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PAPER

Motion and color processing in school-age children and adults: an ERP study

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Abstract

Stimuli designed to selectively elicit motion or color processing were used in a developmental event-related potential study with adults and children aged 6, 7 and 8. A positivity at posterior site INZ (P-INZ) was greater to motion stimuli only in adults. The P1 and N1 were larger to color stimuli in both adults and children, but earlier to motion stimuli only in adults. Finally, the P2 was larger to color stimuli in adults but larger to motion stimuli in children, and earlier to motion stimuli only in children. The findings across components indicate development from middle childhood to adulthood in aspects of both the motion and color processing systems indexed by this paradigm, but are consistent with an hypothesis of a more protracted time course of development for the motion as compared to the color processing system.

Numerous studies have detailed the anatomy and function of the dorsal and ventral visual pathways. The two processing streams are completely segregated from the level of the retinal ganglion cells to the lateral geniculate nucleus (LGN), and remain largely separate, with some cross-talk, at the cortical level (DeYoe & Van Essen, 1988; Livingstone & Hubel, 1988; Sawatari & Callaway, 1996; Schiller & Malpeli, 1978; Shapely, Kaplan & Soodak, 1981; Ungerleider & Haxby, 1994; Ungerleider & Mishkin, 1982; Yabuta & Callaway, 1998; Young, 1992; Zeki, Watson, Lueck, Friston, Kennard & Frackowiak, 1991). Cortically, the dorsal stream receives input preferentially from the magnocellular layers of the LGN and includes areas of posterior parietal cortex such as MT/V5, while the ventral stream receives input from both the magnocellular and parvocellular layers of the LGN and includes anterior regions of the inferior temporal lobe such as V4 (Gulyás, Heywood, Popplewell, Roland & Cowey, 1994; Livingstone & Hubel, 1988; Merigan & Maunsell, 1993; Ungerleider & Haxby, 1994; Ungerleider & Mishkin, 1982; Yabuta & Callaway, 1998; Zeki *et al*., 1991). Functionally, dorsal stream cells respond rapidly but transiently and are highly responsive to moving stimuli with low spatial frequency and low contrast; responses in the ventral stream are comparatively sustained and preferential to colored stimuli with high spatial frequency, dedicated to fine analysis of the visual scene in terms of color, texture, fine pattern, and form (Goebel, Muckli & Singer, 1999; Livingstone & Hubel, 1988; Merigan, 1989; Schiller, Logothetis & Charles, 1990; Schiller & Malpeli, 1978; Tootell, Reppas, Kwong, Malach, Born, Brady, Rosen & Belliveau, 1995).

While much is known about the anatomy and function of these two visual processing streams in monkeys and adult humans, few studies have specifically investigated the normal courses of development of the two streams. In kittens, Y cells in the retinogeniculate pathway, which innervate magnocellular layers of the LGN, have a later and longer developmental time course than X cells, which primarily innervate parvocellular layers of the LGN (Sherman, 1985). In monkeys, the ventral pathway reportedly develops at the same rate or at a 1-month lag as compared to the dorsal pathway (Bachevalier, Hagger & Mishkin, 1991; Distler, Bachevalier, Kennedy, Mishkin & Ungerleider, 1996). In humans, post-mortem anatomical evidence is mixed, suggesting in some cases that networks for processing visual motion may develop in advance of networks for processing color (e.g. in studies of the development of horizontal connections in layers of V1; Burkhalter, Bernardo & Charles, 1993) and in other cases that ventral pathway development occurs more quickly than dorsal pathway development

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(e.g. in studies of the development of LGN layers; Hickey, 1977). In behaving infants, results are also mixed (see Johnson, Mareschal & Csibra, 2001), with some findings indicating faster dorsal stream development (e.g. Dobkins, Anderson & Lia, 1999) and others faster ventral stream development (e.g. Atkinson, 1992).

Few studies of dorsal and ventral stream processing have been conducted with school-age children, although anatomical and MRI evidence indicates that extrastriate visual cortex continues to develop at least until late adolescence (Giedd, Blumenthal, Jeffries, Castellanos, Liu, Zijdenbos, Paus, Evans & Rapoport, 1999; Yakovlev & Lecours, 1967). One pair of psychometric studies with children aged 6 to 16 years has shown that color thresholds decrease to reach adult levels at about puberty, but motion thresholds remain higher than adults' across this age range (Hollants-Gilhuijs, Ruijter & Spekreijse, 1998a, 1998b). Similarly, others have reported that motion coherence processing develops more slowly than form coherence processing between ages 6 and 10 (Gunn, Cory, Atkinson, Braddick, Wattam-Bell, Guzzetta & Cioni, 2002). A study of ventral stream processing using a contour detection task reported improvement between the ages of 5 and 14 years (Kovács, Kozma, Fehér & Benedek, 1999), and a separate study of dorsal stream processing using an illusory flicker-contrast task likewise found improvement through the primary school years to age 10 (Barnard, Crewther & Crewther, 1998). Another study has reported that the use of binocular cues to control movement is not mature by the age of 11 (Watt, Bradshaw, Clarke & Elliot, 2003). Across studies and methods, it is clear that some visual perceptual skills continue to develop throughout childhood. Moreover, while somewhat equivocal, the behavioral studies suggest that some abilities related to the dorsal pathway may show more protracted development than some abilities related to the ventral pathway.

The results across behavioral studies are suggestive, but more direct functional evidence of visual processing is necessary in order to fully delineate the developmental time courses of dorsal and ventral stream processing. The recording of event-related potentials (ERPs) can provide such evidence. ERPs are voltage fluctuations in the ongoing electroencephalogram in response to controlled stimulus presentations, and have proven sensitive to cortical activation patterns underlying sensory and perceptual processes (e.g. see Rugg & Coles, 1995). Previous developmental ERP investigations of dorsal and ventral stream processing have yielded mixed results, with some authors reporting a more extended time course of maturation for ventral stream color processing (Crognale, Kelly, Weiss & Teller, 1998; Gordon & McCulloch, 1999) and other authors reporting earlier maturation of ventral as compared to dorsal stream processing (Crewther, Crewther, Barnard & Klistorner, 1996; Klistorner, Crewther & Crewther, 1996; Crewther, Crewther, Klistorner & Kiely, 1999). In studies comparing complex tasks tapping the ventral (face processing) and dorsal (planning of target-directed saccades) pathways, it has been concluded that at least some aspects of dorsal pathway function are slower to develop than some aspects of ventral pathway function (see Johnson *et al*., 2001).

