**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. It 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, varying the length of their contours to better understand how filling-in processes develop through 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 the manipulation of contour extent.

**Introduction**

von Helmholz observed that vision relied 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](#_ENREF_58)). 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. 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 ([Murray et al. 2002](#_ENREF_40); [Foxe et al. 2005](#_ENREF_19); [Li et al. 2006](#_ENREF_33); [Shpaner et al. 2009](#_ENREF_51)). The bulk of this processing occurs prior to the viewer’s awareness of the object ([Murray et al. 2002](#_ENREF_40)) or the application of semantic knowledge to identify it or make judgments regarding its characteristics ([Murray et al. 2006](#_ENREF_39)). These automatic completion processes have been extensively studied in adults using psychometrics, electrophysiology, and neuroimaging, but little is known about their development across childhood. Are they similarly automatic? Is the timecourse of completion the same? Are the same regions of the brain implicated?

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 1900](#_ENREF_45); [Kanizsa 1976](#_ENREF_27)). These stimuli have proven very useful for studying contour completion specifically and the binding of features into objects more generally ([Csibra et al. 2000](#_ENREF_8)) 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 ([Sugawara and Morotomi 1991](#_ENREF_55); [Herrmann et al. 1999](#_ENREF_25); [Murray et al. 2002](#_ENREF_40); [Foxe et al. 2005](#_ENREF_19); [Fiebelkorn et al. 2010](#_ENREF_17)).

Electrophysiological investigations have pointed to a two-phase model of contour completion with two temporally distinct phases of processing ([Foxe et al. 2005](#_ENREF_19); [Murray et al. 2006](#_ENREF_39)). These conform to Tulving and Schacter’s ([1990](#_ENREF_56)) dissociation of a perceptual phase of functioning from a higher-level conceptual phase (see also [Doniger et al. 2001](#_ENREF_14); [Doniger et al. 2002](#_ENREF_12)). 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](#_ENREF_51)). The second “conceptual” phase lasts from approximately 230 to 400 ms and 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](#_ENREF_13); [Doniger et al. 2001](#_ENREF_14); [Foxe et al. 2005](#_ENREF_19); [Sehatpour et al. 2006](#_ENREF_46)) (Figure 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](#_ENREF_40); [Sehatpour et al. 2008](#_ENREF_47)). The VEP component associated with this phase is the Ncl (closure-related negativity). 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 Ncl. Both of these processing phases have been source-localized to the lateral occipital complex (LOC) ([Foxe et al. 2005](#_ENREF_19); [Sehatpour et al. 2006](#_ENREF_46); [Sehatpour et al. 2008](#_ENREF_47)), a system of ventral visual stream brain regions long-associated with visual object processing ([Grill-Spector et al. 1998](#_ENREF_23); [Murray et al. 2002](#_ENREF_40); [Murray et al. 2004](#_ENREF_38); [Foxe et al. 2005](#_ENREF_19); [Murray et al. 2006](#_ENREF_39); [Shpaner et al. 2009](#_ENREF_51); [Fiebelkorn et al. 2010](#_ENREF_17); [Altschuler et al. 2012](#_ENREF_3); [Knebel and Murray 2012](#_ENREF_28); [Shpaner et al. 2012](#_ENREF_50)).

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](#_ENREF_8)). 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 and Deouell 2009](#_ENREF_61)). 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 (1977](#_ENREF_41)) observed in adult visual processing in general. Adults detect configuration-based differences in visual stimuli more often than differences between local elements. [Carey and Diamond (1977](#_ENREF_7)) 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 et al. (2003](#_ENREF_37)) 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](#_ENREF_44)) 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 Ncl-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 Ncl 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 and Kellman 1992](#_ENREF_49); [Ringach and Shapley 1996](#_ENREF_43)) and the timing of the *IC-effect* ([Murray et al. 2002](#_ENREF_40); [Altschuler et al. 2012](#_ENREF_3)). 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](#_ENREF_3))). 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 et al. 1995](#_ENREF_35); [Grill-Spector et al. 1998](#_ENREF_23)). 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 o – 10 o of visual angle (Fig 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. The development of size-invariant object representation in the inferior temporal cortex of macaques has been shown to be experience-dependent ([Li and DiCarlo 2010](#_ENREF_32)). However, evidence in humans is equivocal.

