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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 230-400 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.

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INTRODUCTION

von Helmholtz 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 Helmholtz, H., 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, H.A. et al., 1990), and yet, the visual system seamlessly “fills in” the missing information (Pessoa, L. & De Weer, P., 2003). As Helmholtz 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 (Murray, M.M. et al., 2002; Proverbio, A.M. & Zani, A., 2002; Foxe, J.J. et al., 2005; Brodeur, M. et al., 2006; Li, W. et al., 2006; Shpaner, M. et al., 2009). The bulk of this processing occurs prior to the viewer’s awareness of the object (Vuilleumier, P. et al., 2001) or the application of semantic knowledge to identify it or make judgments regarding its characteristics (Murray, M.M. et al., 2006). These automatic completion processes have been extensively studied in adults using psychometrics, electrophysiology, and neuroimaging (e.g., Ffytche, D.H. & Zeki, S., 1996; Ringach, D. & Shapley, R., 1996; Mendola, J.D. et al., 1999; Ohtani, Y. et al., 2002; Halko, M.A. et al., 2008). Developmental explorations have studied this process in infancy (e.g., Csibra, G., 2001; Otsuka, Y. et al., 2004; Bremner, J.G. et al., 2012), but the use 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, B. 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 (Schumann, F., 1900; Kanizsa, G., 1976). These stimuli have proven very useful for studying contour completion specifically and the binding of features into objects more generally (Csibra, G. et al., 2000) because simple rearrangements of elements of identical stimulus energy give rise to considerably different percepts (Figure 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 (Sugawara, M. & Morotomi, T., 1991; Herrmann, C.S. et al., 1999; Murray, M.M. et al., 2002; Foxe, J.J. et al., 2005; Fiebelkorn, I.C. et al., 2010).

Electrophysiological investigations have pointed to a two-phase model of contour completion with two temporally distinct phases of processing (Foxe, J.J. et al., 2005; Murray, M.M. 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, G.M. et al., 2001; Doniger, G.M. 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, M. 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, G.M. et al., 2000; Doniger, G.M. et al., 2001; Foxe, J.J. et al., 2005; Sehatpour, P. et al., 2006) (Figure 2). This latter phase is thought to reflect more effortful processes that rely on active comparison with existing neural representations of objects (Murray, M.M. et al., 2002; Sehatpour, P. 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) (Pegna, A.J. et al., 2002; Foxe, J.J. et al., 2005; Sehatpour, P. et al., 2006; Sehatpour, P. et al., 2008), a system of ventral visual stream brain regions long-associated with visual object processing (Grill-Spector, K. et al., 1998; Murray, M.M. et al., 2002; Murray, M.M. et al., 2004; Foxe, J.J. et al., 2005; Murray, M.M. et al., 2006; Shpaner, M. et al., 2009; Fiebelkorn, I.C. et al., 2010; Altschuler, T.S. et al., 2012; Knebel, J. & Murray, M.M., 2012; Shpaner, M. et al., 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, G. et al., 2000). This finding seems to indicate that contour integration is in place very early in development. However, subsequent work strongly suggested that gamma-band response measures are often confounded by subtle saccadic eye movements (Yuval-Greenberg, S. & Deouell, L.Y., 2009). Such effects are only likely to be magnified in infancy. In our view, electrophysiology has not yet offered clear evidence as to whether contour completion processes mature with age.

If automatic contour integration relies on reference to global stimulus configuration in the processing of discrete elements, this may reflect a bias that Navon, D. (1977) observed in adult visual processing in general. Adults detect configuration-based differences in visual stimuli more often than differences between local elements. Carey, S. and Diamond, R. (1977) suggested that adults’ ability to encode configuration results in an advantage over children in recognizing previously-seen versus novel faces. This suggests that this strategy may develop from a focus on local elements in childhood to one on global information in adulthood. For example, Mondloch, C.J. et al. (2003) observed that faster processing of global relative to local processing of hierarchical figures (larger shapes composed of the arrangement of smaller shapes) emerged between 10 and 14 years of age. Scherf et al’s (2009) developmental comparison of hierarchical figure processing detected a local bias in children and adolescents through 17 years-of-age, but this could be manipulated by cueing attention to local or global information. Taken together, these paradigms offer a strong suggestion that global versus local strategies for object processing change over childhood, but an unclear picture of the trajectory. This suggests to us that contour completion processing is also likely to alter.

The goal here is to trace the developmental trajectory of perceptual contour completion from 6 years-of-age to adulthood using a cross-sectional sampling approach. A number of clear predictions can be made. If perception of ICs relies on later more effortful processing in earlier childhood, then Phase-one processing (the *IC-Effect*) may be absent until later in development and IC-processing may instead rely exclusively on later N_{cl} -related processes. Perhaps a more likely scenario is that early automatic processing emerges relatively early in development, but is found to be weaker in early childhood with Phase-two N_{cl} processing playing a more prominent role for younger children.

Additionally, visual filling-in processes are not impervious to experimental manipulations of inducer parameters. Variations in, for example, retinal extent relative to the size of the shape they induce, have been shown to influence the subjective perception of illusion strength (Shipley, T.F. & Kellman, P.J., 1992; Ringach, D. et al., 1996) and the timing of the *IC-effect* (Murray, M.M. et al., 2002; Altschuler, T.S. et al., 2012). In Altschuler et al (2012), we systematically manipulated contour length, inducer diameter, and the proportion of real contour to illusory contour – known as support ratio (see Figure 2 in Altschuler et al (2012)). The latency of the *IC-effect* changed, but only in response to the manipulation of support ratio. Somewhat to our surprise, the amplitude of the *IC-effect* was entirely invariant to manipulations previously associated with illusion strength. Functional neuroimaging work has associated the LOC with visual processing of objects that is invariant with regard to their size or the perspective from which they are viewed (Malach, R. et al., 1995; Grill-Spector, K. et al., 1998). This is in contrast to hierarchically earlier retinotopic regions which do show sensitivity to variations in stimulus energy, as reflected in amplitude modulations of the C1 and P1 components of the VEP (Di Russo, F. et al., 2002; Foxe, J.J. et al., 2008). In our 2012 study, images of different size, projecting different images upon the retina, produced indistinguishable activations in LOC neuronal populations. As long as the gap between inducers was not too large relative to the overall size of the potential object, the contour fragments were bound, leading to the perception of a single object. The two-phase model would posit that this occurs via automatic reference to the viewer's knowledge of similar stimulus configurations.

In the present study, as in our adult study, we manipulated the absolute length of illusory contours (referred to here as “extent”) across a range of 4°-10° of visual angle (Figure 1). Although this manipulation resulted in no variation of the *IC-effect* whatsoever in adults, we reasoned that the human brain does not come “ready-made” to execute such instantaneous references to spatial groupings. Rather, these would likely be tuned via multiple exposures across development to ultimately produce reliable inferences. This is supported by the observation of the experience-dependent development of size-invariant object representation in the inferior temporal cortex of non-human primates (Li, N. & DiCarlo, J.J., 2010) and by human fMRI work showing that improved recognition of objects through practice correlated with increases in LOC activation (Grill-Spector, K. et al., 2000).

To summarize, this study employed high-density electrical mapping to test whether contour completion processes change over neurotypical development from 6 years of age to adulthood, using electrophysiological indices of IC processing, varying contour extent across a range of 4°-10°.

METHODS & MATERIALS

Participants

63 neurotypical individuals (34 female) in four age cohorts participated: 6-9 years of age (N = 16), 10-12 years of age (N= 17), 13-17 years of age (N = 18), and 19-31 years of age (N = 12). Mean ages and standard deviations for each cohort are summarized in Table 1. All

participants reported normal or corrected-to-normal vision, normal hearing, and were tested for normal tri-chromatic vision (Ishihara, S., 2008). Adults gave written informed consent and those younger than 18 provided assent, with their parent or guardian giving informed consent. The City College of New York, Montefiore Medical Center, and Albert Einstein College of Medicine Institutional Review Boards approved all procedures and all procedures were conducted in accordance with the tenets of the Declaration of Helsinki (Rickham, P.P., 1964).

All child and young adult participants had a Full Scale IQ > 85 (Wechsler, D., 1999), see Table 1 for summary. They were also screened for receptive (Dunn, L.M. & Dunn, D.M., 2007) and expressive language (Semel, E. et al., 2003), and social communication and daily living skills (Sparrow, S. et al., 2005). Head trauma, seizures, Attention Deficit Disorder, psychiatric, learning, or developmental disorders, or having a first-degree relative with a developmental disorder constituted exclusionary criteria. Adults were not formally assessed but were functioning as undergraduate or graduate students and reported no significant neurological, psychiatric or developmental histories.