It is important to establish the typical courses of development for the dorsal and ventral visual streams not only to chart possible maturational asynchronies but also to establish a comparative baseline. Systems with longer maturation timelines may be more vulnerable to atypical experience or input, simply by virtue of having a wider time window during which to be influenced by all types of experiences. Accumulating evidence from studies with atypical populations suggests that the magnocellular or dorsal system may be more vulnerable to atypical experience. For example, the results of a number of studies of adults and children with dyslexia are consistent in implicating deficiencies in the dorsal stream, while ventral stream function remains intact (e.g. Livingstone, Rosen, Drislane & Galaburda, 1991; Lovegrove, 1996; Stein, 2003; see Olson & Datta, 2002, for a discussion of the role of IQ and Hari & Renvall, 2001, for a discussion of the role of attention in some findings). There is also evidence of selective impairment of the dorsal system in Williams' syndrome, autism, and hemiplegia (Atkinson *et al.*, 1997; Braddick, Atkinson & Wattam-Bell, 2003; Gunn *et al*., 2002; Spencer, O'Brien, Riggs, Braddick, Atkinson & Wattam-Bell, 2000) and of selective enhancement of the dorsal stream in the deaf (Armstrong, Neville, Hillyard & Mitchell, 2002; Neville & Bavelier, 2000). By establishing the typical developmental course of various visual functions, atypical development can be more profitably explored.

Clearly, more developmental research is necessary to clarify the normal maturational time courses of the dorsal and ventral visual pathways in children; in particular, neuroimaging research employing stimuli that have been shown to selectively tap each processing stream and paradigms that are engaging for young children is needed. Neville and colleagues have designed an ERP paradigm with stimuli specifically created to selectively activate either the magnocellular or the parvocellular system (Armstrong *et al*., 2002; Neville & Bavelier, 2000). Magnocellular stimuli consist of motion in grayscale, low spatial frequency gratings and parvocellular stimuli consist of color changes in isoluminant, high spatial frequency gratings. In their original study with adults, Neville and colleagues found that both motion and color stimuli elicited the typical visual components P1 and

N1, with motion stimuli eliciting an additional early focal positivity (termed P-INZ), a minimal P1, and an early and prominent N1 (Armstrong *et al.*, 2002). Recently, Mitchell and Neville (2004) used this paradigm with adults and two groups of children, ages 6–7 and 8–10 years. For the most part, they replicated previous findings with adults; they also reported evidence for different developmental time courses for motion and color processing in children and extended maturation of the dorsal stream. In both groups of children, ERPs to centrally presented motion stimuli were less adult-like than ERPs to color stimuli: the P-INZ was not clearly larger to motion stimuli in children as it was in adults, the P1 and N1 were not earlier to motion stimuli in children as they were in adults, and the N1 was larger to color stimuli only in children.

Considering the paucity of data concerning the typical course of functional development of the two visual processing streams and the success of the Armstrong *et al.* (2002) paradigm in preferentially eliciting activation within the two streams, in the current study we adapted the paradigm for greater ease of use with school-age children and more closely investigated the developmental time courses of these systems in groups of adults and 6-, 7- and 8-year-old children. The primary goal of the study was to compare ERPs elicited by motion stimuli designed to elicit activity within the dorsal stream and color stimuli designed to elicit activity within the ventral stream, as in previous reports (Armstrong *et al.*, 2002; Mitchell & Neville, 2004). A secondary goal was to chart the developmental course of the ERP components of interest. To our knowledge, the P-INZ has not been reported in the literature outside of the Armstrong *et al.* paradigm. In contrast, there is some consensus regarding the neural sources of both the visual P1 and N1 components: the generator of the P1 appears to lie within ventrolateral occipital cortex in extrastriate area 19 (Clark & Hillyard, 1996), while a distributed array of generators in ventral visual areas (Clark & Hillyard, 1996) or along the occipital-parietal border (Mangun, Hillyard & Luck, 1993) contributes to the N1; thus, both components reflect early visual processing. In adults, the P1 has been linked with parvocellular (ventral) processing while the N1 has been linked with magnocellular (dorsal) processing (Kubovà, Kuba, Spekreijse, & Blakemore, 1995; Mangun *et al.*, 1993). Developmental studies with school-age children have shown that both the amplitude and latency of P1 and N1 decrease across childhood (Brecelj, Strucl, Zidar & Tekavcic-Pompe, 2002; Buchsbaum, Henkin & Christiansen, 1974).

We predicted that in adults our simplified paradigm would elicit the same effects as the more complex version: a P-INZ component largest to motion stimuli, a P1 largest to color stimuli, and an N1 largest and earliest to motion stimuli (Armstrong *et al.*, 2002). Evidence reviewed above suggests that aspects of both visual processing streams may still be developing during the 6- to 8-year-old period but that the dorsal pathway may be slower to mature than the ventral pathway. Therefore, we predicted that neither ERPs to motion nor color stimuli in 6- to 8-year-old children would be identical to ERPs in adults; that is, that neither the dorsal nor the ventral system, as indexed by ERPs in this paradigm, is fully developed by the age of 8. Further, we hypothesized that the ERPs elicited by color stimuli would be more adult-like than the ERPs elicited by motion stimuli; that is, that we would find evidence for a more protracted course of development for dorsal stream processing. Finally, we predicted overall larger and longer latency P1 and N1 components in children as compared to adults.

Methods

Subjects

A total of 80 participants included 16 adults (7 female), average age 22;4 (SD 3;5); 20 6-year-olds (9 female), average age 6;6 (SD 0;3); 21 7-year-olds (8 female), average age 7;5 (SD 0;3); and 23 8-year-olds (12 female), average age 8;4 (SD 0;3). All participants were right-handed (Oldfield, 1971), native English speakers with no history of neurological dysfunction. All were volunteers who were paid for their participation. Socioeconomic status of children's families ranged from lower middle to upper class on the Hollingshead Index of Social Position, with a middle-class average. Adults reported normal or corrected-to-normal visual acuity and normal color vision. All children had normal or corrected-to-normal binocular visual acuity as tested by the Kindergarten Snellen chart and normal color vision as assessed by Matsubura tests (a children's version of Ishihara tests).