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 o – 10 o.

**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 2008](#_ENREF_26)). 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 1964](#_ENREF_42)).

All child and young adult participants had a Full Scale IQ > 85 ([Wechsler 1999](#_ENREF_60)), see Table 1 for summary. They were also screened for receptive ([Dunn and Dunn 2007](#_ENREF_15)) and expressive language ([Semel et al. 2003](#_ENREF_48)), and social communication and daily living skills ([Sparrow et al. 2005](#_ENREF_54)). 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 x 1024 pixel resolution or 75 cm from a monitor with 1680 x 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 (Fig 1). Either the 90o 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 20o - 180o and thereafter held constant for all presentations. Retinal eccentricity was manipulated, with stimuli subtending 4o, 7o, and 10o of visual angle, (calculated for the IC condition) presented in pseudo-random order equiprobably over each block. To hold support ratio ([Ringach and Shapley 1996](#_ENREF_43)) constant for the three levels at 54%, inducers were 2.1o, 3.8 o, and 5.6 o in diameter respectively (Fig 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 (Fig 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. 6-9-year-olds 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 o 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*

Continuous EEG was acquired through a Biosemi ActiveTwo system from a 72- electrode montage, digitized at 512 Hz and referenced to the Common Mode Sense (CMS) and the Driven Right Leg (DRL). Continuous EEG epochs from -150 msec 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. An artifact rejection criterion of ± 100 - 150 μV was applied to reject trials with eye or muscle movement. Average number of trials per condition is shown by age cohort in Table 1. Channels with excessive noise were interpolated if possible or turned off and excluded from further analysis.

*Statistical analyses*

Statistical analyses were guided by previous ERP work on IC processing in adults (e.g., [Murray et al. 2002](#_ENREF_40); [Shpaner et al. 2009](#_ENREF_51)) 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 Ncl, typically spanning ~230- 400 ms and also largest at lateral occipital scalp locations ([Doniger et al. 2000](#_ENREF_13); [Doniger et al. 2001](#_ENREF_14); [Foxe et al. 2005](#_ENREF_19); [Murray et al. 2006](#_ENREF_39); [Shpaner et al. 2012](#_ENREF_50)).

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 Ncl. 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 o, 7o, and 10o). Significance criteria was α < 0.05. Differences between IC conditions at both latencies were also regressed upon age as a continuous variable and the resulting R2 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 was 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 and Buchwald 1991](#_ENREF_24); [Foxe and Simpson 2002](#_ENREF_21)). 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 x axis, scalp region on the y axis. *T*-test results are coded by color (Fig 3). 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. The latencies analyzed were based on the maximal amplitude effects with the N1 and Ncl timeframes, as determined from substraction 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 in Figure 4.

*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 et al. 2012](#_ENREF_3)) 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 et al. 2011](#_ENREF_5); [Brandwein et al. 2012](#_ENREF_4)). The area beneath the curve for the 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; η2partial = 0.47) indicated the presence of an *IC-effect* collapsed across age cohort, hemiscalp, and extent manipulation (Table 3; Fig 5). A main effect of age cohort (F(3,59) = 3.612; p = 0.02; η2partial = 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 V) and the two youngest groups: 6-9-year-olds (1.1 V; p = 0.04) and 10-12-year-olds (1.1 V; 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 (R2 = 0.015, F(1,61) = 0.92; p = 0.34) or quadratically (R2 = 0.016, F(2,60) = 0.48; p = 0.62) (Fig 6).

Considering the strong 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 V; 10-12 =- 0.137 V; 13-17 =- 0.348 V; 19-31 = -1.167 V (Table 3) but did not emerge as significant (F(3,59) = 1.49; p = 0.23; η2partial =0.07).