Stimuli & Task

Subjects sat in a dimly-lit, sound-attenuated booth 60 cm from a monitor with 1280×1024 pixel resolution or 75 cm from a monitor with 1680×1050 pixel resolution. They viewed four black Pacman-shaped disks, presented equidistant from central fixation, against a gray background, arrayed like the number four on a die (Figure 1). Either the 90° angle that comprised the “mouths” pointed toward the center, such that the perception of an illusory square was induced (IC Condition), or three of the mouths were rotated away from the center (No-IC Condition). These conditions were presented in random order and equiprobably. In the No-IC condition, the location of the non-rotated inducer varied randomly. For the other inducers, the amount of rotation was generated randomly in a range from 20° - 180° and thereafter held constant for all presentations. Retinal eccentricity was manipulated, with stimuli subtending 4° , 7° , and 10° of visual angle, (calculated for the IC condition) presented in pseudo-random order equiprobably over each block. To hold support ratio (Ringach, D. et al., 1996) constant for the three levels at 54%, inducers were 2.1° , 3.8° , and 5.6° in diameter respectively (Figure 1).

Stimuli were presented for 500 ms with an 800-1400 ms stimulus-onset asynchrony varying according to a square wave distribution. Ten to fifteen 3-minute blocks (as necessary to acquire sufficient trials) were administered, with breaks to accommodate fatigue. Task instructions referred only to an orthogonal color detection task which focused participants on the center of the display monitor. Murray et al (2002) have shown that explicit attention to ICs is unnecessary to elicit the *IC-effect* in adults. These procedures were undertaken to encourage a passive relationship to IC presentation, and avoid biasing participants towards perception of the illusion. Color detection stimuli consisted of a centrally-presented red fixation-square 4 pixels in area. Every 1-10 seconds, the dot changed to green for 160 ms with the inter-stimulus-interval varying pseudo-randomly on a time-course uncorrelated with that of the Pacman stimuli (Figure 1). Subjects clicked the mouse button with their right index finger for each perceived color change. The changes were effectively imperceptible without foveating, providing a good measure of fixation. Average accuracy for the fixation task is summarized in Table 1. The 6-9-year-old age group performed slightly more poorly than other age groups. Once this became apparent, an Eyelink 1000 eye-tracking camera (SR Research Ltd., Ottawa, Ontario) was used for as many members of the 6-9-year-old cohort as possible (7) to ensure that fixation was not more than 2° from center.

A debriefing questionnaire assessed participants' ability to perceive the illusion. Printed images of IC and No-IC triangles with an open-ended request to “describe what you see”

elicited an indication that triangles were seen in the IC condition in 93% of participants, regardless of the order of administration of the conditions. When shown IC and No-IC conditions in a square configuration and asked to identify the square, 100% of participants pointed to the IC condition resembling the one seen during the experiment.

Data acquisition and EEG preprocessing

Continuous EEG was acquired through a Biosemi Active Two system from a 72-electrode montage, digitized at 512 Hz and referenced to the Common Mode Sense (CMS) and the Driven Right Leg (DRL). EEG epochs from -150 ms before stimulus onset to 1000 ms after were averaged for each subject for each condition and level of manipulation using BESA 5.1.8 EEG software (Gräfelfing, Germany). Trials were baseline-corrected across an epoch of -80 to +20 ms and low-pass filtered at 45 Hz with a 24 db/octave roll-off. Given that children's evoked responses are of larger amplitude and that they also typically show greater levels of background noise, artifact rejection criteria were chosen on an individual participant basis within a range of ± 100 -150 μ V and applied via a BESA-generated algorithm to reject trials with eye or muscle movement, as recommended by Luck (2005). Average number of trials per condition is shown by age cohort in Table 1. Channels with excessive noise were interpolated and three external electrodes were so consistently noisy in younger subjects that they were turned off in all participants and excluded from further analysis. These were the two mastoid leads (M1 and M2) and the nosetip electrode, which wasn't well tolerated by younger children.

Statistical analyses

Statistical analyses were guided by previous ERP work on IC processing in adults (e.g., Murray, M.M. et al., 2002; Shpaner, M. et al., 2009) which has produced the two-phase model described earlier. Accordingly, the primary analyses were focused relative to the *IC-effect* over scalp regions where the visual N1 response was largest in amplitude (lateral occipital scalp represented best at scalp-sites PO3 and PO4), and the early time window was centered on the peak latency of the N1. The later time window was defined relative to the N_{cl} , typically spanning ~230-400 ms and also largest at lateral occipital scalp locations (Doniger, G.M. et al., 2000; Doniger, G.M. et al., 2001; Foxe, J.J. et al., 2005; Murray, M.M. et al., 2006; Shpaner, M. et al., 2012).

Specifically, the first window encompassed the 30 ms window centered on the N1 of the grand average waveform of each age cohort and level of extent. This was identified as the most negative point between 100 and 250 ms averaged across IC conditions (IC and No-IC) and hemiscalp (PO3 and PO4). A 300-400 ms window was chosen to encompass the N_{cl} . Waveforms were re-referenced to an anterior midline frontal scalp site (AFz). These two time windows were subjected to 2x2x3 repeated-measures ANOVAs in SPSS 15.0 with a between-subjects factor of age cohort (6-9, 10-12, 13-17, 19-31), and within-subjects factors of IC condition (IC vs. No-IC), hemiscalp (PO3, PO4), and eccentricity (4°, 7°, and 10°). Significance criterion was set at an $\alpha < 0.05$. Differences between IC conditions at both latencies were also regressed upon age as a continuous variable and the resulting R^2 values tested for significance. The results are depicted as a scatter plot.

To assess whether our measures were sensitive to the range of contour extent manipulation, a P1 analysis was conducted on the 30 ms window surrounding the first positive peak of the grand average waveforms between 60 and 150 ms for each age group and extent condition at electrodes PO3 and PO4. This employed the same methods as above.

Additionally, we observed that, although the *IC-effect* was statistically equivalent across age groups, it varied greatly in proportion to the overall amplitude of the VEP. To assess the

significance of this relative difference, we ran an additional post-hoc ANOVA on the ratio of the difference between IC and No-IC during the N1 timeframe (the *IC-effect*) and P1 amplitude.

Onset latency of VEP responses were calculated using point-wise paired *t*-tests collapsed across eccentricities for each age cohort. This identified the first time point where the *t*-test exceeded the 0.05 alpha criterion for 11 consecutive time points at 3 adjacent electrodes. The consecutive time points approach is a conservative control for inflation of type I error due to multiple comparisons (Guthrie, D. & Buchwald, J.S., 1991; Foxe, J.J. & Simpson, G.V., 2002). The requirement of 3 adjacent electrodes controls for spurious effects based on the fact that activity at any channel should be correlated with activity at adjacent channels. The results are displayed as a statistical cluster-plot, with latency on the \times axis, scalp region on the y axis. *T*-test results are coded by color. The white dotted line roughly divides scalp areas which are posterior to center from those which are anterior to center.

Dipole source modeling

The intracranial sources of effects were modeled using BESA's least squares algorithm, fitting two symmetrical dipoles to explain the maximal amount of variance in the overall signal. A 4-shell ellipsoidal head model was employed with a radius of 90 mm. A scalp thickness of 6mm and skull thickness of 7 mm were assumed. The latencies analyzed were based on the maximal amplitude effects with the N1 and N_{C1} timeframes, as determined from subtraction waveforms. The stability of the model was challenged by altering the location of the dipoles and re-fitting. Results for the difference between IC and No-IC conditions collapsed across contour extent are shown along with their goodness-of-fit (i.e., percent variance explained) for each age cohort in Talairach coordinates (mm) and the Brodmann Area in which they are estimated to be situated.

Signal-to-Noise (SNR) ratio

SNR was measured by comparing amplitude in a pre-stimulus period as an estimate of noise, to amplitudes in a window of 90-200 ms to allay concerns that any differences between conditions or group might be due to differences in signal strength. Methods are summarized in (Altschuler, T.S. et al., 2012) and results displayed in Table 1.

RESULTS

N1 Analysis

The maximum negative deflection in the 100-250 ms period averaged across IC conditions and hemiscalp was selected as the N1 peak for each extent in each age cohort. This latency decreased with age as has been previously observed (Brandwein, A.B. et al., 2011; Brandwein, A.B. et al., 2012). The integrated amplitude over a 30 ms window centered on this latency (Table 2) was submitted to analysis to compare the amplitude of the difference between IC conditions across the four age cohorts, two hemiscalps, and three levels of retinal eccentricity (extent).