Stimuli and tasks

Features of the stimuli were quantifiable along chromatic, spatial frequency, and motion dimensions. All stimuli were vertically oriented sinusoidal spatial frequency gratings presented on a gray background. Each stimulus was approximately $2 \times 2°$ with edges filtered by a ramp function in order to reduce high frequency artifacts. The color or P stimulus, designed to activate the ventral visual pathway, consisted of an isoluminant blue and green high spatial frequency grating; at randomly varying intervals (500–1000 ms), the blue bars changed to red

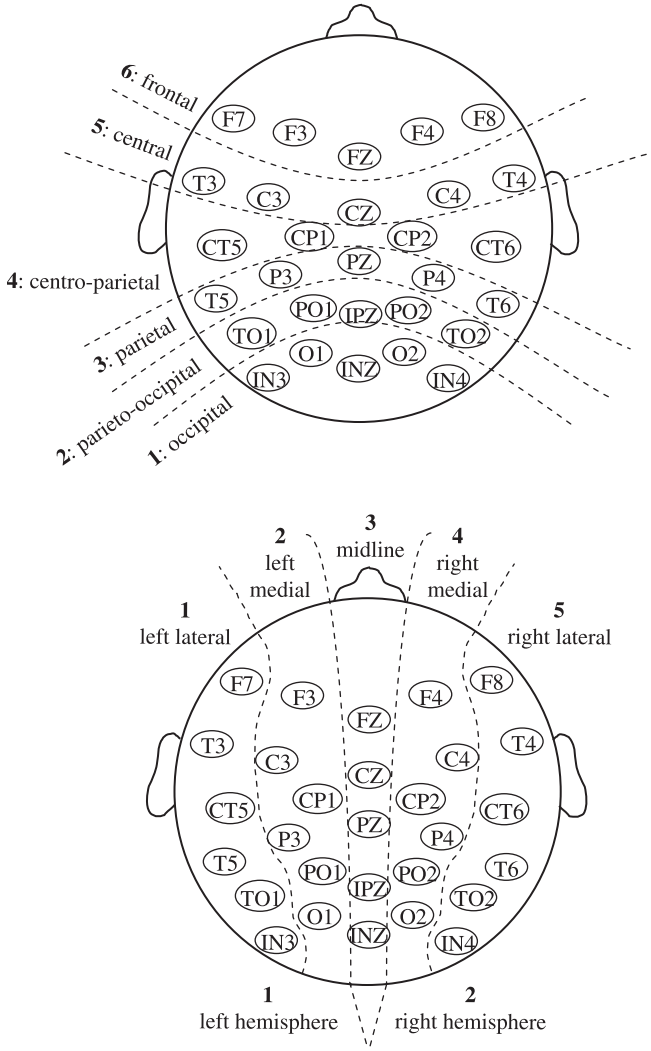

Figure 1 *Schematic representation of electrode configuration and analysis factors. Top: 6 possible levels of the anterior/posterior factor. Bottom: 3 possible levels of the lateral/medial/midline factor and 2 possible levels of the hemisphere factor.*

for 100 ms, then changed back to blue, creating the perception of a flash of red with no transverse movement or luminance or pattern change. The color stimulus had a spatial frequency of 9 cycles/degree. The motion or M stimulus, designed to activate the dorsal visual pathway, consisted of a low spatial frequency grayscale grating with low luminance contrast of 4%; at randomly varying intervals (500–1000 ms), the bars of the grating moved transversely to the right at a velocity of 13.7°/s for 100 ms (the stimulus itself remained stationary). The motion stimulus had a spatial frequency of 1 cycle/degree. Refer to Figure 1 in Armstrong *et al*. (2002) for pictorial depictions of the stimuli. Both motion and color stimuli had a mean luminance of 8.5 candles/meter^2. Stimuli were presented only at the center of a monitor located 46 in. directly in front of the subject (cf. Armstrong *et al*., 2002; Mitchell & Neville, 2004, which used both central and peripheral presentations). In order to keep subjects engaged, at random intervals, the motion stimulus was replaced by a picture of one of the seven dwarves and the color stimulus was replaced by a picture of one of seven characters from Winnie the Pooh; appearance of these cartoons required a button-press response (cf. Armstrong *et al*., 2002; Mitchell & Neville, 2004, in which the task was to detect a black square). Three hundred twenty instances each of motion and color stimuli were presented in separate blocks, each lasting about 5 min (cf. Armstrong *et al*., 2002, in which each block lasted one hour).

Procedure

Subjects were given a brief tour of the laboratory, any questions were answered, and children were asked to sign an assent form while parents signed a consent form; adult participants signed a consent form. After the cap was in place (see details below), subjects were seated in a comfortable chair in an electrically shielded, sound-attenuating booth. They were instructed to keep their eyes at the center of the monitor in front of them where they would see a colored square (P or color condition) or a grayish square (M or motion condition), and were told to watch for the Pooh characters (color condition) or the dwarves (motion condition) that would sometimes appear at that location instead of the square. They held a response box in their laps and were instructed to press a button whenever a cartoon character appeared; response hand was counterbalanced across subjects across the motion and color conditions. Subjects were told that if they found all the characters (i.e. pressed a button at the appearance of each character), they would get to see the characters all together at the end (at the end of the trials, a large picture with all seven dwarves appeared in the motion condition, and a large picture with all the Pooh characters appeared in the color condition). Order of presentation of motion and color conditions was counterbalanced across subjects. A short practice session (with the motion stimulus for subjects in the motion-first order or the color stimulus for subjects in the color-first order and 3 different target pictures) preceded the actual test sessions.

EEG/ERP recording and analysis

Electroencephalogram (EEG) was recorded from 29 tin electrodes mounted in an elastic cap (Electro-Cap International). The array included 10 sites from the

International 10–20 system and an additional 19 sites interspersed among these so as to form a regular grid covering primarily the posterior portion of the head (see Figure 1). Electrodes were also placed beneath the lower right eye and at the outer canthi of the left and right eyes in order to monitor eye movements (EOG); in addition, recordings from FP1/2 were used to reject trials that were contaminated by eyeblink artifacts. Activity at the right mastoid was recorded during the experiment, but all on-line recordings were referenced to the left mastoid (except the horizontal eye channel, a bipolar recording between left and right outer canthi); recordings were re-referenced to averaged mastoids in the final data averaging (see Armstrong *et al.*, 2002; Mitchell & Neville, 2004, for similar methods). Eye electrode impedances were maintained below 10 KΩ, mastoid electrodes below 2 KΩ, and scalp electrodes below 3 KΩ.

