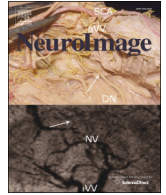




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The effort to close the gap: Tracking the development of illusory contour processing from childhood to adulthood with high-density electrical mapping

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ARTICLE INFO

Article history:

12 Accepted 12 December 2013

13 Available online xxx

ABSTRACT

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

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Q3 Introduction

von Helmholtz observed that vision relies on more than stimulation of the retina, “*remiscences of previous experiences act in conjunction with present sensations to produce a perceptual image.*” (von Helmholtz, 1910). Poor lighting, occlusion, and the fact that the retina is a variegated and somewhat discontinuous surface produce incomplete, two-dimensional low-level representations of objects. Changes in perspective or viewing distance of a given object result in projection of vastly different images onto this surface. Indeed, the retina contains a so-called blind-spot of nearly 2 mm in diameter where the axons of the optic nerve exit (Quigley et al., 1990), and yet, the visual system seamlessly “fills in” the missing information (Pessoa and De Weer,

2003). As 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 (Brodeur et al., 2006; Foxe et al., 2005; Li et al., 2006; Murray et al., 2002; Proverbio and Zani, 2002; Shpaner et al., 2009). The bulk of this processing occurs prior to the viewer's awareness of the object (Vuilleumier et al., 2001) or the application of semantic knowledge to identify it or make judgments regarding its characteristics (Murray et al., 2006). These automatic completion processes have been extensively studied in adults using psychometrics, electrophysiology, and neuroimaging (e.g., Ffytche and Zeki, 1996; Halko et al., 2008; Mendola et al., 1999; Ohtani et al., 2002; Ringach and Shapley, 1996). Developmental explorations have studied this process in infancy (e.g., Bremner et al., 2012; Csibra, 2001; Otsuka et al., 2004), but the use

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

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

Electrophysiological investigations have pointed to a two-phase model of contour completion with two temporally distinct phases of processing (Foxe et al., 2005; Murray et al., 2006). These conform to Tulving and Schacter's (1990) dissociation of a perceptual phase of functioning from a higher-level conceptual phase (see also Doniger et al., 2001; Doniger et al., 2002). The "perceptual" phase has been associated with a modulation of VEP amplitude during the timeframe of the N1

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

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

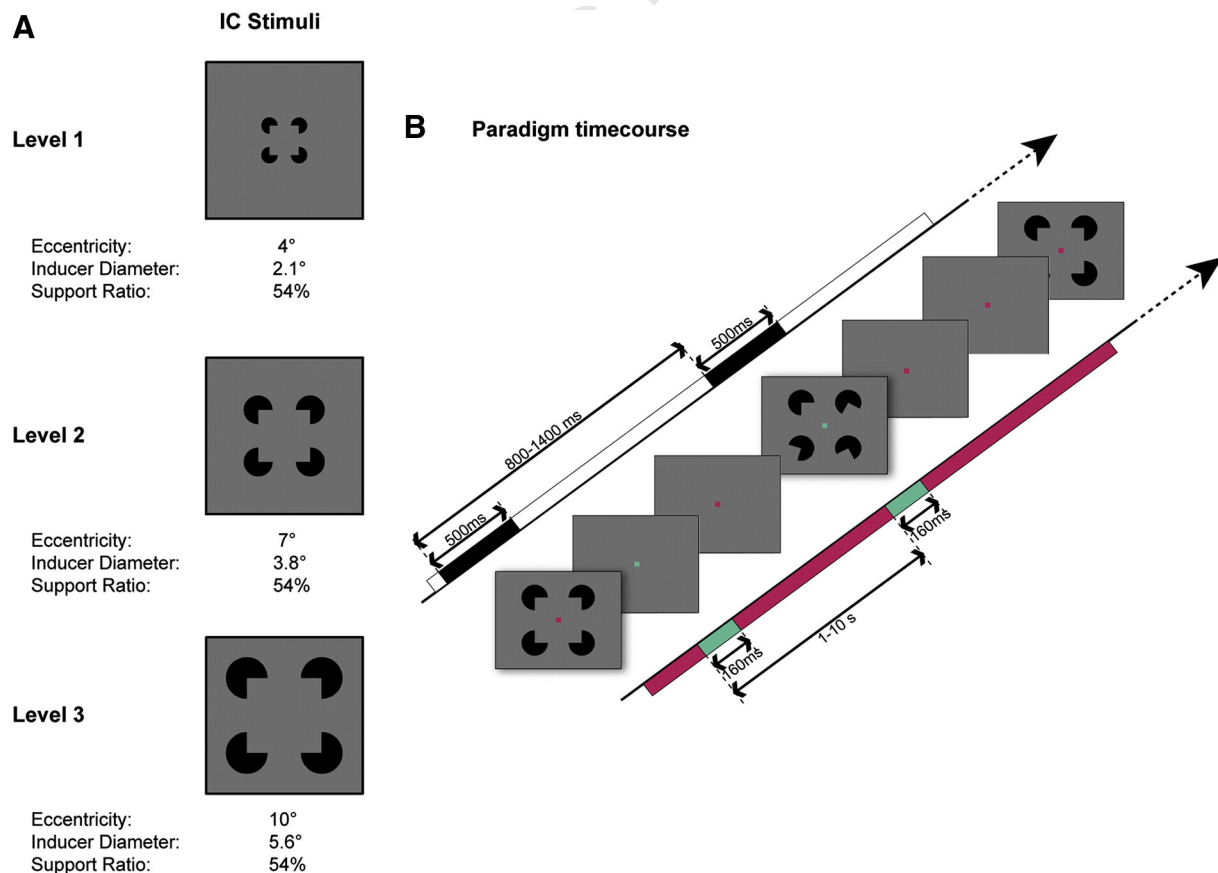


Fig. 1. Stimuli & paradigm. A. Stimuli in illusion-inducing (IC) condition with 3 experimental manipulations of contour extent. B. Paradigm time-course.