A main effect of IC condition ($F_{(1, 59)} = 51.506$; $p < 0.001$; $\eta_{\text{partial}}^2 = 0.47$) indicated the presence of an *IC-effect* collapsed across age cohort, hemiscalp, and extent manipulation (Table 3; Figure 3). A main effect of age cohort ($F_{(3, 59)} = 3.612$; $p = 0.02$; $\eta_{\text{partial}}^2 = 0.16$) indicated a difference in VEP magnitudes collapsed across IC condition, hemiscalp, and extent (Table 3). This main effect is driven by significant mean differences between adults (-3.2 μV) and the two youngest groups: 6-9-year-olds (1.1 μV ; $p = 0.04$) and 10-12-year-olds (1.1 μV ; $p = 0.03$). No interactions attained significance.

The regression of IC difference (i.e., *IC-effect*) upon age as a continuous variable was not significant whether data were fitted linearly ($R^2 = 0.015$, $F_{(1,61)} = 0.92$; $p = 0.34$) or quadratically ($R^2 = 0.016$, $F_{(2,60)} = 0.48$; $p = 0.62$) (Figure 4).

Considering the differences in overall VEP magnitude across age groups, we compared the *IC-effect* magnitude as a proportion of P1 magnitude collapsed across hemiscalp for each condition and age group. Voltages increased with age: 6-9 = $-0.087 \mu\text{V}$; 10-12 = $-0.137 \mu\text{V}$; 13-17 = $-0.348 \mu\text{V}$; 19-31 = $-1.167 \mu\text{V}$ (Table 3) but did not emerge as significant ($F_{(3,59)} = 1.49$; $p = 0.23$; $\eta_{\text{partial}}^2 = 0.07$).

N_{cl} Analysis

The integrated amplitude across the period from 300-400 ms was submitted to analysis to compare the amplitude of the difference between IC conditions (i.e. the N_{cl} component) for the four age cohorts, two hemiscalps, and 3 levels of extent.

A main effect of condition ($F_{(1, 59)} = 48.254$; $p < 0.001$; $\eta_{\text{partial}}^2 = 0.45$) indicated a difference between IC conditions collapsed across age cohort, hemiscalp, and extent manipulation (Figure 3). A main effect of age cohort ($F_{(3,59)} = 24.118$; $p < 0.001$; $\eta_{\text{partial}}^2 = 0.55$), indicated a difference of VEP magnitude collapsed across IC conditions, hemiscalp, and extent. This was driven by significant mean differences between all age contrasts except 10-12-year-olds vs. 13-17-year-olds. In contrast to the effect during the N1 processing timeframe, a significant interaction of IC condition \times age cohort was present ($F_{(3, 59)} = 5.284$; $p = 0.0027$; $\eta_{\text{partial}}^2 = 0.21$). The comparison of differences between IC conditions (Bonferroni adjusted) was significant through childhood and adolescence but not in adulthood (Table 3) 10-12-year-olds: $-2.015 \mu\text{V}$ ($p < 0.001$); 6-9-year-olds: $-1.669 \mu\text{V}$ ($p < 0.001$); 13-17-year-olds: $-0.638 \mu\text{V}$ ($p = 0.047$); 19-31-year-olds: $-0.4 \mu\text{V}$ ($p = 0.30$). This was echoed by the regression of IC difference upon age as a continuous variable, which was significant whether modeled linearly ($R^2 = 0.141$, $F_{(1,61)} = 9.98$; $p = 0.002$) or quadratically ($R^2 = 0.145$, $F_{(2,60)} = 5.105$; $p = 0.009$) (Figure 4).

P1 Analysis

In the absence of any magnitude differences during the N1 and N_{cl} timeframes as a function of the extent manipulation, the P1 timeframe for each age group and condition was submitted to analysis. The P1 component is thought to reflect early registration of spatial stimulus parameters and has shown systematic modulation to the manipulation of stimulus extent in adults (Di Russo, F. et al., 2002; Murray, M.M. et al., 2002; Snyder, A.C. et al., 2012). A main effect of extent ($F_{(2,59)} = 4.985$; $p = 0.013$ (Greenhouse-Geisser corrected); $\eta_{\text{partial}}^2 = 0.078$) confirmed our participants' sensitivity to the range of manipulation (Figure 5). This was driven by a significant contrast between the 4° and 10° conditions ($6.8 \mu\text{V}$ versus $6.1 \mu\text{V}$; $p = 0.011$). The contrast between 7° and 10° approached significance ($6.7 \mu\text{V}$ versus $6.1 \mu\text{V}$; $p = 0.056$).

Spatio-temporal activity across scalp areas and time

Paired *t*-tests between IC conditions revealed the overall spatio-temporal patterns of IC-related activity (Figure 6). A white dotted guideline divides regions anterior to central regions from those posterior to central regions. General trends for periods of activity can be seen across developmental groups.

Topographies

Spline-interpolated potential maps depict voltage across the scalp surface for the difference between IC and No-IC conditions (Figure 7). Posterior views for each age cohort and extent

showed the greatest voltage over occipital and/or occipito-temporal regions. Seven representative latencies across the epoch are presented, including average N1 latencies for the two oldest age cohorts (171 ms), two youngest (228 ms), and three spanning the N_{c1} (300, 350, 400 ms). Activity was apparent in the N1 time frame for all age groups. While activity was restricted to this latency for adults, the two younger groups show activity that continues into the N_{c1} time-window that is of even greater magnitude. 13-17-year-olds lie in between, with more discrete activity during the N1, similar to that observed in adults, as well as activity in the N_{c1} time-frame in 6-9 and 10-12 year olds. Anterior views collapsed across extent (Figure 8) show activity over frontal and fronto-central regions for every group except adults in the N_{c1} timeframe. Note that the spline interpolation procedure used here (BESA 5.1.8 EEG software, Gräefeling, Germany) projects inferred potential distributions over inferior scalp regions where no electrodes were actually placed.

Dipole Models

Two symmetrical dipole current sources were modeled for the 30 ms window centered on the N1 (*IC-effect*) and the 40 ms window centered on the N_{c1} derived from the global field power (GFP) (Skrandies, W., 1995) of the subtraction of IC and No-IC conditions averaged across contour extent. Separate color-coded maps show solutions for each age group, with the color of the dipole cartoon matching the color of the Talairach coordinates given (Figure 9). During the N1, solutions for all groups overlap and fits exceed 92% of explained variance. The coordinates for all age groups fall approximately within Brodmann Area (BA) 19 which encompasses lateral occipital cortex as estimated on Talairach Client software (Lancaster, J.L. et al., 1997; Lancaster, J.L. et al., 2000). Solutions for the N_{c1} processing time-frame overlap roughly for 6-17 year-olds falling in BA 19 and 37 - lateral occipital and occipito-temporal areas. The fits of these estimates exceed 94% explained variance. There was no peak in GFP during the N_{c1} time-frame in adults, obviating the logic of fitting a dipole solution. However, we attempted a model for the sake of consistency. The solution accounting for the greatest amount of variance was estimated to fall close to the inferior temporal gyrus in BA 20. Only 76% of the variance was explained by this model.

DISCUSSION

To investigate the developmental trajectory of contour completion processes, we presented stimuli composed of non-continuous contours. One condition induced the illusory perception of continuous contours whereas a second control condition did not. Neurotypical participants ranged from 6-31 years of age. Extent and inducer diameter were varied to hold support ratio constant with the idea that presenting contour fragments over increasing spatial extents would reveal the limits of the visual system's ability to interpolate said contours, and that those limits might change with age if this ability is experience-dependent. We worked from a well-tested theoretical model that has identified temporally and functionally dissociable processing phases using electrophysiology- the first was an automatic, perceptual phase occurring between 100-200 ms (associated with the N1 processing timeframe), and the second later conceptual phase (230-400 ms) which has been associated with the analysis of higher-level ambiguous objects.

Early Perceptual Phase Processing of Illusory Contours

An adult-like difference between contour conditions was observed during the "perceptual" phase in all the four age groups, including the youngest group tested (6-9 year olds). This analysis was constrained to the timeframe of the N1 of each age group for each extent condition, since the N1 is a stable component of the VEP (Di Russo, F. et al., 2002; Foxe, J.J. et al., 2003) and has a stereotypical morphology by age two (Lippe, S. et al., 2007). N1 latency varied inversely with age, from approximately 226 ms in 6-9-year-olds to 165 ms in

adults (Table 2). This shortening of N1 latency is an already well-characterized effect (Lippe, S. et al., 2007; Brandwein, A.B. et al., 2011).