The EEG was amplified with Grass 7P511 amplifiers (–3dB cutoff, bandpass .01 to 100 Hz) and digitized on-line at 256 Hz. ERPs were time-locked to the onset of a color change in the P condition and the onset of motion in the M condition. Off-line, separate ERPs to motion and color stimulus presentations were averaged for each subject at each electrode site over a 700 ms epoch using a 200 ms pre-stimulus-onset baseline. Trials contaminated by eye movements, muscular activity, amplifier blocking, electrical noise or behavioral responses were rejected during averaging and were not included in analyses. Data were first analyzed using standard artifact rejection parameters and were subsequently inspected on an individual basis and re-analyzed with more stringent rejection parameters when necessary. Average number of useable trials in the motion condition for adults was 242.4 (SD 53.2), for 8-year-olds was 176.7 (SD 61.6), for 7-year-olds was 135.4 (SD 75.9) and for 6-year-olds was 163.6 (SD 50.7). For the color condition, average number of useable trials was 246.4 (SD 46.3) for adults, 171.7 (SD 52.8) for 8-year-olds, 146.8 (SD 64.4) for 7-year-olds and 152.4 (SD 62.1) for 6-year-olds.

ERP component peak amplitudes and latencies were measured at specific electrode sites within specific time windows, as described below.[1] ERP measures of peak amplitude and latency were analyzed with repeated-measures analyses of variance (ANOVAs; SPSS GLM). The Greenhouse-Geisser correction for nonsphericity was applied to all within-subjects measures with more than two levels; corrected *p*-values are reported below. As detailed below, the between-subjects factor was group (adult, 6, 7, 8) and within-subject factors included stimulus type (motion, color) and measures of electrode location (anterior/posterior [6 possible levels], hemisphere [2 possible levels], lateral/medial/midline [3 possible levels]; refer to Figure 1). Peak amplitude measures were normalized based on a method previously used with developmental ERP data (e.g. Holcomb, Coffey & Neville, 1992) according to the formula (score – mean/stdev) in which score is an average amplitude value (one for each condition and site for each subject), mean is the mean amplitude across all subjects within each group, and stdev is the standard deviation of the mean.

[1] Automated peak amplitude and latency measurement routines identified the 'highest' or 'lowest' data point within the specified time window at each site for each condition and participant. In order to reduce the possibility of identifying local maxima or minima, we further constrained these measures by requiring that the identified data point be 'higher' or 'lower' than the preceding and following three data points.

Results

Visual inspection

Grand-average ERP waveforms for adults from this simplified version of the paradigm appeared similar in componentry to those for the previous version of the task (see Armstrong *et al.*, 2002), and the three specific components previously identified and measured were measured here as well (see Figure 2). The P-INZ to motion stimuli was clearly present at the INZ site and was measured at INZ within the 95–190 ms time window. A P1 was evident at the lateral sites of the three most posterior levels of the anterior/posterior factor, and was measured from 100 to 200 ms post-onset. The large negative peak N1 was measured at medial and lateral electrode sites at all levels of the anterior/posterior factor within a 150–300 ms post-onset time window. In addition, a subsequent positivity not measured previously (Armstrong *et al.*, 2002; Mitchell & Neville, 2004) but clearly defined in the present waveforms, termed P2, was measured within the 200–330 ms window along the midline and medial sites of the two most posterior levels of the anterior/posterior factor.

In children (see Figures 3, 4 and 5), the overall morphology of the waveforms was similar to that in adults, although there were clear developmental differences. Most striking was the apparent lack of a condition effect for the P-INZ, which appeared substantially larger to motion stimuli in adults. Conversely, the P2 that seemed larger to color stimuli in adults seemed larger to motion stimuli in all three groups of children. While the N1 appeared earlier to motion stimuli in adults, the opposite seemed to be the case in children. Despite these differences, the overall componentry of the waveforms was similar in adults and children and the same four components were measured in children, within the same time

