, in order to better understand how filling-in processes develop across childhood and adolescence. Our results suggest that, while adults complete contour boundaries in a single discrete period during the automatic perceptual phase, children display an immature response pattern—engaging in more protracted processing across both timeframes and appearing to recruit more widely distributed regions which resemble those evoked during adult processing of higher-order ambiguous figures. However, children older than 5 years of age were remarkably like adults in that the effects of contour processing were invariant to manipulation of contour extent.

Introduction

von Helmholz observed that vision relies on more than stimulation of the retina, "*reminiscences of previous experiences act in conjunction with present sensations to produce a perceptual image*." (von Helmholz, 1910). Poor lighting, occlusion, and the fact that the retina is a variegated and somewhat discontinuous surface produce incomplete, two-dimensional low-level representations of objects. Changes in perspective or viewing distance of a given object result in projection of vastly different images onto this surface. Indeed, the retina contains a so-called blind-spot of nearly 2 mm in diameter where the axons of the optic nerve exit (Quigley et al., 1990), and yet, the visual system seamlessly "fills in" the missing information (Pessoa and De Weer, 2003). As Helmholz inferred, perception might be more reasonably characterized as an interaction between relatively impoverished sensory representations and internally-generated representations that have been encoded through experience. Such interpolation of visual input has been observed electrophysiologically during the automatic filling-in of certain types of fragmented contours, with related modulations of brain activity observed within 90–150 ms of stimulus presentation (Brodeur et al., 2006; Foxe et al., 2005; Li et al., 2006; Murray et al., 2002; Proverbio and Zani, 2002; Shpaner et al., 2009). The bulk of this processing occurs prior to the viewer's awareness of the object (Vuilleumier et al., 2001) or the application of semantic knowledge to identify it or make judgments regarding its characteristics (Murray et al., 2006). These automatic completion processes have been extensively studied in adults using psychometrics, electrophysiology, and neuroimaging (e.g., Ffytche and Zeki, 1996; Halko et al., 2008; Mendola et al., 1999; Ohtani et al., 2002; Ringach and Shapley, 1996). Developmental explorations have studied this process in infancy (e.g., Bremner et al., 2012; Csibra, 2001; Otsuka et al., 2004), but the use

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of fixation duration in such studies allows only an implied measure of neural processing. A behavioral study in children suggests that completion processes are still developing from 6 until at least 12 years-of-age (Hadad et al., 2010), however, no one has characterized neural processing using electrophysiology across multiple stages of development. We don't know whether completion processes are similarly automatic to adulthood, whether their timecourse is the same, or whether the same regions of the brain are implicated in children.

One of the primary approaches to understanding these contour integration processes has involved the use of a class of stimuli with incomplete contours that nonetheless induce perception of complete contours, known as illusory contour (IC) stimuli (Kanizsa, 1976; Schumann, 1900). These stimuli have proven very useful for studying contour completion specifically and the binding of features into objects more generally (Csibra et al., 2000) because simple rearrangements of elements of identical stimulus energy give rise to considerably different percepts (Fig. 1). In the illusion-inducing configuration, viewers describe continuous contours between inducing elements, contours which form a two-dimensional object that appears to be superimposed on the background. In the non-inducing arrangement, they describe only the inducers. Robust modulation of the visual-evoked potential (VEP) time-locked to the presentation of these conditions provides an index of the neural contributions underlying this perceived change in contour completeness (Fiebelkorn et al., 2010; Foxe et al., 2005; Herrmann et al., 1999; Murray et al., 2002; Sugawara and Morotomi, 1991).

Electrophysiological investigations have pointed to a two-phase model of contour completion with two temporally distinct phases of processing (Foxe et al., 2005; Murray et al., 2006). These conform to Tulving and Schacter's (1990) dissociation of a perceptual phase of functioning from a higher-level conceptual phase (see also Doniger et al., 2001; Doniger et al., 2002). The "perceptual" phase has been associated with a modulation of VEP amplitude during the timeframe of the N1 component (occurring between 90 and 200 ms in adult observers). This manifests as a response of increased negativity for illusion-inducing compared to non-illusion-inducing conditions over lateral–occipital scalp locations. Referred to as the *IC-effect*, this negative modulation is associated with automatic filling-in of object boundaries (Shpaner et al., 2009). The second "conceptual" phase lasts has been seen in response to peripherally presented IC stimuli or to the presentation of fragmented objects that are difficult to identify (Doniger et al., 2000, 2001; Foxe et al., 2005; Sehatpour et al., 2006) (Fig. 2). This latter phase is thought to reflect more effortful processes that rely on active comparison with existing neural representations of objects (Murray et al., 2002; Sehatpour et al., 2008). The VEP component associated with this phase is the N_{cl} (closure-related negativity, lasting from approximately 230 to 400 ms). Murray et al. (2006) differentiated these phases functionally, finding the *IC-effect* was correlated only with accurate detection of boundary completion and not with discerning differences between ICs of varying shape. Shape judgments were only associated with modulations of the later N_{cl}. Both of these processing phases have been source-localized to the lateral occipital complex (LOC) (Foxe et al., 2005; Pegna et al., 2002; Sehatpour et al., 2006, 2008), a system of ventral visual stream brain regions long-associated with visual object processing (Altschuler et al., 2012; Fiebelkorn et al., 2010; Foxe et al., 2005; Grill-Spector et al., 1998; Knebel and Murray, 2012; Murray et al., 2002, 2004, 2006; Shpaner et al., 2009, 2012).