Posterior topographies of the *IC-Effect* (Figure 7) showed voltage distributions focused over lateral occipital scalp areas. Dipole models were nearly identical in every age group (Figure 9), estimating generators of this effect to be located in the region of Brodmann Area 19, a lateral occipital region which corresponds very well with previous fMRI studies identifying the LOC as sensitive to IC processing (Mendola, J.D. et al., 1999; Murray, M.M. et al., 2002).

Overall VEP magnitude, as indexed by P1 amplitude (Table 3), was quite large in the youngest sample, decreasing rather dramatically with age. This is a common finding in developmental ERP studies (Gomes, H. et al., 2001; Brandwein, A.B. et al., 2011). To our knowledge, there is as yet no widely accepted explanation for this difference across age-groups. One highly plausible cause, however, may be found in the properties of the volume conductor itself – that is, the nature of the intervening structures between the electrodes and the neural tissue generating the measured currents. Children have thinner more immature skulls that continue to thicken across childhood (e.g., Adeloje, A. et al., 1975), and this thickening undoubtedly increases the intervening resistivity (Cuffin, B.N., 1993; Akhtari, M. et al., 2002). The skull, which is a relatively poor conductor, plays an especially large role in attenuating EEG signals (Lanfer, B. et al., 2012). Additionally, it is possible that age-related changes in cortical tissue impact signal conduction (Grieve, P.G. et al., 2003). Thus, in comparing responses between adults and children, one might suppose that concentrating on relative changes in amplitude (i.e. ratios) makes the most sense. In adults, the ratio of IC difference during the perceptual phase to the P1 was ten times that of the youngest children. This represents a substantial modulation of ongoing activity in adults, whereas it obviously represents a more moderate modulation in younger children. However, when ratios were assessed statistically rather than absolute amplitudes, the difference was not robust, leaving this observation and the methodological question of whether the use of ratios or absolute values represents the more meaningful approach for future investigations. We would nevertheless argue that this difference is suggestive of the relative immaturity of this automatic early-phase contour-integration mechanism in younger children.

Later Conceptual Phase Processing of Illusory Contours

Key differences between adults and children emerged during the “conceptual” processing timeframe. Unlike the early phase, differences between contour-forming and non-contour-forming conditions varied significantly with age during this timeframe, with the greatest amplitude modulations apparent in the two youngest groups (6-9 and 10-12 year-olds), followed by the 13-17-year-old group. In contrast, no significant difference was observed during this timeframe in adults. Although the developmental trajectory did not follow an entirely neat step-like decrease across age groups, since the 10-12 year-old group showed slightly greater modulations during this timeframe than the youngest cohort, the overall pattern across age-groups suggests amplification of conceptual-phase relative to perceptual-phase processing in younger children, a pattern that begins to reverse during adolescence and is fundamentally different by adulthood. In adults, only the automatic perceptual-phase appears obligatory for analysis of this stimulus class. This general pattern points to a protracted developmental trajectory whereby contour-integration processes involve multiple temporal phases of processing within object-recognition areas during childhood, but as visual experience is acquired across childhood, the encoding of these stimuli becomes ever more automatic, shifting from a reliance on later processing to a consolidation of processing into early automatic processing - a *late-to-early* consolidation model.

Inverse source localization produced strong fits within lateral occipital and occipito-temporal regions for all three childhood age groups. On the other hand, adults, who showed no effect during the conceptual timeframe, showed no second peak in global field power, and unsurprisingly, source analysis produced a poor fitting model (Figure 9). In addition, more distributed networks appeared to be implicated in children than in adults (Figure 6). Topographic mapping for both of the younger groups showed greater activity over fronto-central scalp (Figure 8), suggesting possible recruitment of conceptual-level mechanisms (Sehatpour, P. et al., 2008). One possible alternative explanation that cannot be definitively ruled out is that this fronto-central focus might represent the positive pole of the lateral occipital dipoles. We believe that this is unlikely, however, since all three of the child groups have highly similar bilateral LOC activity in this timeframe but the older group shows no such frontal topography.

What Do These Developmental Differences Mean?

The present results point to significantly more protracted contour closure processes in childhood than adulthood. Two phases of amplitude modulation occurred in the period between approximately 150-400 ms in children and adolescents in contrast to the single discrete and relatively punctate early process observed in adults (~150-220ms). Moreover, prior to adolescence, the second processing phase appears to have been of greater magnitude than the first, although we did not make a direct statistical comparison.

In considering boundary completion of Kanizsa type illusory contours, we considered what may be the simplest version of completion processes. These stimuli, which rely on only a few inducers to drive contour integration mechanisms, could be considered impoverished in terms of their ‘objectness’ relative to the objects typically encountered by the visual system. Certainly, prior work has investigated the neural mechanisms of object closure for considerably more complex objects from highly fragmented inputs. This latter case of completion may be closer to the parsing of an everyday visual scene in which many of the objects we view are partially occluded by other objects, or otherwise degraded due to poor viewing conditions. For example, Doniger et al. (2000) presented participants with line drawings of common objects in a recognition task where they employed the so-called ‘ascending method of limits’ design. They began by presenting participants with line-drawings of everyday objects (airplanes, dogs and the like), but on initial presentation, only 30% of the pixels of the original drawing were displayed. With this few pixels, object-identification is impossible. They then repeated presentation with an additional 10% of the pixels added back, and continued this process of adding pixels until the participant could successfully “close” (or recognize) the object. This procedure allowed for examination of the VEP to the fragmentation level at which the image was ultimately recognized, which in neurotypical individuals is still quite fragmented, and for comparison of this response to the responses to the preceding fragmentation levels when the objects were not explicitly recognized. This revealed gradual increases in activity in the LOC in the 230-400 ms timeframe, with no evidence for modulation during the earlier N1 processing timeframe, contrasting with the modulations seen for simple Kanizsa figures. This later onset and more protracted timeframe suggested a less automatic process – one that appeared to present a greater challenge to the visual system. Subsequent intracranial work in humans (Sehatpour, P. et al., 2008) revealed the involvement in this process of a distributed network involving not only the LOC, but also prefrontal cortex, and the hippocampal formation. This led Sehatpour and colleagues to propose a model whereby the LOC facilitates on-line matching of incoming sensory stimuli to mnemonic object representations stored in the hippocampal formation, while the prefrontal cortex limits the matching options by generating hypotheses.

In a subsequent version of the fragmented picture study, certain objects were shown to participants a second time. With repeated images participants could successfully close the

image in its most degraded version, and when they did, a VEP difference was seen during the earlier N1 latency (Doniger, G.M. et al., 2001). It is presumed that rather than accessing object representations at the “conceptual” level, the visual system can begin closure sooner because it has access to a sensory trace laid down when closure was achieved on the previous presentation of the image. It is conceivable that the automatic closure seen in the present study is, similarly based on lower-level cues derived from contour extent (hence our reference to it as “perceptual”) and therefore relies on a certain amount of exposure. When the limits of such processes are taxed or sufficient expertise has not yet been acquired, the system cannot rely on parametric cues to complete contour fragments automatically. Studies in higher primates have pointed to size-invariant object processing as a mechanism that is tuned over multiple exposures (Li, N. et al., 2010). An interpretation was put forth in a study of closure processes in schizophrenia patients whereby deficiencies in posterior visual processing were compensated for by additional frontal activity during the later timeframe (Fuxe, J.J. et al., 2005). The general lack of exposure that children have to even simple stimulus configurations such as the Kanizsa stimuli may be similarly compensated for here.

The greater recruitment of fronto-central regions pointed to by anterior topographies (Figure 9) suggests that children may employ so-called conceptual-level processes to accomplish the closure adults achieve with low-level perceptual mechanisms. However, the characterization of the later phase as “conceptual” stems from a decade of work during which participants executed tasks demanding their attention to stimuli that required closure. Here, although no explicit manipulation of attentional load was included, an orthogonal task at the fixation point appeared to require the continuous attention of participants, and there was never any explicit need for participants to pay attention to the Kanizsa inducers at any point throughout the experiment. Indeed, if anything, they would likely have acted as potential distracters from the central task. Thus, the present data suggest that second stage conceptual-level processing and recruitment of more distributed networks also occurs relatively automatically in children and adolescents. It is noteworthy that this second stage of processing is essentially absent in our adult group, whereas in many of our previous studies, this was not the case. Again, the likely explanation here is that in all but one of those studies, our adult participants were asked to actively engage in a task involving the presence, absence or shape of the IC stimuli, and this likely invoked protracted processing. Thus, it would appear that later conceptual processing can be arrested in adults. In only one of our previous studies (experiment 2 of Murray, M.M. et al., 2002) were adults not required to perform a task on the IC stimuli, but unfortunately we did not analyze the later conceptual phase in that study. Even so, those adults were not required to engage in an orthogonal task, so presumably some attentional resources could have been directed towards examining the Kanizsa stimuli. Overall, the current results suggest that adults may be very efficient at filtering out the essentially distracting Kanizsa inputs, and that only early automatic closure processes are invoked in the mature brain. It will fall to future work to expressly determine the role of attentional load on this stage of processing. The interested reader is pointed to the work of Seghier and Vuilleumier (2006) who offer a similar account of early low-level versus late high-level framing of IC processing in their review of the fMRI literature.