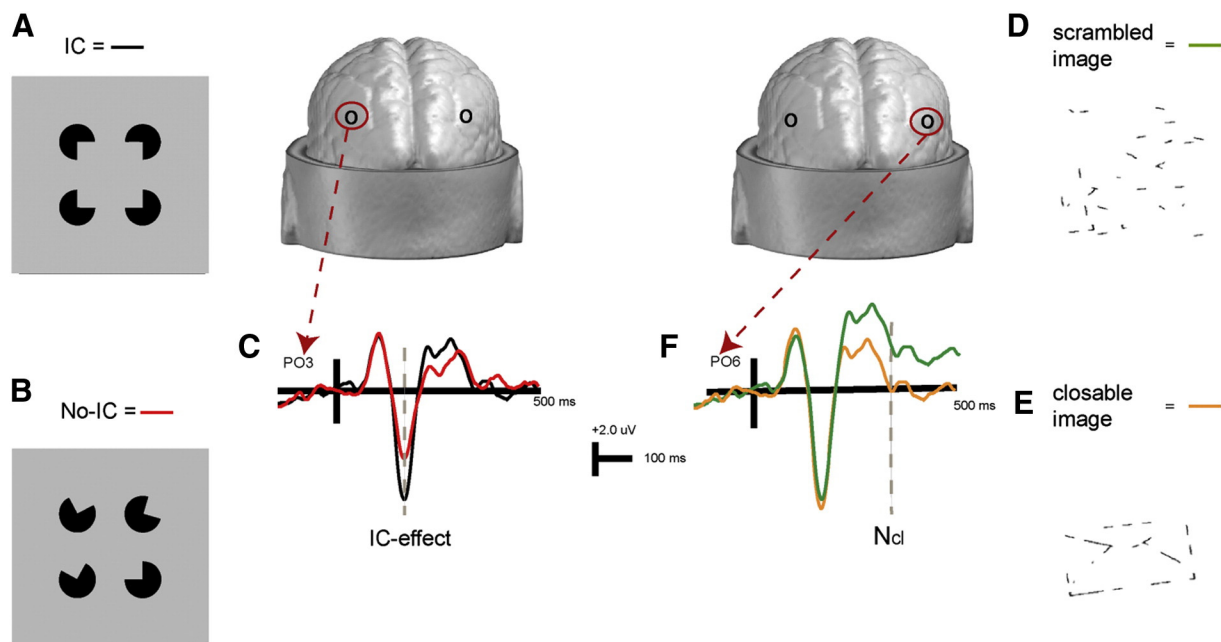


Fig. 2. Effect examples. A. IC stimulus in illusion-inducing (IC) condition. B. IC stimulus in non-illusion-inducing (No-IC) condition. C. Exemplar *IC-effect* (Altschuler et al., 2012). D. Exemplar ambiguous fragmented scrambled image. E. Exemplar identical closable image. F. Exemplar N_{cl} . Adapted from Sehatpour et al. (2006) for illustrative purposes.

135 strongly suggested that gamma-band response measures are often con-
 136 found by subtle saccadic eye movements (Yuval-Greenberg and
 137 Deouell, 2009). Such effects are only likely to be magnified in infancy.
 138 In our view, electrophysiology has not yet offered clear evidence as to
 139 whether contour completion processes mature with age.

140 If automatic contour integration relies on reference to global stimu-
 141 lus configuration in the processing of discrete elements, this may reflect
 142 a bias that Navon (1977) observed in adult visual processing in general.
 143 Adults detect configuration-based differences in visual stimuli more
 144 often than differences between local elements. Carey and Diamond
 145 (1977) suggested that adults' ability to encode configuration results
 146 in an advantage over children in recognizing previously seen versus
 147 novel faces. This suggests that this strategy may develop from a
 148 focus on local elements in childhood to one on global information in
 149 adulthood. For example, Mondloch et al. (2003) observed that faster
 150 processing of global relative to local processing of hierarchical figures
 151 (larger shapes composed of the arrangement of smaller shapes)
 152 emerged between 10 and 14 years of age. Scherf et al.'s (2009) develop-
 153 mental comparison of hierarchical figure processing detected a local
 154 bias in children and adolescents through 17 years-of-age, but this
 155 could be manipulated by cueing attention to local or global information.
 156 Taken together, these paradigms offer a strong suggestion that global
 157 versus local strategies for object processing change over childhood,
 158 but an unclear picture of the trajectory. This suggests us that contour
 159 completion processing is also likely altered.

160 **Q4** The goal here is to trace the developmental trajectory of perceptual
 161 contour completion from 6 years-of-age to adulthood using a cross-
 162 sectional sampling approach. A number of clear predictions can be
 163 made. If perception of ICs relies on later more effortful processing in
 164 earlier childhood, then Phase-one processing (the *IC-Effect*) may be
 165 absent until later in development and IC-processing may instead rely
 166 exclusively on later N_{cl} -related processes. Perhaps a more likely scenario
 167 is that early automatic processing emerges relatively early in develop-
 168 ment, but is found to be weaker in early childhood with Phase-two N_{cl}
 169 processing playing a more prominent role for younger children.

170 Additionally, visual filling-in processes are not impervious to exper-
 171 imental manipulations of inducer parameters. Variations in, for exam-
 172 ple, retinal extent relative to the size of the shape they induce, have

173 been shown to influence the subjective perception of illusion strength
 174 (Ringach and Shapley, 1996; Shipley and Kellman, 1992) and the timing
 175 of the *IC-effect* (Altschuler et al., 2012; Murray et al., 2002). In Altschuler
 176 et al. (2012), we systematically manipulated contour length, inducer
 177 diameter, and the proportion of real contour to illusory contour—
 178 known as support ratio (see Fig. 2 in Altschuler et al. (2012)). The laten-
 179 cy of the *IC-effect* changed, but only in response to the manipulation of
 180 support ratio. Somewhat to our surprise, the amplitude of the *IC-effect*
 181 was entirely invariant to manipulations previously associated with illu-
 182 sion strength. Functional neuroimaging work has associated the LOC
 183 with visual processing of objects that is invariant with regard to their
 184 size or the perspective from which they are viewed (Grill-Spector
 185 et al., 1998; Malach et al., 1995). This is in contrast to hierarchically
 186 earlier retinotopic regions which do show sensitivity to variations in
 187 stimulus energy, as reflected in amplitude modulations of the C1 and
 188 P1 components of the VEP (Di Russo et al., 2002; Foxe et al., 2008).
 189 In our 2012 study, images of different size, projecting different images
 190 upon the retina, produced indistinguishable activations in LOC neuronal
 191 populations. As long as the gap between inducers was not too large
 192 relative to the overall size of the potential object, the contour frag-
 193 ments were bound, leading to the perception of a single object. The two-phase
 194 model would posit that this occurs via automatic reference to the
 195 viewer's knowledge of similar stimulus configurations.

196 In the present study, as in our adult study, we manipulated the abso-
 197 lute length of illusory contours (referred to here as “extent”) across a
 198 range of 4° – 10° of visual angle (Fig. 1). Although this manipulation re-
 199 sulted in no variation of the *IC-effect* whatsoever in adults, we reasoned
 200 that the human brain does not come “ready-made” to execute such in-
 201 stantaneous references to spatial groupings. Rather, these would likely
 202 be tuned via multiple exposures across development to ultimately pro-
 203 duce reliable inferences. This is supported by the observation of the
 204 experience-dependent development of size-invariant object represen-
 205 tation in the inferior temporal cortex of non-human primates (Li and
 206 DiCarlo, 2010) and by human fMRI work showing that improved recog-
 207 nition of objects through practice correlated with increases in LOC acti-
 208 vation (Grill-Spector et al., 2000).

209 To summarize, this study employed high-density electrical mapping
 210 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°.