*Ncl Analysis*

The area beneath the curve for the period of 300 – 400 ms was submitted to analysis to compare the amplitude of the difference between IC conditions (i.e. the Ncl 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; η2partial = 0.45) indicated a difference between IC conditions collapsed across age cohort, hemiscalp, and extent manipulation (Fig 5). A main effect of age cohort (F(3,59) = 24.118; p = 0.00000000026; η2partial = 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 x age cohort was present (F(3, 59) = 5.284; p =0. 0027; η2partial = 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 V ( p = 0.000000052); 6-9-year-olds: -1.669 V (p = 0.0000052); 13-17-year-olds: -0.638 V (p = 0.047); 19-31-year-olds : -0.4 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 (R2 = 0.141, F(1,61) = 9.98; p = 0.002) or quadratically (R2 = 0.145, F(2,60) = 5.105; p = 0.009) (Fig 6).

*P1 Analysis*

In the absence of any magnitude differences during the N1 and Ncl 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 ([Murray et al. 2002](#_ENREF_40); [Snyder et al. 2012](#_ENREF_53)). A main effect of extent (F(1,59) = 4.985; p = 0.013 (Greenhouse-Geisser corrected*);* η2partial = 0.078 confirmed our participants’ sensitivity to the range of manipulation (Fig 9). This was driven by a significant contrast between the 4 o and 10 o conditions (6.8 V versus 6.1 V; p = 0.011). The contrast between 7 o and 10 o approached significance (6.7 V versus 6.1 V; p = 0.056).

*Onset latencies*

Paired *t*-tests between IC conditions revealed the overall spatio-temporal patterns of IC-related activity (Fig 3). The oldest cohort displayed one significant and relatively punctate phase of IC processing prior to 400 ms which onset at ~ 155ms and continued for ~90 ms, with activity confined mainly to occipital and parietal-occipital scalp locations. Later modulations of much smaller amplitude occurred after 430 ms and included central scalp locations (a white dotted guideline divides regions anterior to central regions from those posterior to central regions). 13-17 year olds displayed an early phase onsetting at ~175ms and continuing until ~270. Processing resumed after ~300 ms and was measured across a greater extent of the scalp than in the adults. 6-9 year olds showed some occipital activity as early as 140 ms with parietal occipital activity onsetting at ~150 ms and continuing until ~250 ms. This early phase included central scalp locations. Activity resumes only 20ms later and continued past 500 ms, with a very wide scalp distribution, including over frontal regions. 10-12 year olds proved to be the most divergent from adults, showing almost one continuous processing phase onsetting at ~205 ms with sustained activity apparent until at least 500ms.

*Topographies*

Spline-interpolated potential maps depict voltage across the scalp surface for the difference between IC and No-IC conditions (Fig 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 Ncl (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 Ncl 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 Ncl time-frame in 6-9 and 10-12 year olds. Anterior views collapsed across extent (Fig 8) show activity over frontal and fronto-central regions for every group except adults in the Ncl timeframe.

*Dipole Models*

Two symmetrical dipole current sources were modeled for 30 ms N1 and 40 ms Ncl windows derived from the global field power 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 (Fig 4). 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 et al. 1997](#_ENREF_29); [Lancaster et al. 2000](#_ENREF_30)). Solutions for the Ncl 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 Ncl 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 to 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 identifies temporally and functionally dissociable processing phases – 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.

***The Development of Early Perceptual Processing of Illusory Contours***

An adult-like difference between contour conditions was observed during the perceptual phase in all the four age groups. 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 et al. 2002](#_ENREF_11); [Foxe et al. 2003](#_ENREF_18)) and has a stereotypical morphology by age two ([Lippe et al. 2007](#_ENREF_34)). N1 latency varied inversely with age, from approximately 226 ms in 6-9-year-olds to 165 ms in adults (Table 2). This is an already well-characterized effect ([Brandwein et al. 2011](#_ENREF_5)), but confirmed that the adult-like relationship between the peak of early IC processing and the visual N1 is seen across ages. This N1/IC correspondence was corroborated by statistical cluster plots in which the onset of differential activity was seen to occur in the N1 timeframe for all age-groups.