Anatomical Considerations Concerning Conceptual Phase Processing of Illusory Contours

The magnitude of conceptual phase processing across the developmental period measured here generally decreases from the youngest to oldest participants, but not in a linear fashion. It is in the second period – that of late childhood to early adolescence (9-12 years old) – where we measured the largest magnitude. Parallel non-linear effects in the anatomical development literature may point to some of the mechanisms underlying this pattern. Histological analyses suggest that pruning of excess synapses doesn't begin until late childhood or early adolescence (Huttenlocher, P.R., 1990). Childhood increases in gray

matter volume as measured by MRI are followed in adolescence by decreases, peaking at approximately 11-12 years of age and decreasing thereafter (Caviness, V.S., Jr. et al., 1996; Giedd, J.N. et al., 1999). The use of resting-state fMRI as an index of functional connectivity suggests a shift in processing modes during the transition from late childhood to young adulthood, from segregated processing within local nodes to processing across more distributed nodes (Fair, D.A. et al., 2009). Diffusion tensor imaging (DTI) assays of white matter development also suggest that late childhood into adolescence is a highly dynamic period (Barnea-Goraly, N. et al., 2005; Schmithorst, V.J. & Yuan, W., 2010; Lebel, C. & Beaulieu, C., 2011). For example, Qiu et al. (2008) showed that while overall measures of white matter structural integrity increased from 6-23 years-of-age, only 9-12 year-olds demonstrated regressive as well as progressive changes in measures of diffusivity. A great deal of the observed structural changes occurred in frontal, right-temporal, and occipital regions. Schmithorst et al (2010) have suggested that understanding of the structural changes occurring during this period would be well-served by not limiting analyses to linear models and by breaking out 9-12 year olds as their own group, and the current results accord well with this suggestion.

Response Invariance as a Function of Spatial Extent Manipulations

In a previous study conducted in adults, we manipulated the absolute spatial extent of ICs and revealed invariance in the magnitude and latency of the *IC-effect* as well as the overall VEP during the perceptual timeframe (Altschuler, T.S. et al., 2012). These effects are replicated here. Also in that earlier study, the *IC-effect* was invariant to manipulations of relative contour length. However, in that case, the early sensory-evoked VEP (i.e. the N1) did vary in amplitude, since manipulating relative contour length involved changing the absolute size of the inducing elements (i.e. the Pacmen). The current study did not compare manipulations of absolute and relative contour but we do see adult-like invariance of both the IC-effect and overall VEP amplitude to the manipulation of absolute contour extent in children from 6-years-of-age on.

Realizing that invariance to the extent manipulation could be interpreted as the visual system's lack of sensitivity to the range of the manipulations employed here, we also compared amplitudes during the earlier P1 timeframe (approximately 60-150 ms) since activity during this timeframe is thought to index early spatial processing within dorsal and ventral visual stream sources (Foxye et al 2005; Molholm et al, 2006). Indeed, previous manipulations of spatial extent have resulted in changes in P1 amplitude (Murray, M.M. et al., 2002; Snyder, A.C. et al., 2012), although the direction of that change is in dispute. Here, extent varied inversely with P1 amplitude in accord with Snyder et al (Snyder, A.C. et al., 2012). This demonstrates that, despite the invariance of either the early or late contour completion phases or the overall N1 to systematic manipulation of extent from 4° to 10°, the measures used here are sufficiently sensitive to measure the visual system's encoding of such a manipulation.

Children older than 6 years of age were remarkably like adults in that the amplitude of both the early and late effects were invariant to the manipulation of contour extent. DeLoache, J.S. et al. (2004) observed that children between 18-30 months-of-age made frequent attempts to perform actions with miniature versions of familiar objects without taking into account their actual size – for example, trying to enter a toy car. These observations suggest that the developmental trajectory of visual object processing in early childhood includes a point at which children may be less efficient at integrating their knowledge of an object with their perception of its scale. At that point in development, we posit that the contour extent manipulation might well tax the limits of contour integration processes – a question for future exploration.

CONCLUSION

We sought to better understand the developmental trajectory of contour completion processes in a cohort of children of schooling age because these processes contribute to the most elemental steps of delimiting objects from the rest of space. Our approach was to probe the vulnerability of electrophysiological markers of these processes across a range of contour integration extents. The data suggest a generally less efficient, more effortful, and more protracted set of contour completion processes that mature across childhood. Even in adolescents, the data suggest that these processes have not yet reached adult-like patterns of maturity.

Evidence of atypical boundary detection (Vandenbroucke, M.W.G. et al., 2008), an atypical bias toward processing global stimulus configurations (Fiebelkorn, I.C. et al., 2012), and delays in the development of other sensory processes (Fuxe, J.J. et al., 2013) in persons with an autism spectrum disorder suggest to us that these differences in contour integration may have application toward understanding the broad phenotype of this wide-spread syndrome. These data offer a developmental baseline from which we can begin to make comparisons.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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Highlights

- We describe a developmental trajectory for contour closure processes in humans 6-31
- Adults integrate contour fragments automatically in a single discrete phase
- Children and adolescents showed more protracted processing than adults
- Children and adolescents recruited more widely distributed regions than adults
- Closure related electrophysiological indices are invariant to the manipulation of contour extent

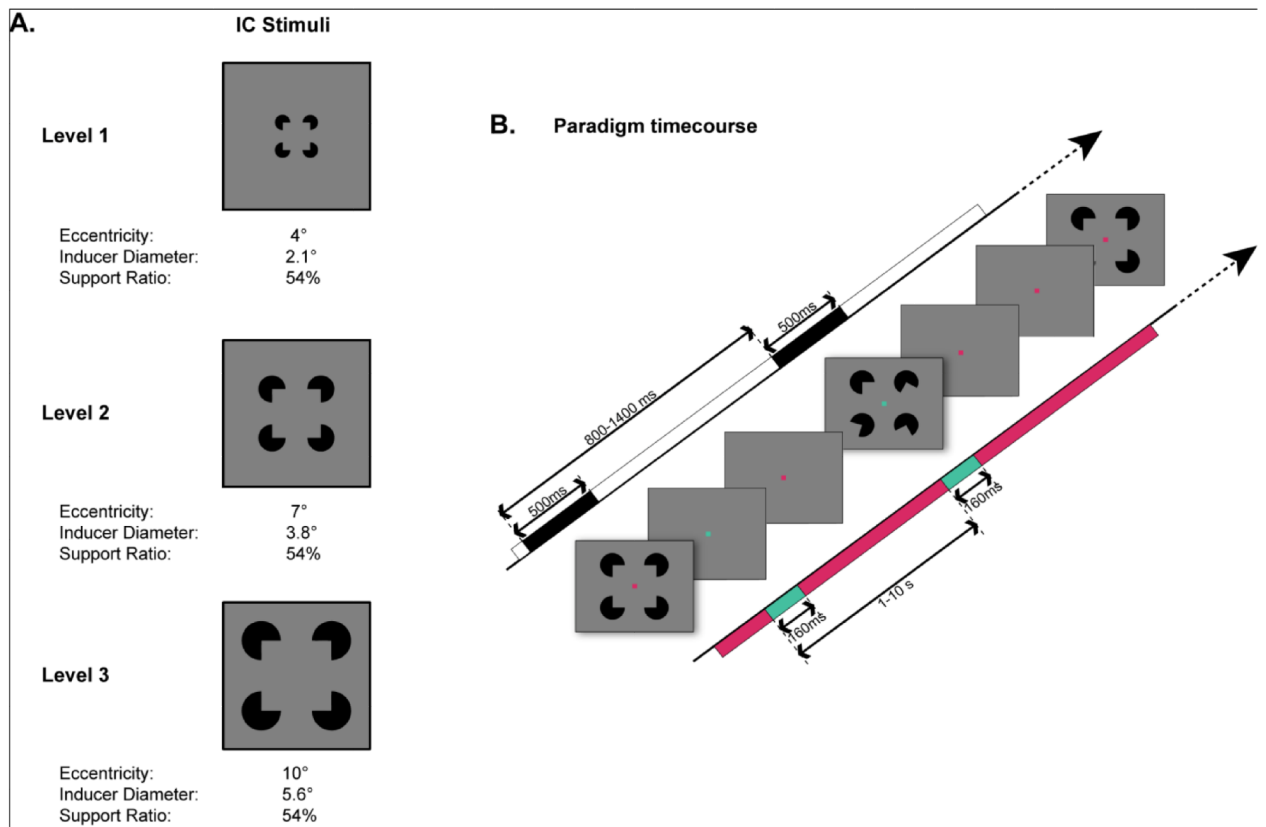


Figure 1. Stimuli & Paradigm A. Stimuli in illusion-inducing (IC) condition with 3 experimental manipulations of contour extent. B. Paradigm time-course.