214 Methods & materials

215 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). 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).

All child and young adult participants had a full scale IQ > 85 (Wechsler, 1999), see Table 1 for summary. They were also screened for receptive (Dunn and Dunn, 2007) and expressive language (Semel et al., 2003), and social communication and daily living skills (Sparrow 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 and developmental histories.

239 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 (Fig. 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° to 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 and Shapley, 1996) constant for the three levels at 54%, inducers were 2.1°, 3.8°, and 5.6° 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 toward perception of the illusion. Color detection stimuli consisted of a centrally-presented red fixation-square 4 pixels in area. Every 1–10 s, 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. 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 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). 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 μV 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 et al., 2002; Shpaner 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

t1.1 **Table 1**
t1.2 Participant descriptive and behavioral data.

| t1.3 | 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 |
|------|-----------------------------------|---------------|-------------------------------|-------------------------------|--------------------------------|-----------------------------------|
| t1.4 | 6–9 year olds | 16 (9) | 8.03 (0.86) | 113.07 (12.23) | 81.78 (18.44) | 151.42 (32.06) |
| t1.5 | 10–12 year olds | 17 (7) | 11.56 (0.91) | 116.50 (12.97) | 93.56 (6.57) | 155.16 (42.26) |
| t1.6 | 13–17 year olds | 18 (9) | 15.01 (1.12) | 112.18 (13.87) | 95.56 (3.94) | 194.94 (48.99) |
| t1.7 | 19–31 year olds | 12 (9) | 23.25 (3.44) | Not assessed | 97.73 (1.78) | 175 (50.32) |

t2.1 **Table 2**
t2.2 N1 latencies across age group and condition.

| t2.3 | | Condition 1 (4°) | Condition 2 (7°) | Condition 3 (10°) |
|------|-----------------|------------------|------------------|-------------------|
| t2.4 | 6–9 years-old | 209–239 ms | 216–246 ms | 209–239 ms |
| t2.5 | 10–12 years-old | 217–247 ms | 210–240 ms | 218–248 ms |
| t2.6 | 13–17 years-old | 171–201 ms | 167–197 ms | 166–196 ms |
| t2.7 | 19–31 years-old | 152–182 ms | 150–180 ms | 148–178 ms |

314 regions where the visual N1 response was largest in amplitude (lateral
315 occipital scalp represented best at scalp-sites PO3 and PO4), and the
316 early time window was centered on the peak latency of the N1. The
317 later time window was defined relative to the N_{cl} , typically spanning
318 ~230–400 ms and also largest at lateral occipital scalp locations
319 (Doniger et al., 2000, 2001; Foxe et al., 2005; Murray et al., 2006;
320 Shpaner et al., 2012).

321 Specifically, the first window encompassed the 30 ms window
322 centered on the N1 of the grand average waveform of each age cohort
323 and level of extent. This was identified as the most negative point be-
324 tween 100 and 250 ms averaged across IC conditions (IC and No-IC)
325 and hemiscalp (PO3 and PO4). A 300–400 ms window was chosen
326 to encompass the N_{cl} . Waveforms were re-referenced to an anterior
327 midline frontal scalp site (AFz). These two time windows were sub-
328 jected to $2 \times 2 \times 3$ repeated-measures ANOVAs in SPSS 15.0 with a
329 between-subjects factor of age cohort (6–9, 10–12, 13–17, 19–31),
330 and within-subjects factors of IC condition (IC vs. No-IC), hemiscalp
331 (PO3, PO4), and eccentricity (4°, 7°, and 10°). Significance criterion
332 was set at an $\alpha < 0.05$. Differences between IC conditions at both la-
333 tencies were also regressed upon age as a continuous variable and
334 the resulting R^2 values tested for significance. The results are depicted
335 as a scatter plot.

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

342 Additionally, we observed that, although the *IC-effect* was statistical-
343 ly equivalent across age groups, it varied greatly in proportion to the
344 overall amplitude of the VEP. To assess the significance of this relative
345 difference, we ran an additional post-hoc ANOVA on the ratio of the dif-
346 ference between IC and No-IC during the N1 timeframe (the *IC-effect*)
347 and P1 amplitude.

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

t3.1 **Table 3**
t3.2 Component & effect amplitudes across age group.

| t3.3 | | P1 amplitude (μ V) | N1 amplitude (μ V) | N1 IC condition mean diff (μ V) | N_{cl} IC condition mean diff (μ V) & significance | Ratio of IC condition mean diff (N1) to P1 amplitude (μ V) |
|------|-------|----------------------------|----------------------------|---|--|--|
| t3.4 | 6–9 | 12.453 | 1.1362 | –1.082 | –1.669 ($p = 0.0000052$) | 0.087 |
| t3.5 | 10–12 | 7.739 | 1.1251 | –1.064 | –2.015 ($p = 0.00000052$) | 0.137 |
| t3.6 | 13–17 | 4.408 | –0.7821 | –1.534 | –0.638 ($p = 0.047$) | 0.348 |
| t3.7 | 19–31 | 1.474 | –3.2067 | –1. | –0.4 ($p = 0.30$) | 1.167 |

Dipole source modeling

361

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

Signal-to-noise (SNR) ratio

375

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

Results

381

N1 Analysis

382

383 The maximum negative deflection in the 100–250 ms period aver-
384 aged across IC conditions and hemiscalp was selected as the N1 peak
385 for each extent in each age cohort. This latency decreased with age as
386 has been previously observed (Brandwein et al., 2011, 2012). The inte-
387 grated amplitude over a 30 ms window centered on this latency
388 (Table 2) was submitted to analysis to compare the amplitude of the
389 difference between IC conditions across the four age cohorts, two
390 hemiscalps, and three levels of retinal eccentricity (extent).

391 A main effect of IC condition ($F_{(1, 59)} = 51.506$; $p < 0.001$;
392 $\eta^2_{\text{partial}} = 0.47$) indicated the presence of an *IC-effect* collapsed across
393 age cohort, hemiscalp, and extent manipulation (Table 3; Fig. 3). A main
394 effect of age cohort ($F_{(3,59)} = 3.612$; $p = 0.02$; $\eta^2_{\text{partial}} = 0.16$) indi-
395 cated a difference in VEP magnitudes collapsed across IC condition,
396 hemiscalp, and extent (Table 3). This main effect is driven by significant
397 mean differences between adults (–3.2 μ V) and the two youngest
398 groups: 6–9-year-olds (1.1 μ V; $p = 0.04$) and 10–12-year-olds
399 (1.1 μ V; $p = 0.03$). No interactions attained significance.

400 The regression of IC difference (i.e., *IC-effect*) upon age as a contin-
401 uous variable was not significant whether data were fitted linearly
402 ($R^2 = 0.015$, $F_{(1,61)} = 0.92$; $p = 0.34$) or quadratically ($R^2 = 0.016$,
403 $F_{(2,60)} = 0.48$; $p = 0.62$) (Fig. 4).