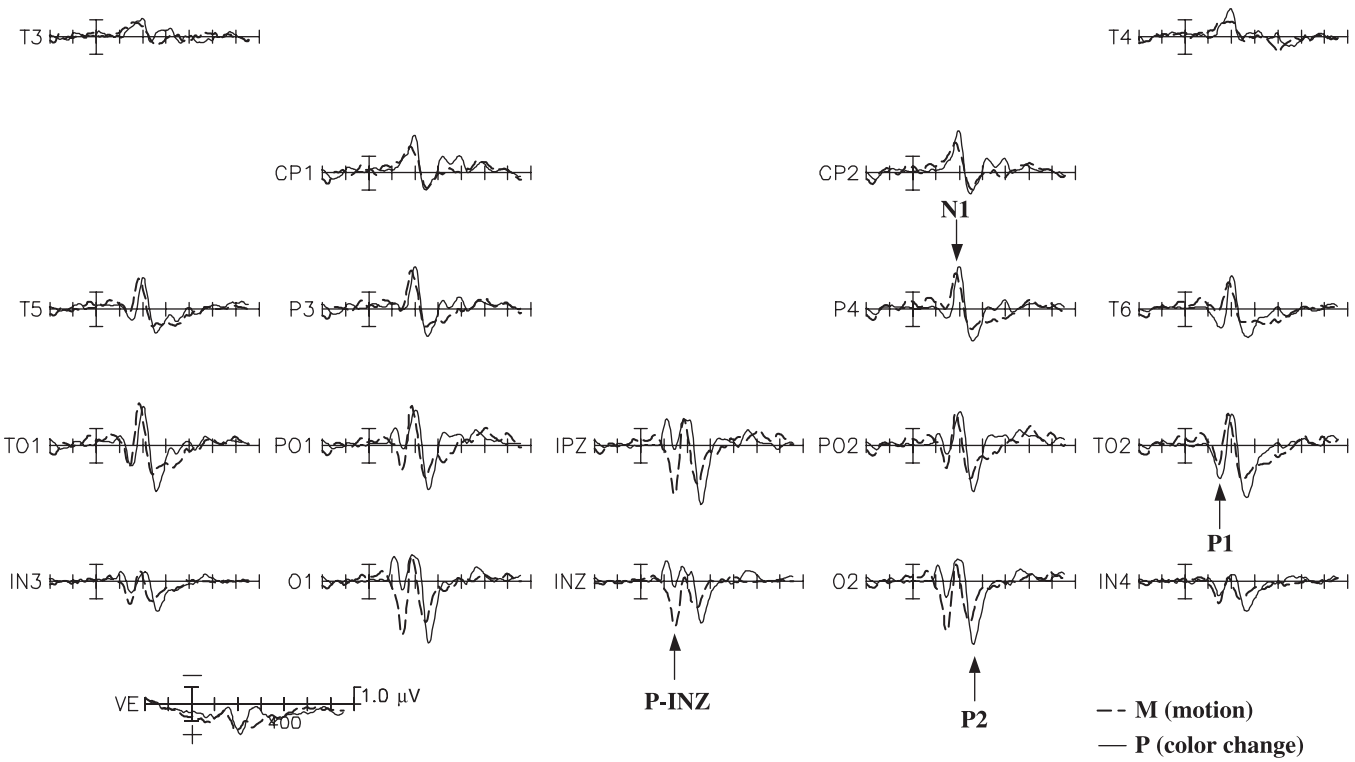

Figure 2 *Grand average ERP waveforms for adults. Component P-INZ is identified at the INZ site, P2 at the O2 site, P1 at the TO2 site, and N1 at the P4 site. Anterior sites are toward the top, left hemisphere sites are on the left, and the site VE represents activity recorded from beneath the right eye here and in all subsequent ERP figures. As per convention, note that negative is 'plotted up' in all ERP figures.*

windows, as were measured in adults. Reported below are the results of these analyses for the four components in general terms, followed by specific results involving group and condition effects for each of the components of interest.

General componentry and development

Analyses of non-normalized amplitude data (preserving the main effect of group) revealed the typical developmental pattern in which amplitudes were larger in children for most components (main effect of group for P-INZ, $F(3, 76) = 9.9$, $p < .001$; for P1, $F(3, 76) = 9.4$, $p < .001$; for N1, $F(3, 76) = 9.6$, $p < .001$). The P2 was largest in 8-year-olds but of similar amplitude in the other three groups (group, $F(3, 76) = 5.7$, $p < .001$).

Also consistent with previous reports, latencies of the P1 ($F(3, 76) = 5.3$, $p < .01$) and N1 ($F(3, 76) = 16.7$, $p < .001$) decreased with age, while there was no main effect of group for latency of the P-INZ ($p = .2$) or P2 ($p = .8$).

Analyses of normalized amplitude data investigating the distribution of components revealed that, across groups and conditions, P1 was larger at occipital than centro-parietal sites and larger over the right hemisphere (hemisphere, $F(1, 76) = 13.1$, $p < .001$; anterior/posterior, $F(2, 152) = 21.5$, $p < .001$), N1 was earlier over the left hemisphere at anterior medial sites (hemisphere, $F(1, 76) = 9.6$, $p < .01$; anterior/posterior, $F(5, 380) = 28.3$, $p < .001$; lateral/medial, $F(1, 76) = 9.7$, $p < .01$; hemisphere × lateral/medial, $F(1, 76) = 20.3$, $p < .001$), and P2 was largest at occipital midline sites (i.e. INZ; anterior/posterior, $F(1, 76) = 90.3$, $p < .001$; medial/midline, $F(2, 152) = 4.2$, $p < .001$; anterior/posterior × medial/midline, $F(2, 152) = 11.0$, $p < .001$). The distribution of the P2 shifted from more midline in 6-year-olds to more medial in 8-year-olds and adults (anterior/posterior × group, $F(3, 76) = 10.9$, $p < .001$; medial/midline × group, $F(6, 152) = 4.2$, $p < .001$; anterior/posterior × midline/medial × group, $F(6, 152) = 6.8$, $p < .001$).

In summary, as predicted, the early visual components tended to be larger and later in children; however, the P-INZ and P2 did not show typical decreases in latency with age. The P1 and N1 appeared similarly distributed in children and adults, while the distribution of the P2 shifted laterally with age.

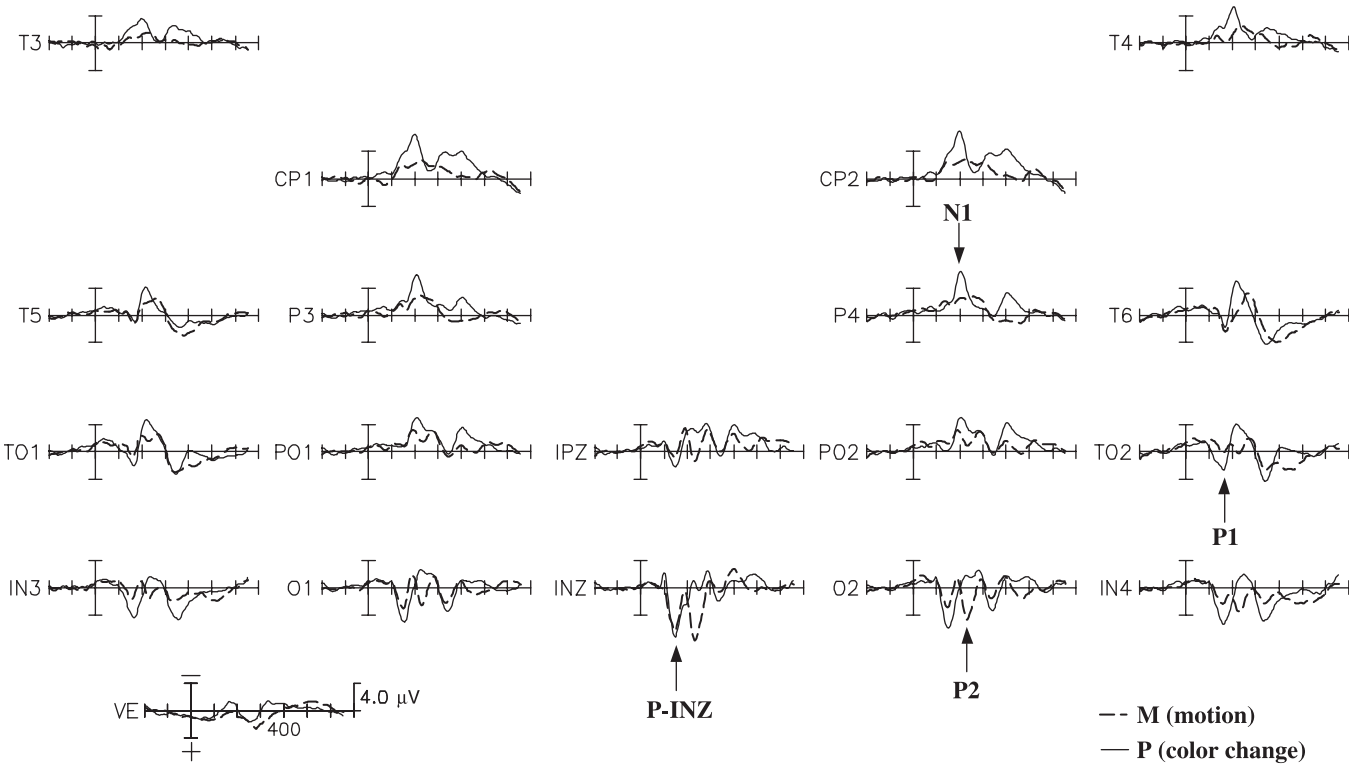

Figure 3 *Grand average ERP waveforms for 6-year-olds. Components of interest are identified.*