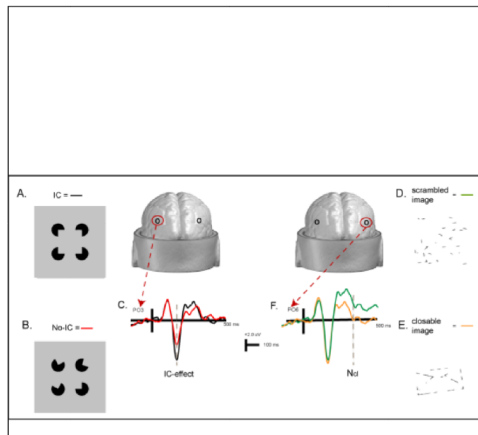


Figure 2.

Effect examples A. IC stimulus in illusion-inducing (IC) condition. B. IC stimulus in non-illusion-inducing (No-IC) condition. C. Exemplar *IC-effect* (Altschuler et al., 2012). D. Exemplar ambiguous fragmented scrambled image. E. Exemplar identical closable image. F. Exemplar N_{CI} (adapted from Sehatpour, P. et al., 2006 for illustrative purposes).

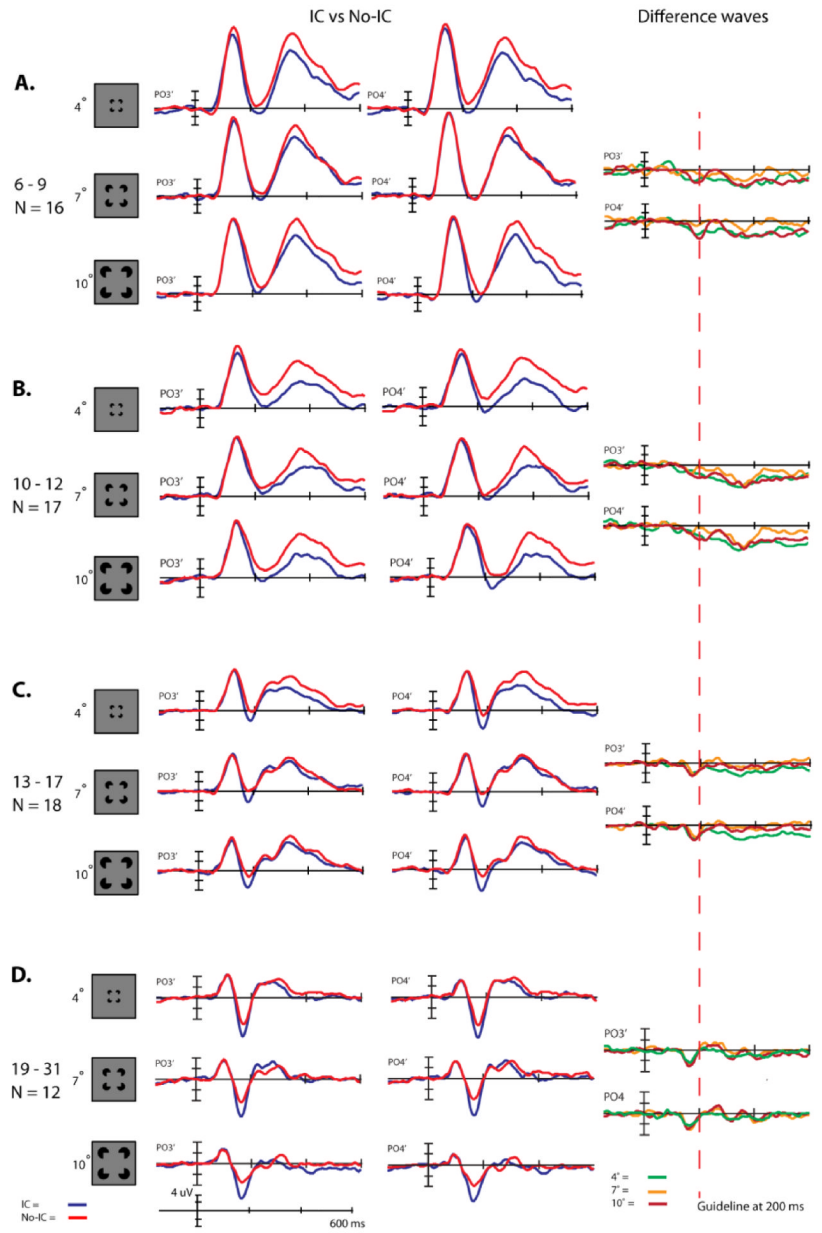


Figure 3. VEP Waveforms IC versus No-IC and subtraction waves for each condition and age group (A – D). Effect wave forms show IC condition (blue) & No-IC condition (red) from -150 to $+600$ ms at electrodes PO3 and PO4. Waves are referenced to electrode AFz. Difference waves depict each condition of contour extent 4° (green), 7° (orange), 10° (burgundy).

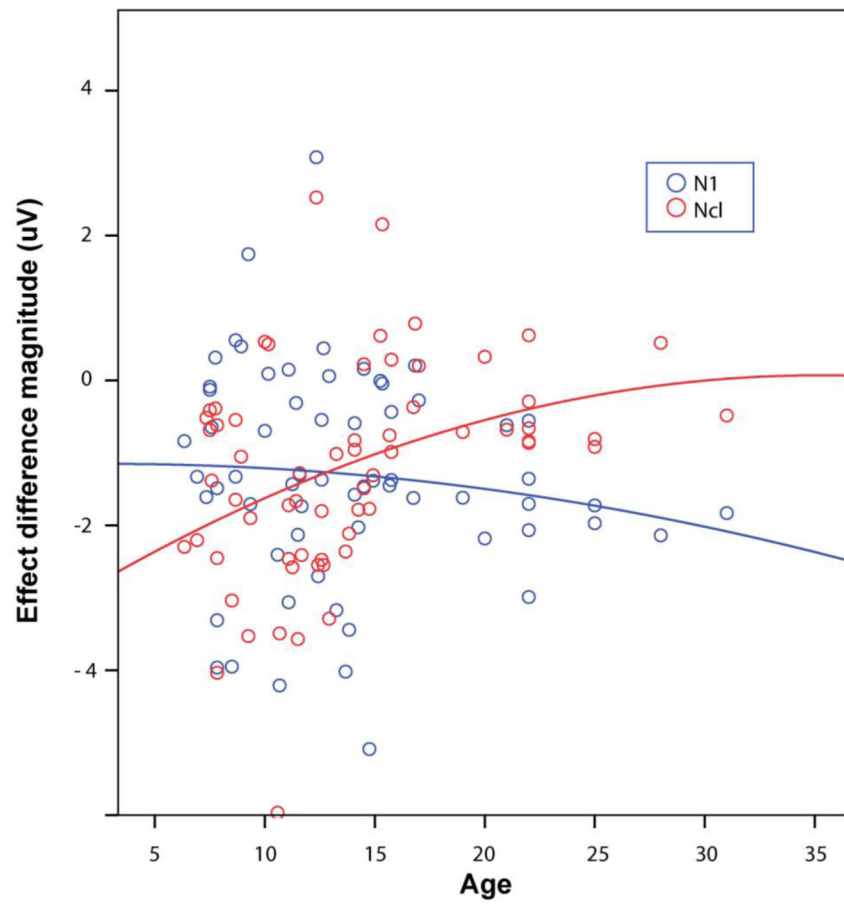


Figure 4. Regression analysis Difference amplitudes during N1 (blue) and N_{cl} (red) latencies regressed upon age. Data are collapsed across hemiscalp and contour extent. Quadratic regression is significant for N_{cl} but not for N1 latency.