404 Considering the differences in overall VEP magnitude across
405 age groups, we compared the *IC-effect* magnitude as a proportion
406 of P1 magnitude collapsed across hemiscalp for each condition
407 and age group. Voltages increased with age: 6–9 = –0.087 μ V;
408 10–12 = –0.137 μ V; 13–17 = –0.348 μ V; and 19–31 = –1.167 μ V
409 (Table 3) but did not emerge as significant ($F_{(3,59)} = 1.49$; $p = 0.23$;
410 $\eta^2_{\text{partial}} = 0.07$).

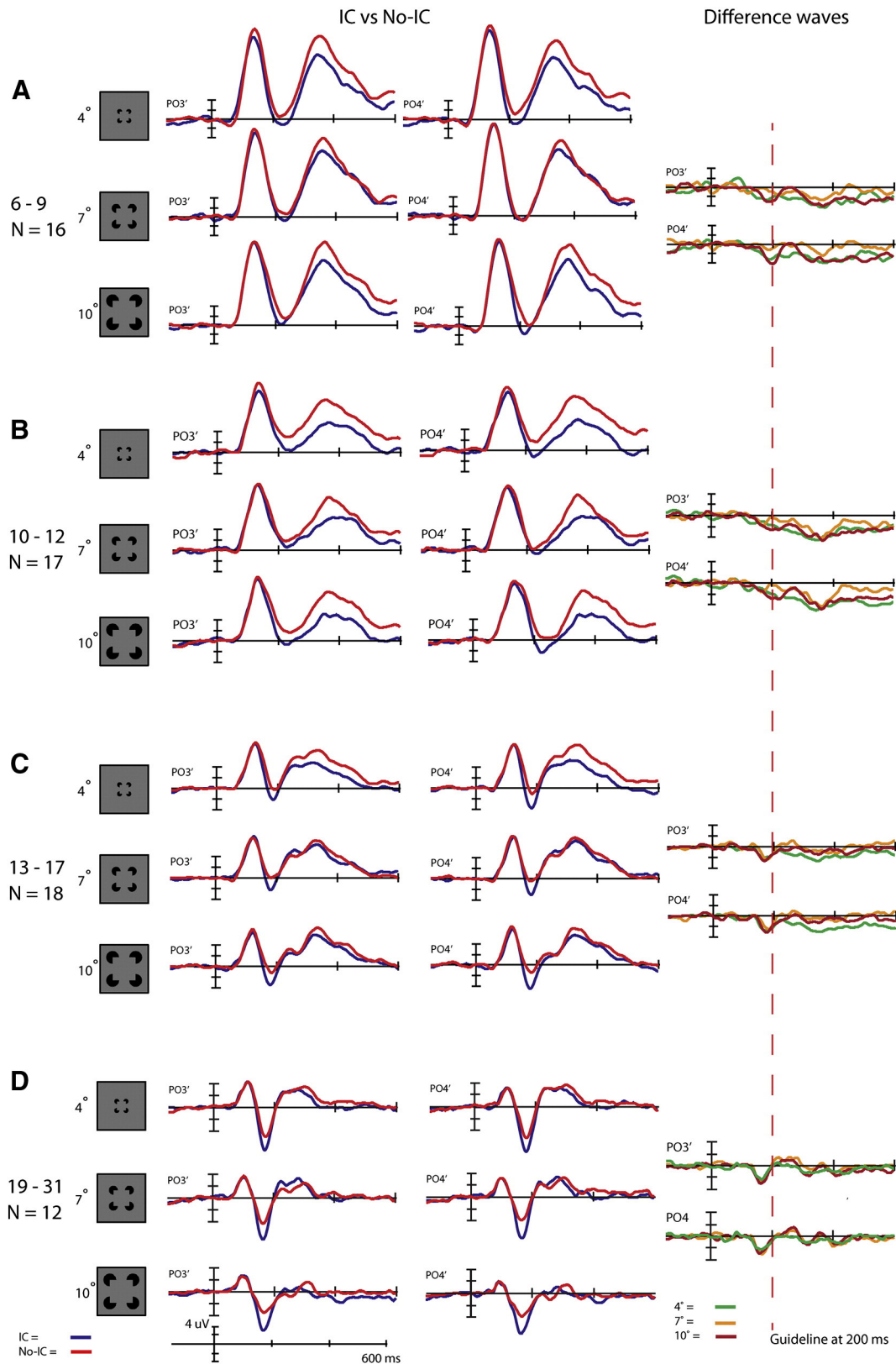


Fig. 3. VEP waveforms. IC versus No-IC and subtraction waves for each condition and age group (A–D). Effect wave forms show IC condition (blue) & No-IC condition (red) from -150 to $+600$ ms at electrodes PO3 and PO4. Waves are referenced to electrode AFz. Difference waves depict each condition of contour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

411 N_{cl} analysis

412 The integrated amplitude across the period from 300 to 400 ms was
413 submitted to analysis to compare the amplitude of the difference

between IC conditions (i.e. the N_{cl} component) for the four age cohorts, 414
two hemiscalps, and 3 levels of extent. 415

A main effect of condition ($F_{(1, 59)} = 48.254$; $p < 0.001$; $\eta^2_{\text{partial}} = 0.45$) indicated a difference between IC conditions collapsed across 416
0.45) indicated a difference between IC conditions collapsed across 417

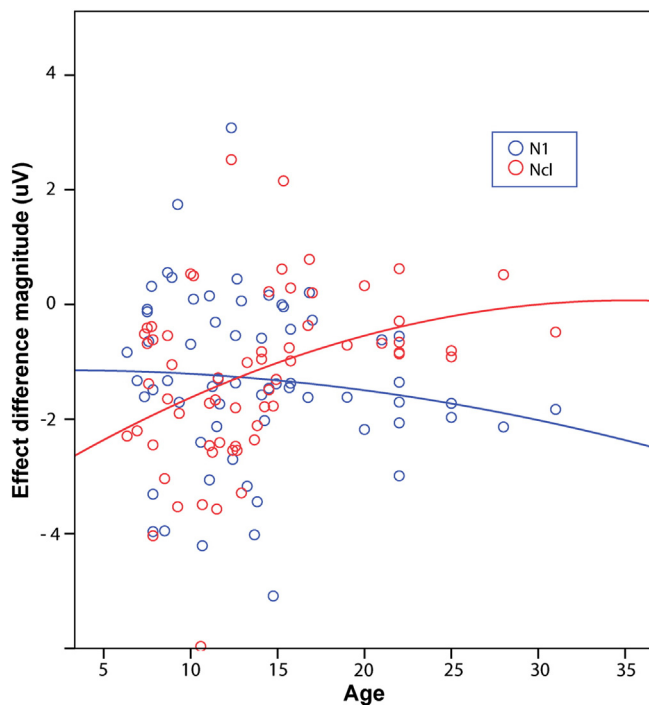


Fig. 4. Regression analysis. Difference amplitudes during N1 (blue) and N_{cl} (red) latencies regressed upon age. Data are collapsed across hemiscalp and contour extent. Quadratic regression is significant for N_{cl} but not for N1 latency.

age cohort, hemiscalp, and extent manipulation (Fig. 3). A main effect of age cohort ($F_{(3,59)} = 24.118$; $p < 0.001$; $\eta^2_{\text{partial}} = 0.55$), 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 ($F_{(3, 59)} = 5.284$; $p = 0.0027$; $\eta^2_{\text{partial}} = 0.21$). 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: $-0.638 \mu\text{V}$ ($p = 0.047$); and 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 ($R^2 = 0.145$, $F_{(2,60)} = 5.105$; $p = 0.009$) (Fig. 4).