Posterior topographies of the *IC-Effect* (Fig 7) showed voltage distributionsfocused over lateral occipital scalp areas. Dipole models were nearly identical in every age group (Fig 4), estimating generators of this effect to be located in BA 19, a lateral occipital region which corresponds with fMRI studies identifying the LOC as sensitive to IC processing ([Mendola et al. 1999](#_ENREF_36); [Murray et al. 2002](#_ENREF_40)).

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 et al. 2001](#_ENREF_22); [Brandwein et al. 2011](#_ENREF_5)). To our knowledge, there is as yet no 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 currents to be measured. Children have thinner more immature skulls that continue to thicken across childhood ([e.g., Adeloye et al. 1975](#_ENREF_1)), and this thickening undoubtedly increases the intervening resistivity ([Cuffin 1993](#_ENREF_9); [Akhtari et al. 2002](#_ENREF_2)). The skull, which is a relatively poor conductor, plays an especially large role in attenuating EEG signals ([Lanfer et al. 2012](#_ENREF_31)). 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 represents a more moderate modulation in younger children. However, when ratios were assessed statistically rather than absolute amplitudes, the difference was not statistically significant, leaving this observation and the methodological question of whether the use of a ratio or absolute values is the more meaningful approach for future investigation. We would nevertheless argue that this difference is suggestive of the relative immaturity of this automatic contour-integration mechanism in younger children.

***The Development of Later Conceptual Phase Processing of Illusory Contours***

Key differences between adults and children occurred during the conceptual processing timeframe. Unlike the early phase, differences between contour-forming and non-contour-forming conditions varied significantly with age, with the greatest differences apparent in 10-12-year-olds, followed by 6-9-year-olds, and 13-17-year-olds. In contrast, no significant difference was seen during this timeframe in adults. Although the developmental trajectory did not follow a neat, step-like decrease across age groups, the picture across age (Fig 6) suggests more conceptual-phase than perceptual-phase processing, which decreases across adolescence and asymptotes to zero in adulthood.

Dipole models produced strong fits within lateral occipital and occipito-temporal locations for all three childhood age groups, however, adults, who showed no effect during the conceptual timeframe, showed no second peak in global field power, and unsurprisingly produced a poorly fitted model (Fig 4). In addition, more distributed networks appeared to be implicated in children than in adults (Fig 3). 6-12 year-olds showed greater activity over fronto-central scalp (Fig 8), suggesting possible recruitment of conceptual-level mechanisms ([Sehatpour et al. 2008](#_ENREF_47)).

***What Do These Developmental Differences Mean?***

The present results point to significantly more protracted contour closure processes in childhood than adulthood. Two distinct amplitude modulations occurred prior to 400 ms in the context of what appeared to be nearly continuous contour-related closure activity in children. This is in contrast to the single discrete and relatively punctate early process observed in adults. Moreover, prior to adolescence, the second processing phase was of greater magnitude.

Previous work has shown that automatic perceptual completion processes in adults default to the conceptual phase timeframe when images that are more challenging to close are presented. Such processing has been seen with degraded images for which, as successively more complete images are shown, one sees a gradual step-like change in the VEP until closure is achieved. This has been theorized to index active matching of incoming sensory stimuli to mnemonic object representations ([Sehatpour et al. 2006](#_ENREF_46)), hence the characterization of conceptual phase processes as more “effortful.” The implication of a more distributed neural network associated with this process has been supported by human intracranial work showing beta-band coherence among distant cortical regions ([Sehatpour et al. 2008](#_ENREF_47)). Synchronous high-frequency oscillatory activity has been proposed as a mechanism whereby anatomically distinct cortical areas may be functionally linked ([Singer and Gray 1995](#_ENREF_52); [von Stein et al. 1999](#_ENREF_59); [Buzsaki and Draguhn 2004](#_ENREF_6)). The synchronous activity of the LOC, prefrontal cortex, and hippocampal formation during the conceptual phase suggested a model in which the hippocampal formation serves as the repository of learned object representations and the prefrontal cortex limits matching options by generating hypotheses. It is conceivable that automatic perceptual closure based on contour extent cues alone relies on a certain amount of exposure and that, 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 process which is tuned over multiple exposures ([Li and DiCarlo 2010](#_ENREF_32)). 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 ([Foxe et al. 2005](#_ENREF_19)). The lack of exposure that children have to stimulus configurations may be similarly compensated for here.