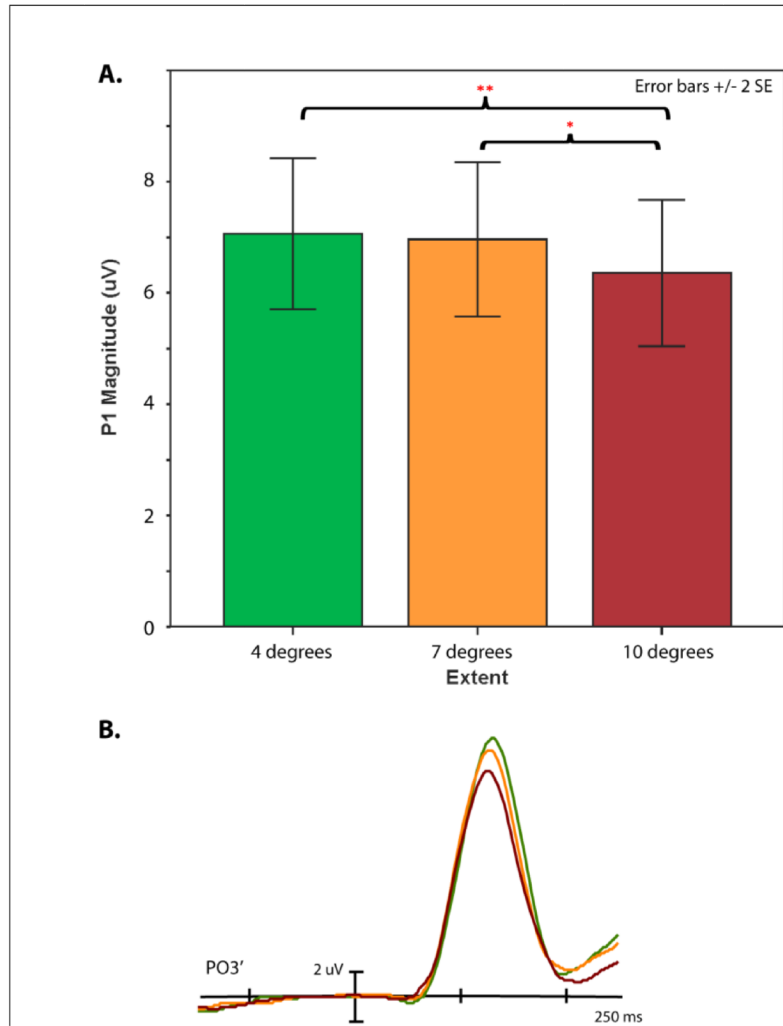


Figure 5.

P1 Main Effect of Extent Manipulation A. Bar graph: P1 magnitude (μV) collapsed across age and IC conditions for each extent. ** The significant contrast between 4° and 10° ($p = 0.011$) drives the effect. *The contrast between 7° and 10° approaches significance ($p = 0.056$). B. The average waveforms of IC conditions and age groups is shown for each extent condition 4° (green), 7° (orange), and 10° (burgundy) from -150 - $+250$ ms. Electrode PO3 was chosen as representative. Waves are referenced to electrode AFz.

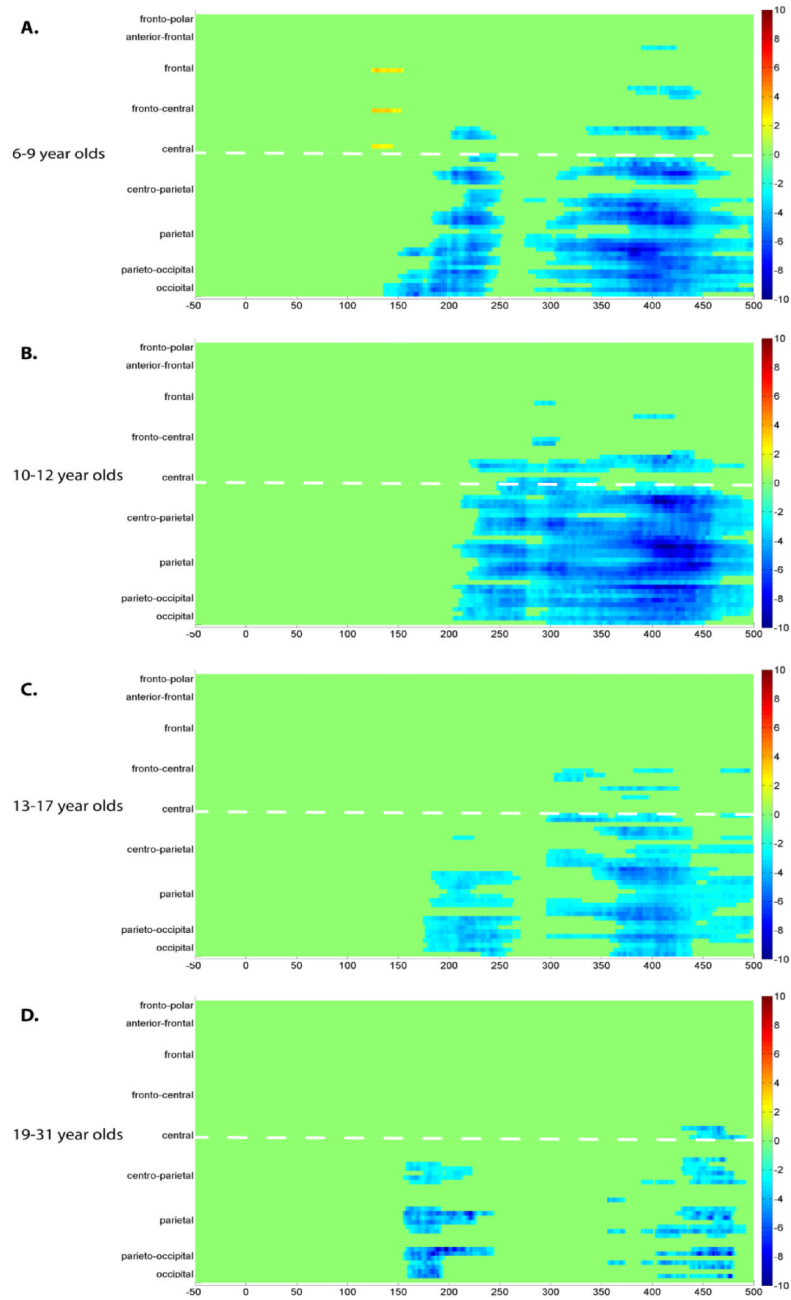


Figure 6.

T maps of difference between IC and No-IC conditions collapsed across extent. Color values indicate the result of point-wise paired t -tests for 10 consecutive points a 3 consecutive electrodes (see Methods), over a -50 to $+500$ ms time period (x-axis) and scalp region (y-axis). $\alpha = 0.05$, baselined from -80 to $+40$ ms, referenced to AFz. A. 6 - 9 year-olds. B. 10 - 12 year-olds. C. 13 - 17 year-olds. D. 19 - 31 year-olds.