434 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 et al., 2002; Murray et al., 2002; Snyder et al., 2012). A main effect of extent ($F_{(2,59)} = 4.985$; $p = 0.013$ (Greenhouse–Geisser corrected); $\eta^2_{\text{partial}} = 0.078$ confirmed our participants' sensitivity to the range of manipulation (Fig. 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 $6.1 \mu\text{V}$; $p = 0.056$).

447 Spatio-temporal activity across scalp areas and time

Paired *t*-tests between IC conditions revealed the overall spatio-temporal patterns of IC-related activity (Fig. 6). A white dotted

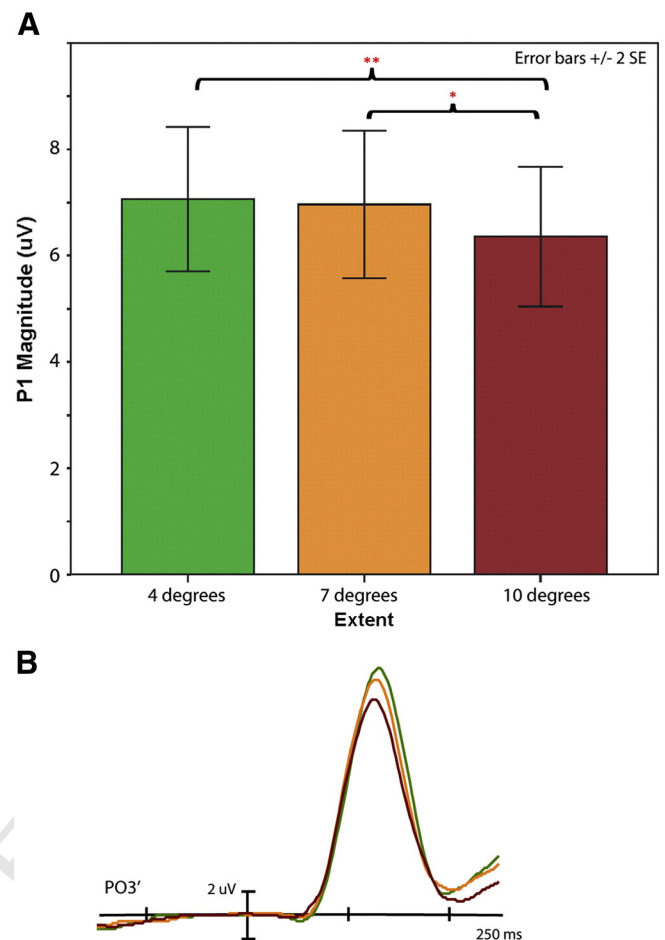
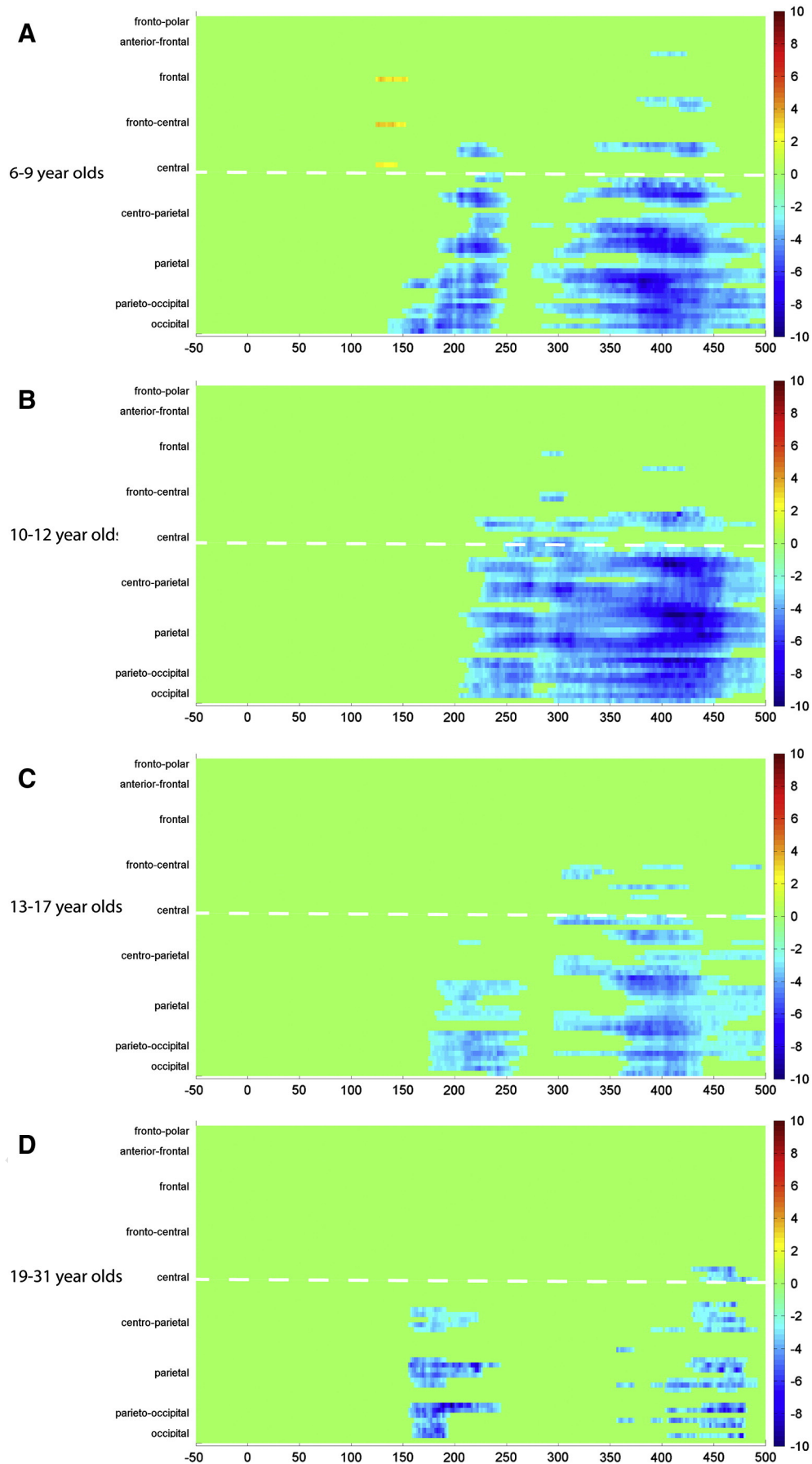


Fig. 5. P1 main effect of extent manipulation. A. Bar graph: P1 magnitude (μV) collapsed across age and IC conditions for each extent. **The significant contrast between 4° and 10° ($p = 0.011$) drives the effect. *The contrast between 7° and 10° approaches significance ($p = 0.056$). B. The average waveforms of IC conditions and age groups is shown for each extent condition 4° (green), 7° (orange), and 10° (burgundy) from -150 to $+250$ ms. Electrode PO3 was chosen as representative. Waves are referenced to electrode AFz.