The greater recruitment of fronto-central regions pointed to by anterior topographies (Fig 9) suggest 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 appeared to require the continuous attention of participants. Although processing occupied the latter time frame and recruitment of more distributed networks may be implicated, the second phase may also occur relatively automatically.

***Response invariance as a function of spatial extent manipulations***

In a previous study, we manipulated the absolute spatial extent of ICs in adults and revealed invariance in the magnitude and latency of the *IC-effect* as well as the overall VEP in the perceptual timeframe ([Altschuler et al. 2012](#_ENREF_3)) just as is seen here. The *IC-effect* was also invariant to our manipulation of relative contour length in adults. However, in that case, the overall VEP did vary. This study has not compared 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.

Realizing that invariance to the extent manipulation could be interpreted as the visual system’s lack of sensitivity to the range of the manipulation employed here, we compared amplitudes during the earlier P1 timeframe (approximately 60 – 150 ms) because this component is thought to index early spatial processing with dorsal and ventral visual stream sources contributing to its generation (Foxe et al 2005; Molholm et al, 2006). It has previously shown sensitivity to the manipulation of stimulus extent ([Murray et al. 2002](#_ENREF_40); [Snyder et al. 2012](#_ENREF_53)) although there is not agreement in which direction such manipulation affects amplitude. Here, extent varied inversely with P1 amplitude in accord with Snyder et al ([Snyder et al. 2012](#_ENREF_53)). 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 o to 10o, our measures are sufficiently sensitive to measure the visual system’s encoding of such a manipulation.

Children older than 5 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 et al. (2004](#_ENREF_10)) observed that children 18-30 months-of-age made frequent attempts to perform actions with miniature versions of familiar objects without taking into account their size – for example, trying to enter a toy car. Their results 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 contour extent manipulation may then tax the limits of contour integration processes – a question for future exploration.

**Conclusion**

We sought to better understand the typical development contour completion because this process contributes 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 extents. A developmental trajectory of less efficient, more effortful, and more protracted contour completion processes that mature over childhood is emerging. The two functionally and temporally distinct phases that have been useful in characterizing adult object processing – consisting of an early automatic and a later conceptual phase – do not appear to emerge finally as distinct until late adolescence.

Evidence of atypical boundary detection ([Vandenbroucke et al. 2008](#_ENREF_57)), an atypical bias toward processing global stimulus configuration ([Fiebelkorn et al. 2012](#_ENREF_16)), and delays in the development of other sensory processes ([Foxe et al. 2009](#_ENREF_20)) in persons on the autism spectrum 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.

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**Table Captions**

Table 1

Participant Descriptive and Behavioral Data

Table 2

N1 Latencies across Age Group and Condition

Table 3

Component & Effect Amplitudes across Age Group

**Figure Captions**

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 Ncl ([adapted from Sehatpour et al. 2006](#_ENREF_46)).

Figure 3 – 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 at 3 consecutive electrodes (see Methods), over a -50 to +500 ms time period (x-axis) and scalp region (y-axis). α = 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 4 – Dipole Models

“Glass brain” and MRI symmetrical dipole models for A. N1 time window (averaged across condition for each age group) and B. Ncl window ( 365 - 405 ms). Dipole colors correspond to age cohorts as indicated.

Figure 5 – 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 4o (green), 7o (orange), 10o (burgundy).

Figure 6 – Regression analysis

Difference amplitudes during N1 (blue) and Ncl (red) latencies regressed upon age. Data are collapsed across hemiscalp and contour extent. Quadratic regression is significant for Ncl but not for N1 latency.

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 (6-12-year-old: 228 ms – blue outline) and the two oldest age groups (13 - 31-year-old: 171 ms – green outline). Three latencies during the Ncl 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 latency for each age group and the center point of the large window encompassing the Ncl processing timeframe are shown.

Figure 9 – P1 Main Effect of Extent Manipulation

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

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