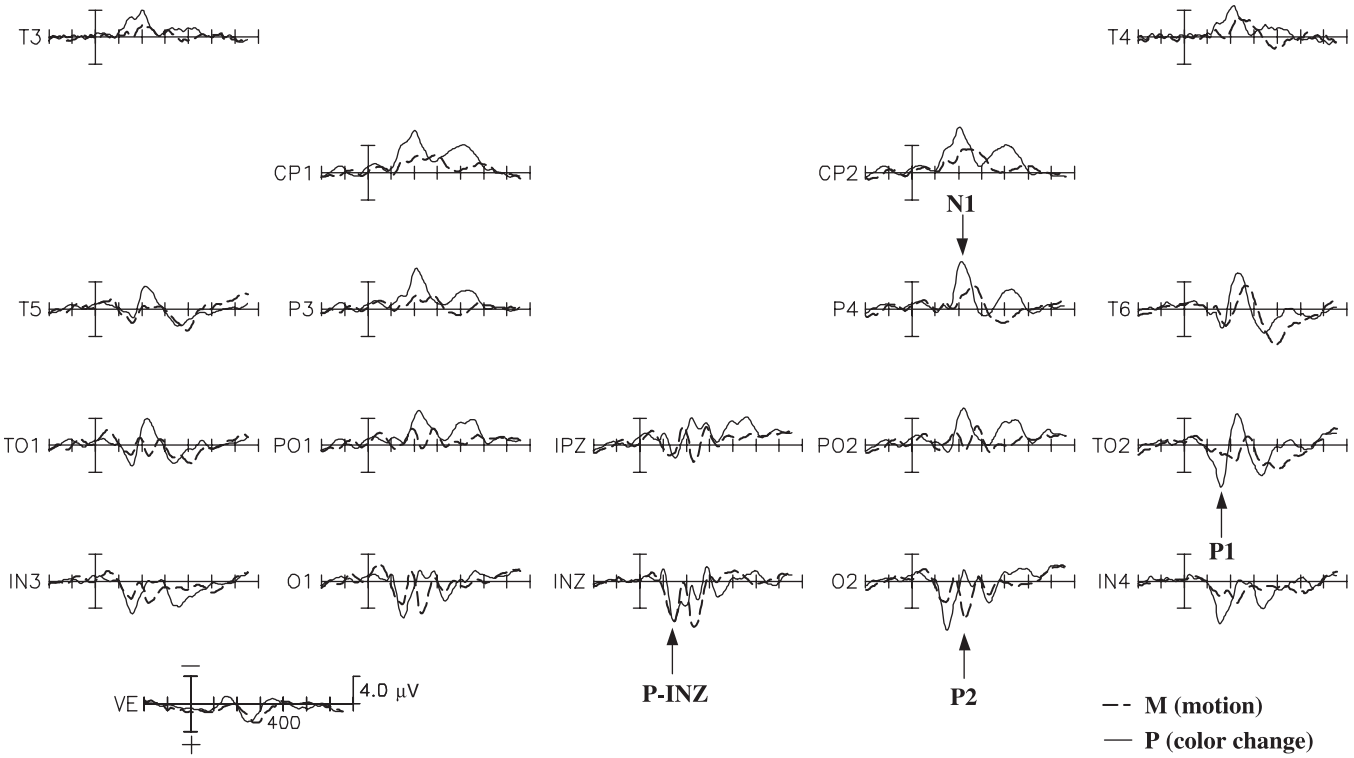

Figure 4 *Grand average ERP waveforms for 7-year-olds. Components of interest are identified.*