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.

453 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 N_{cl} (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_{cl} 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_{cl} 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 N_{cl} timeframe. Note that the spline interpolation procedure used here (BESA 5.1.8 EEG software, Gräfelting, Germany) projects inferred potential distributions over inferior scalp regions where no electrodes were actually placed.



472 *Dipole models*

473 Two symmetrical dipole current sources were modeled for the
 474 30 ms window centered on the N1 (*IC-effect*) and the 40 ms window
 475 centered on the N_{cl} derived from the global field power (GFP)
 476 (Skrandies, 1995) of the subtraction of IC and No-IC conditions averaged
 477 across contour extent. Separate color-coded maps show solutions for
 478 each age group, with the color of the dipole cartoon matching the
 479 color of the Talairach coordinates given (Fig. 9). During the N1, solutions
 480 for all groups overlap and fits exceed 92% of explained variance. The
 481 coordinates for all age groups fall approximately within Brodmann
 482 area (BA) 19 which encompasses lateral occipital cortex as estimated
 483 on Talairach Client software (Lancaster et al., 1997, 2000). Solutions
 484 for the N_{cl} processing time-frame overlap roughly for 6–17 year-olds
 485 falling in BA 19 and 37—lateral occipital and occipito-temporal areas.
 486 The fits of these estimates exceed 94% explained variance. There was
 487 no peak in GFP during the N_{cl} time-frame in adults, obviating the logic
 488 of fitting a dipole solution. However, we attempted a model for the
 489 sake of consistency. The solution accounting for the greatest amount
 490 of variance was estimated to fall close to the inferior temporal gyrus
 491 in BA 20. Only 76% of the variance was explained by this model.

492 **Discussion**

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

509 *Early perceptual phase processing of illusory contours*

510 An adult-like difference between contour conditions was observed
 511 during the “perceptual” phase in all the four age groups, including the
 512 youngest group tested (6–9 year olds). This analysis was constrained
 513 to the timeframe of the N1 of each age group for each extent condition,
 514 since the N1 is a stable component of the VEP (Di Russo et al., 2002; Foxe
 515 et al., 2003) and has a stereotypical morphology by age two (Lippe et al.,
 516 2007). N1 latency varied inversely with age, from approximately
 517 226 ms in 6–9-year-olds to 165 ms in adults (Table 2). This shortening
 518 of N1 latency is an already well-characterized effect (Brandwein et al.,
 519 2011; Lippe et al., 2007).

520 Posterior topographies of the *IC-Effect* (Fig. 7) showed voltage distri-
 521 butions focused over lateral occipital scalp areas. Dipole models were
 522 nearly identical in every age group (Fig. 9), estimating generators of
 523 this effect to be located in the region of Brodmann area 19, a lateral oc-
 524 cipital region which corresponds very well with previous fMRI studies
 525 identifying the LOC as sensitive to IC processing (Mendola et al., 1999;
 526 Murray et al., 2002).

527 Overall VEP magnitude, as indexed by P1 amplitude (Table 3), was
 528 quite large in the youngest sample, decreasing rather dramatically

529 with age. This is a common finding in developmental ERP studies
 530 (Brandwein et al., 2011; Gomes et al., 2001). To our knowledge, there
 531 is as yet no widely accepted explanation for this difference across age-
 532 groups. One highly plausible cause, however, may be found in the prop-
 533 erties of the volume conductor itself—that is, the nature of the interven-
 534 ing structures between the electrodes and the neural tissue generating
 535 the measured currents. Children have thinner more immature skulls
 536 that continue to thicken across childhood (e.g., Adey et al., 1975),
 537 and this thickening undoubtedly increases the intervening resistivity
 538 (Akhtari et al., 2002; Cuffin, 1993). The skull, which is a relatively poor
 539 conductor, plays an especially large role in attenuating EEG signals
 540 (Lanfer et al., 2012). Additionally, it is possible that age-related changes
 541 in cortical tissue impact signal conduction (Grieve et al., 2003). Thus, in
 542 comparing responses between adults and children, one might suppose
 543 that concentrating on relative changes in amplitude (i.e. ratios) makes
 544 the most sense. In adults, the ratio of IC difference during the perceptual
 545 phase to the P1 was ten times that of the youngest children. This repre-
 546 sents a substantial modulation of ongoing activity in adults, whereas it
 547 obviously represents a more moderate modulation in younger children.
 548 However, when ratios were assessed statistically rather than absolute
 549 amplitudes, the difference was not robust, leaving this observation
 550 and the methodological question of whether the use of ratios or abso-
 551 lute values represents the more meaningful approach for future investi-
 552 gations. We would nevertheless argue that this difference is suggestive
 553 of the relative immaturity of this automatic early-phase contour-
 554 integration mechanism in younger children.

555 *Later conceptual phase processing of illusory contours*

556 Key differences between adults and children emerged during the
 557 “conceptual” processing timeframe. Unlike the early phase, differences
 558 between contour-forming and non-contour-forming conditions varied
 559 significantly with age during this timeframe, with the greatest ampli-
 560 tude modulations apparent in the two youngest groups (6–9 and
 561 10–12 year-olds), followed by the 13–17-year-old group. In contrast,
 562 no significant difference was observed during this timeframe in adults.
 563 Although the developmental trajectory did not follow an entirely neat
 564 step-like decrease across age groups, since the 10–12 year-old group
 565 showed slightly greater modulations during this timeframe than the
 566 youngest cohort, the overall pattern across age-groups suggests ampli-
 567 fication of conceptual-phase relative to perceptual-phase processing in
 568 younger children, a pattern that begins to reverse during adolescence
 569 and is fundamentally different by adulthood. In adults, only the auto-
 570 matic perceptual-phase appears obligatory for analysis of this stimulus
 571 class. This general pattern points to a protracted developmental trajec-
 572 tory whereby contour-integration processes involve multiple temporal
 573 phases of processing within object-recognition areas during childhood,
 574 but as visual experience is acquired across childhood, the encoding of
 575 these stimuli becomes ever more automatic, shifting from a reliance
 576 on later processing to a consolidation of processing into early automatic
 577 processing—a *late-to-early* consolidation model.