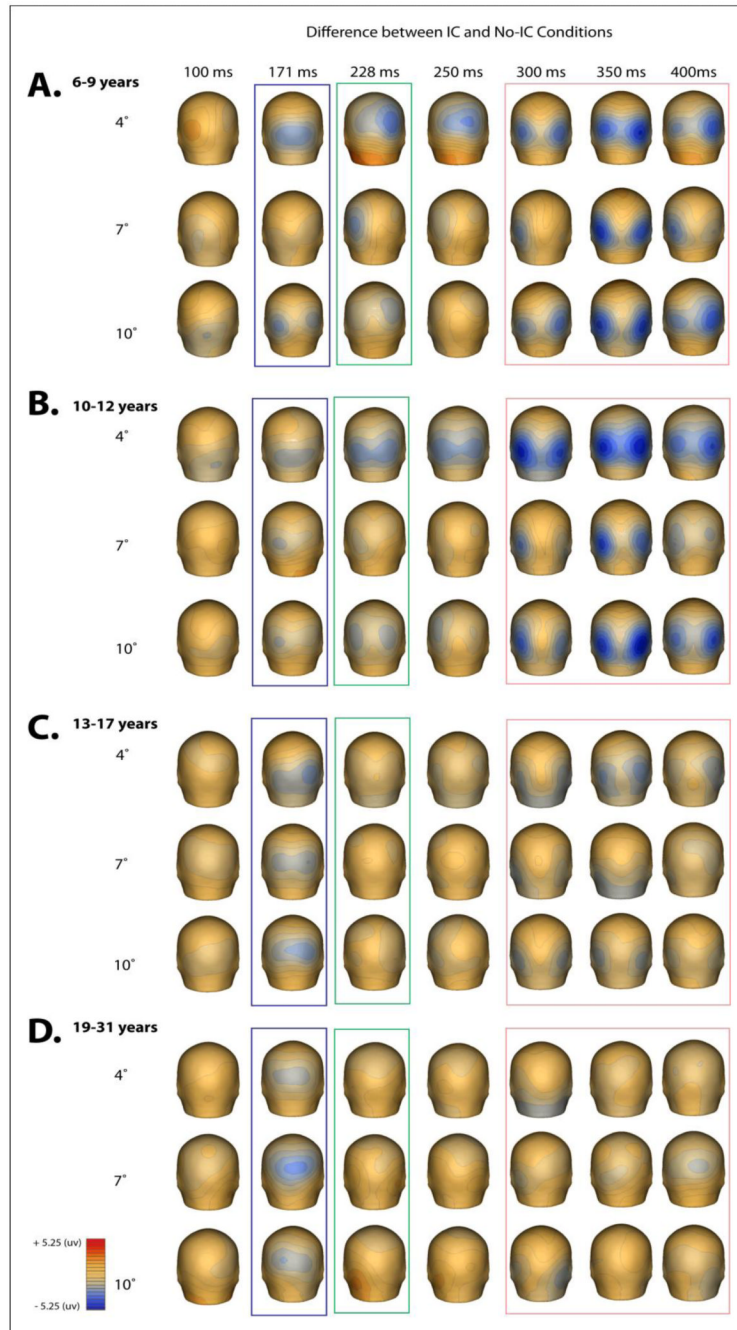


Figure 7.

Topographical Voltage Maps – Posterior View Voltage across the scalp surface for the difference between IC and No-IC conditions across age groups (A – D), contour extent, and time 100 – 400 ms. Average N1 latencies are shown for the two youngest age groups (6-9 and 10-12-year-old: 228 ms – blue outline) and the two oldest age groups (13-17 and 19-31-year-old: 171 ms – green outline). Three latencies during the N_{cl} processing-time frame are shown (red outline).

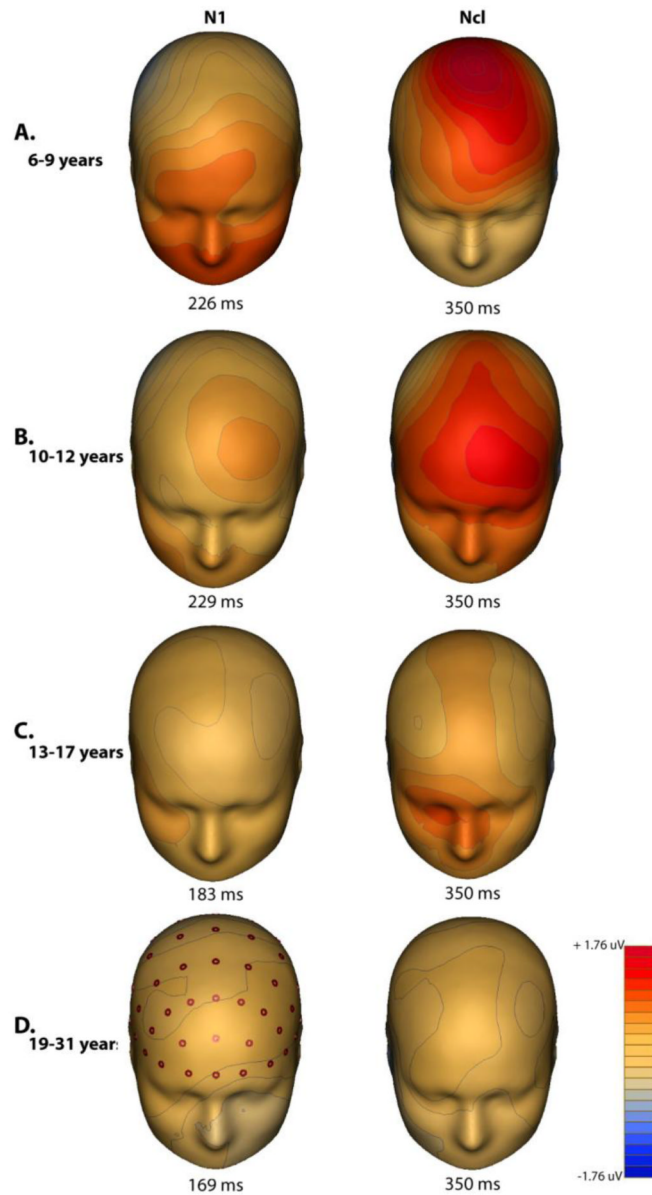


Figure 8. Topographical Voltage Maps – Anterior View Voltage across the scalp surface for the difference between IC and No-IC conditions across age groups (A – D), collapsed across contour extent. The N1 peak latency for each age group and the center point of the window encompassing the N_{c1} processing timeframe are shown. D (left panel) illustrates electrode positions.

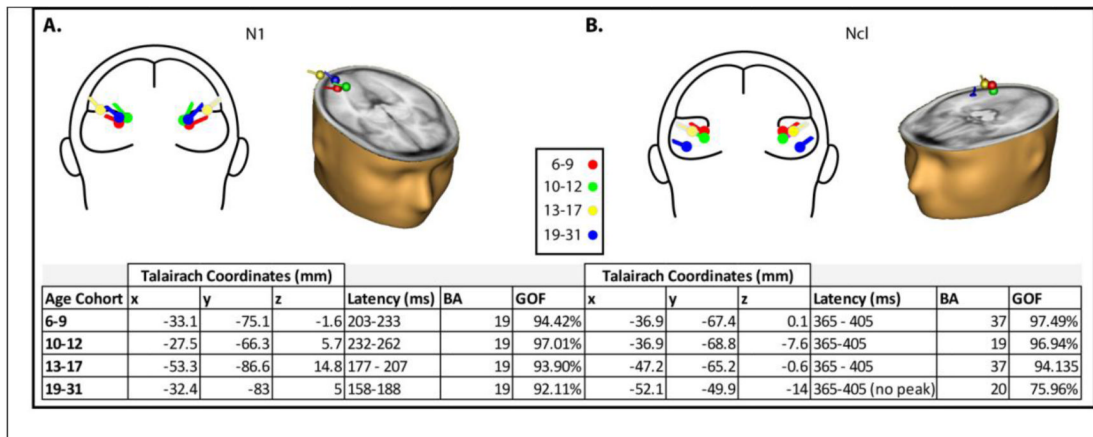


Figure 9.

Dipole Source Localization Models “Glass brain” and MRI dipole models for A. N1 time window (averaged across condition for each age group) and B. N_{cl} window (365 – 405 ms). Dipole colors correspond to age cohorts as indicated. Only right-hemisphere locations are shown as model is symmetrical.

Table 1

Participant Descriptive and Behavioral Data

	Number of Participants (# female)	Mean Age (SD)	Mean Full Scale IQ Score (SD)	Mean Fixation Task Perf. (SD)	Mean Trials per condition (SD)	Signal-to-Noise Ratio (SD) in dBs
6-9 year olds	16 (9)	8.03 (0.86)	113.07 (12.23)	81.78 (18.44)	151.42 (32.06)	27.02 (4.69)
10-12 year olds	17 (7)	11.56 (0.91)	116.50 (12.97)	93.56 (6.57)	155.16 (42.26)	24.96 (5.35)
13-17 year olds	18 (9)	15.01 (1.12)	112.18 (13.87)	95.56 (3.94)	194.94 (48.99)	24.20 (5.29)
19-31 year olds	12 (9)	23.25 (3.44)	Not assessed	97.73 (1.78)	175 (50.32)	22.69 (2.96)

Table 2

N1 Latencies across Age Group and Condition

	Condition 1 (4°)	Condition 2 (7°)	Condition 3 (10°)
6-9 years-old	209-239 ms	216-246 ms	209-239 ms
10-12 years-old	217-247 ms	210-240 ms	218-248 ms
13-17 years-old	171-201 ms	167-197 ms	166-196 ms
19-31 years-old	152-182 ms	150-180 ms	148-178 ms

Table 3

Component & Effect Amplitudes across Age Group

	P1 Amplitude (μV)	N1 Amplitude (μV)	N1 IC Condition Mean Diff (μV)	N_d IC Condition Mean Diff (μV) & Significance	Ratio of IC Condition Mean Diff (N1) to P1 Amplitude (μV)
6-9	12.453	1.1362	-1.082	-1.669 (p = 0.0000052)	0.087
10-12	7.739	1.1251	-1.064	-2.015 (p = 0.000000052)	0.137
13-17	4.408	-0.7821	-1.534	-0.638 (p = 0.047)	0.348
19-31	1.474	-3.2067	-1.	-0.4 (p = 0.30)	1.167