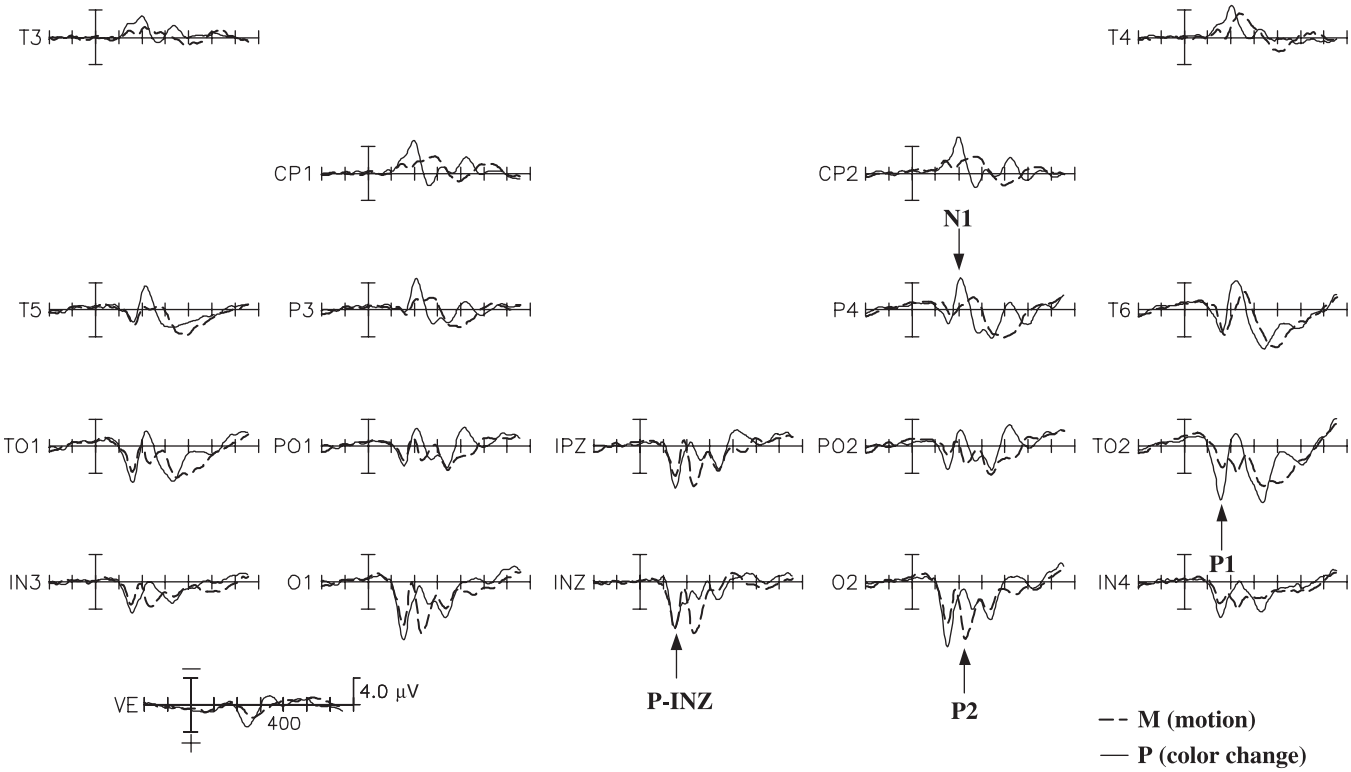

Figure 5 *Grand average ERP waveforms for 8-year-olds. Components of interest are identified.*

P-INZ

In analyses of non-normalized amplitude data (as this component was measured at only one site), the P-INZ was larger to motion stimuli only in adults (condition × group, $F(3, 76) = 3.6$, $p < .05$; see Figure 6). Analyses by group confirmed that the P-INZ elicited by motion and color stimuli was of similar amplitude in 6-year-olds ($p = .11$), 7-year-olds ($p = .62$), and 8-year-olds ($p = .84$), while the P-INZ was substantially larger to motion stimuli in adults ($F(1, 15) = 42.1$, $p < .001$). Follow-up analyses by condition indicated that the amplitude of the P-INZ decreased from childhood to adulthood for both motion (group, $F(3, 76) = 5.5$, $p < .01$) and color (group, $F(3, 76) = 11.3$, $p < .001$) stimuli.

Peak latency of the P-INZ was longer to motion stimuli in adults and shorter to motion stimuli in 7-year-olds, but similar to motion and color stimuli in 6- and 8-year-olds (condition × group, $F(3, 76) = 5.3$, $p < .01$).

In summary, as predicted, motion stimuli elicited a larger P-INZ than color stimuli in adults; however, this effect held only in adults, indicating maturation of this focal response to motion beyond the age of 8. The latency of the P-INZ did not show consistent developmental changes.

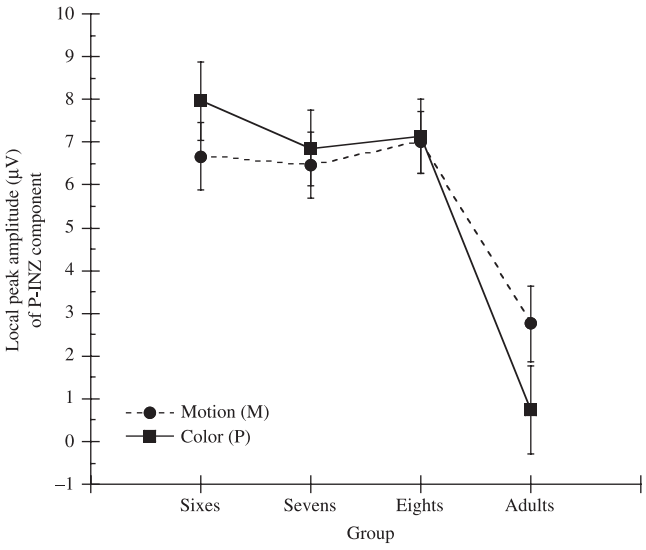

Figure 6 *Plot of amplitude data illustrating the condition by group effect for the P-INZ component at site INZ. The P-INZ was larger to motion stimuli in adults but similar to motion and color stimuli in the three groups of children.*

P1

Across groups, color stimuli elicited a larger P1 than motion stimuli (condition, $F(1, 76) = 34.1$, $p < .001$), particularly at right hemisphere posterior sites (condition × hemisphere, $F(1, 76) = 5.1$, $p < .05$; condition × hemisphere × anterior/posterior, $F(2, 152) = 4.5$, $p < .05$). This P1 effect had a more posterior distribution in children than in adults (anterior/posterior × group, $F(6, 152) = 5.2$, $p < .001$; condition × anterior/posterior × group, $F(6, 152) = 11.2$, $p < .001$).

The main effect of condition such that P1 latency was shorter to motion than to color stimuli ($F(1, 76) = 9.7$, $p < .01$) varied by group (condition × group × anterior/posterior, $F(6, 152) = 2.6$, $p < .05$; see Figure 7). Analyses by group indicated that P1 was earlier to motion stimuli only in adults ($F(1, 15) = 14.4$, $p < .01$); the main effect of condition was not significant in 6-year-olds ($p = .93$), 7-year-olds ($p = .17$), or 8-year-olds ($p = .53$). Analyses by condition showed that P1 latency to motion stimuli was shorter in adults than in children (group, $F(3, 76) = 8.3$, $p < .001$), particularly at parietal and parieto-occipital sites (anterior/posterior × group, $F(6, 152) = 3.6$, $p < .01$). No significant effects were found for the color condition, indicating that P1 latency to motion stimuli showed relatively more developmental change.

In summary, as predicted, color stimuli elicited a larger P1 than motion stimuli in adults; the same pattern was observed in children, suggesting relatively adult-like ventral stream processing. In contrast, motion stimuli elicited an earlier P1 than color stimuli in adults, but this effect was not observed in children, suggesting lagging development of dorsal stream processing.

N1

Overall, the N1 was larger to color stimuli than to motion stimuli ($F(1, 76) = 48.7$, $p < .001$); there were no significant results involving group in normalized amplitude analyses.

While across groups, N1 latency was earlier to color than to motion stimuli (condition, $F(1, 76) = 5.9$, $p < .05$), this effect varied by group. By group, N1 latency was earlier to color stimuli in children but earlier to motion stimuli in adults (see Figure 8), an effect that varied across the scalp (condition × group, $F(3, 76) = 8.1$, $p < .001$; condition × group × anterior/posterior, $F(15, 380) = 2.8$, $p < .01$). In confirmatory follow-up analyses by group, the main effect of condition was significant such that N1 was earlier to color stimuli for 6-year-olds ($F(1, 19) = 5.2$, $p < .05$), 7-year-olds ($F(1, 20) = 6.0$, $p < .05$), and 8-year-olds ($F(1, 22) = 13.6$, $p < .001$) but such that N1 was earlier to motion stimuli in adults ($F(1, 15) = 14.1$, $p < .01$).