578 Inverse source localization produced strong fits within lateral oc-
 579 cipital and occipito-temporal regions for all three childhood age groups.
 580 On the other hand, adults, who showed no effect during the conceptual
 581 timeframe, showed no second peak in global field power, and unsur-
 582 prisingly, source analysis produced a poor fitting model (Fig. 9). In
 583 addition, more distributed networks appeared to be implicated in
 584 children than in adults (Fig. 6). Topographic mapping for both of the
 585 younger groups showed greater activity over fronto-central scalp
 586 (Fig. 8), suggesting possible recruitment of conceptual-level mecha-
 587 nisms (Sehatpour et al., 2008). One possible alternative explanation
 588 that cannot be definitively ruled out is that this fronto-central focus

Fig. 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.

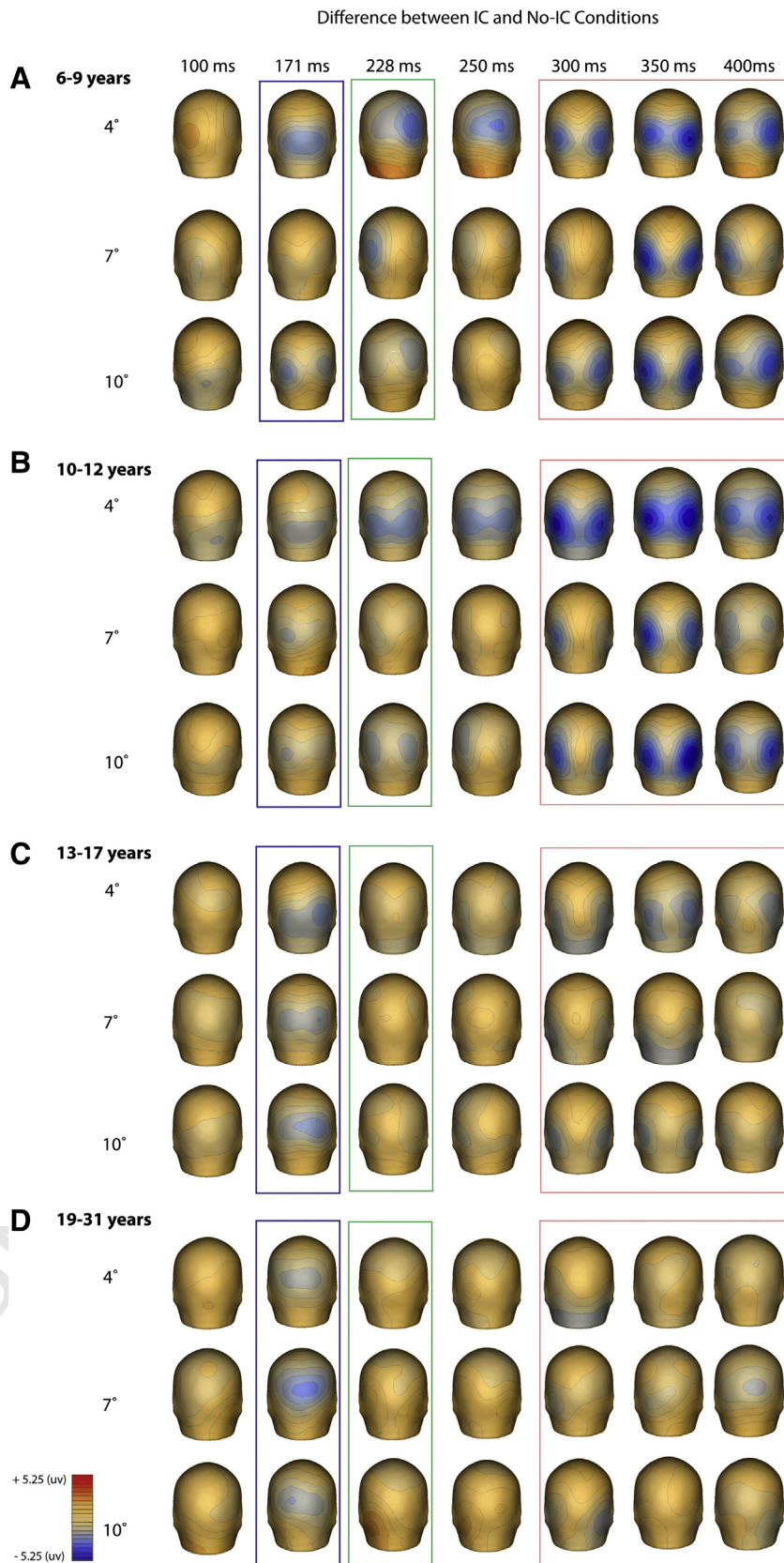


Fig. 7. Topographical voltage maps –posterior view. Voltage across the scalp surface for the difference between IC and No-IC conditions across age groups (A–D), contour extent, and time 100–400 ms. Average N1 latencies are shown for the two youngest age groups (6–9 and 10–12-year-old: 228 ms–blue outline) and the two oldest age groups (13–17 and 19–31-year-old: 171 ms–green outline). Three latencies during the N_{d1} processing-time frame are shown (red outline).

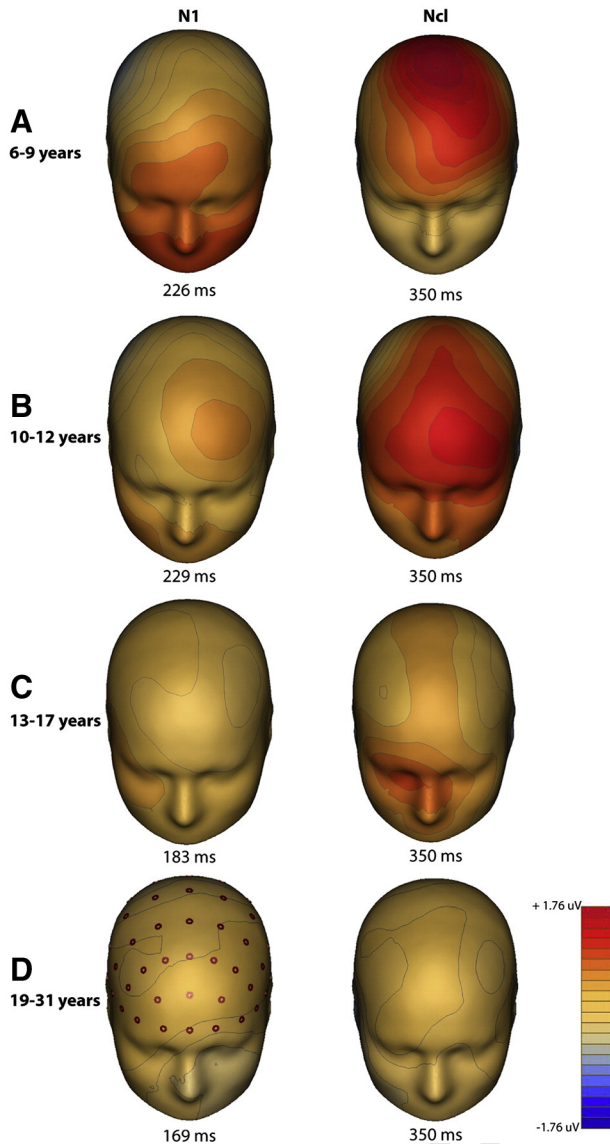


Fig. 8. Topographical voltage maps –anterior view. Voltage across the scalp surface for the difference between IC and No-IC conditions across age groups (A–D), collapsed across contour extent. The N1 peak latency for each age group and the center point of the window encompassing the N_{c1} processing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

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 (~150–220 ms). 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.