The main question driving the present study is whether early IC processing is similarly automatic throughout childhood or whether more effortful processes, like those employed by adults in processing ambiguous stimuli, must be relied upon until some point in childhood. Gamma-band oscillations, thought to index the binding of stimulus features of ICs, have been measured in infants as young as 8 months old (Csibra et al., 2000). This finding seems to indicate that contour integration is in place very early in development. However, subsequent work

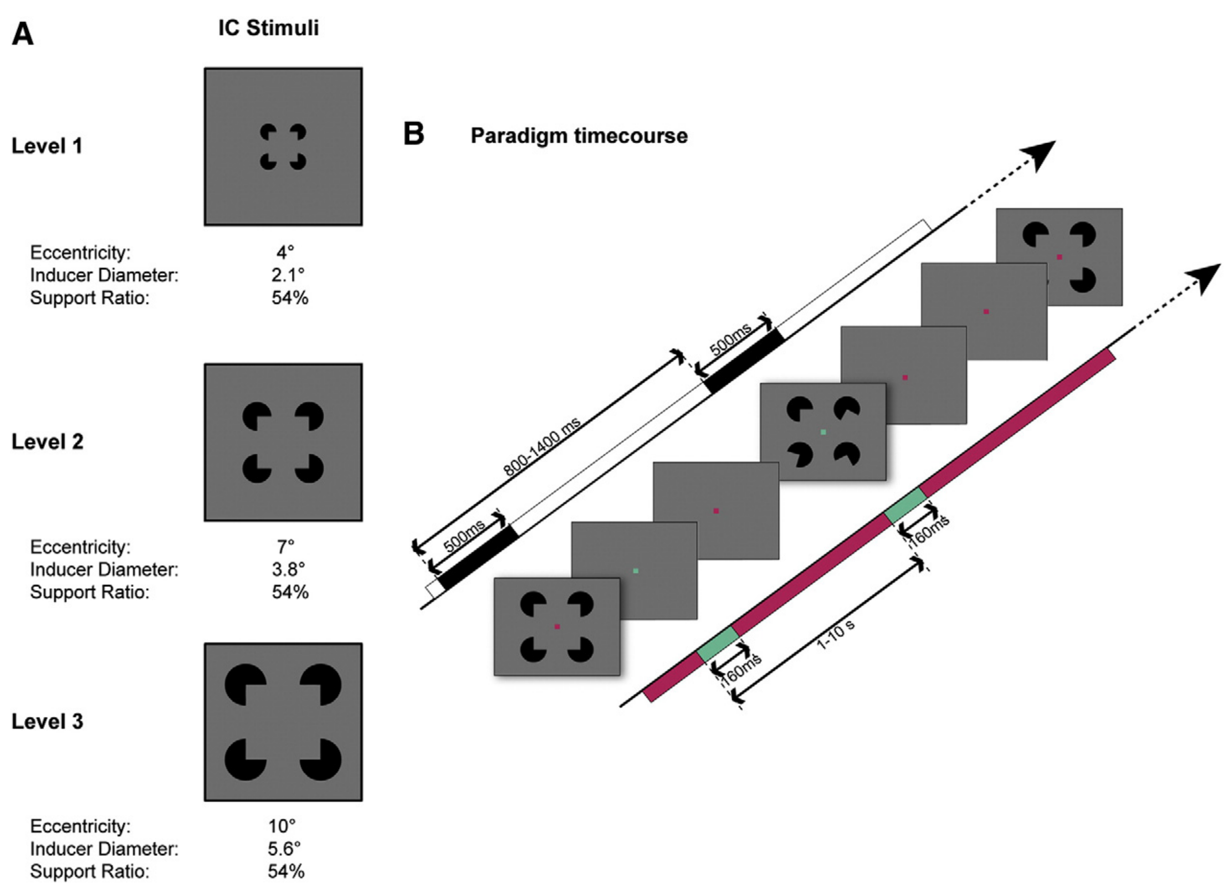

Fig. 1. Stimuli & paradigm. A. Stimuli in illusion-inducing (IC) condition with 3 experimental manipulations of contour extent. B. Paradigm time-course.