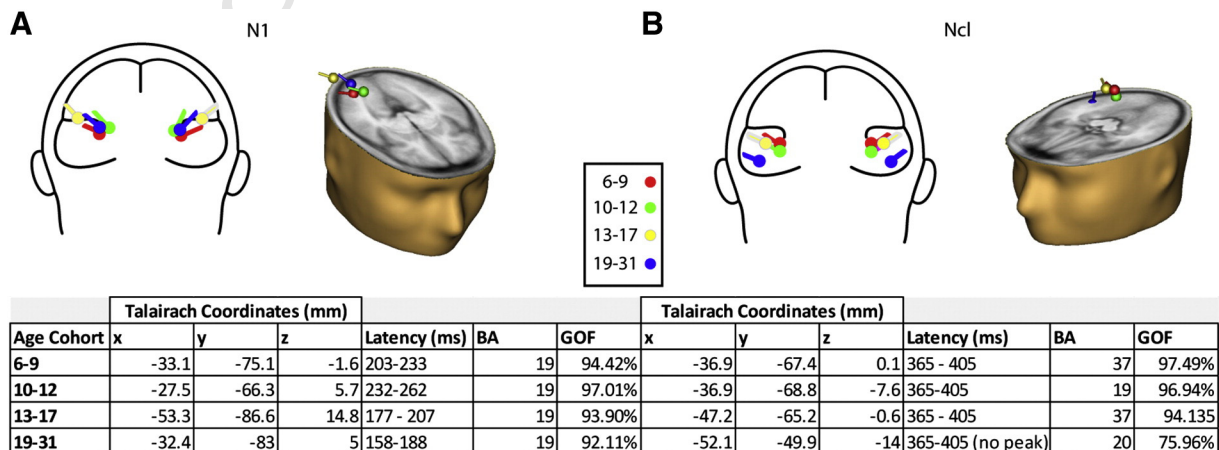


Fig. 9. Dipole source localization models. “Glass brain” and MRI dipole models for A. N1 time window (averaged across condition for each age group) and B. N_{c1} window (365–405 ms). Dipole colors correspond to age cohorts as indicated. Only right-hemisphere locations are shown as model is symmetrical.

632 Subsequent intracranial work in humans (Sehatpour et al., 2008)
633 revealed the involvement in this process of a distributed network in-
634 volving not only the LOC, but also the prefrontal cortex, and the hippo-
635 campal formation. This lead Sehatpour et al. (2008) to propose a model
636 whereby the LOC facilitates on-line matching of incoming sensory
637 stimuli to mnemonic object representations stored in the hippocampal
638 formation, while the prefrontal cortex limits the matching options by
639 generating hypotheses.

640 In a subsequent version of the fragmented picture study, certain objects
641 were shown to participants a second time. With repeated images
642 participants could successfully close the image in its most degraded version,
643 and when they did, a VEP difference was seen during the earlier N1
644 latency (Doniger et al., 2001). It is presumed that rather than accessing
645 object representations at the “conceptual” level, the visual system can
646 begin closure sooner because it has access to a sensory trace laid
647 down when closure was achieved on the previous presentation of the
648 image. It is conceivable that the automatic closure seen in the present
649 study is similarly based on lower-level cues derived from contour extent
650 (hence our reference to it as “perceptual”) and therefore relies on a certain
651 amount of exposure. When the limits of such processes are taxed or
652 sufficient expertise has not yet been acquired, the system cannot rely on
653 parametric cues to complete contour fragments automatically. Studies
654 in higher primates have pointed to size-invariant object processing as
655 a mechanism that is tuned over multiple exposures (Li and DiCarlo,
656 2010). An interpretation was put forth in a study of closure processes
657 in schizophrenia patients whereby deficiencies in posterior visual processing
658 were compensated for by additional frontal activity during the later
659 timeframe (Foxy et al., 2005). The general lack of exposure that
660 children have to even simple stimulus configurations such as the
661 Kanizsa stimuli may be similarly compensated for here.

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

*Anatomical considerations concerning conceptual phase processing of
illusory contours* 698
699

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, 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
et al., 1996; Giedd 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 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 et al.,
2005; Lebel and Beaulieu, 2011; Schmithorst and Yuan, 2010). For
example, Qiu et al. (2008) showed that while overall measures of
white matter structural integrity increased from 6 to 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 and Yuan (2010) have suggested that understand-
ing 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 729

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 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 (Foxy
et al., 2005; Molholm et al., 2006). Indeed, previous manipulations
of spatial extent have resulted in changes in P1 amplitude (Murray
et al., 2002; Snyder 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. (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 et al.
(2004) observed that children between 18 and 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 et al., 2008), an atypical bias toward processing global stimulus configurations (Fiebelkorn et al., 2012), and delays in the development of other sensory processes (Fuxe 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.

Acknowledgments

This study was supported by a grant from the U.S. National Institute of Mental Health (NIMH) to JJJ and SM (RO1-MH085322). The Human Clinical Phenotyping Core, where the children enrolled in this study were recruited and clinically evaluated, is a facility of the Rose F. Kennedy Intellectual and Developmental Disabilities Research Center (IDDR) which is funded through a center grant from the Eunice Kennedy Shriver National Institute of Child Health & Human Development (NICHD P30 HD071593). Ongoing support of The Cognitive Neurophysiology Laboratory is provided through a grant from the Sheryl and Daniel R. Tishman Charitable Foundation. Mr. Altschuler was supported by a Robert Gillece Fellowship through the Program in Cognitive Neuroscience at The City College of New York. The authors would like to express their gratitude to Drs. Hilary Gomes, Hans-Peter Frey, Juliana Bates, Natalie Russo, and Adam Snyder for their valuable input and to Ms. Sarah Ruberman and Mr. Frantzy Acluche for their many hours of work in support of this study. We also extend our heartfelt gratitude to the children and families that have so graciously contributed their time to participate in this research.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.neuroimage.2013.12.029>.

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