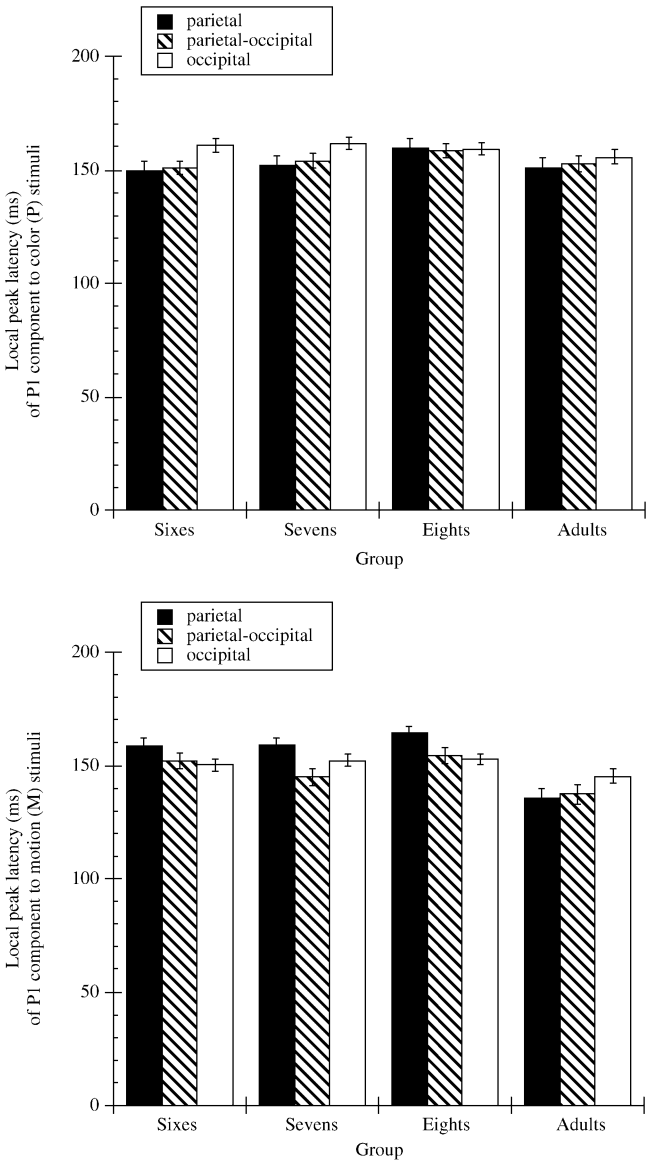

Figure 7 *Graphic representation of the peak latency of the P1 component within each group across lateral posterior sites for color (top) and motion (bottom) stimuli.*

In analyses by condition, N1 latency was significantly shorter in adults than in children for motion stimuli (group, $F(3, 76) = 18.4$, $p < .001$) but not for color stimuli ($p = .10$), indicating greater developmental change for the N1 response to motion stimuli. However, the distribution of the N1 to color stimuli did show change with age, being earliest at posterior and medial sites in adults but not in children (anterior/posterior × group, $F(15, 380) = 5.9$, $p < .001$; lateral/medial × group, $F(3, 76) = 3.3$, $p < .05$).

In summary, color stimuli elicited a larger N1 than motion stimuli in both adults (cf. Armstrong *et al.*, 2002;

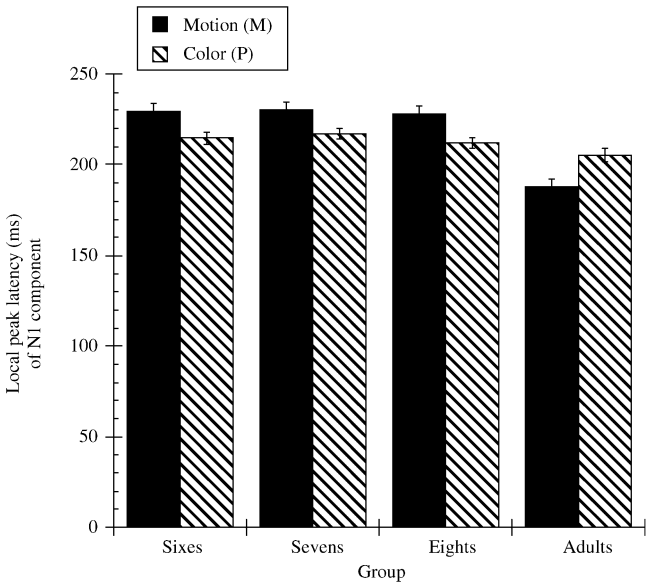

Figure 8 *Graphic representation of the peak latency of the N1 component by group and condition. N1 was earlier to color stimuli in all three groups of children, but earlier to motion stimuli in adults.*

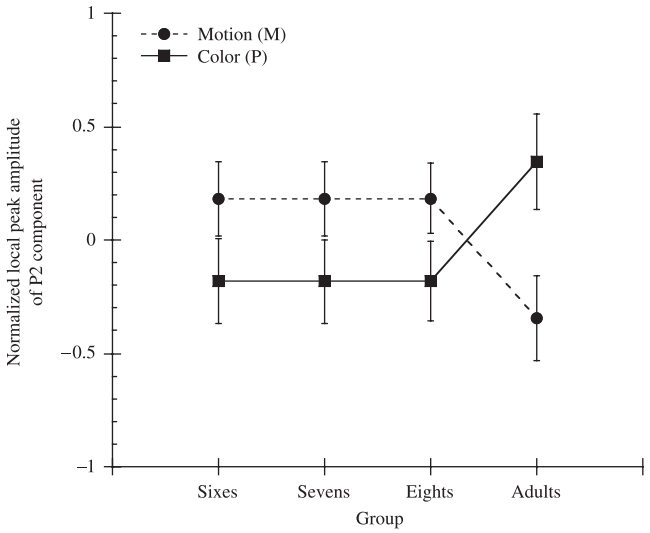

Figure 9 *Plot of normalized amplitude data illustrating the condition by group effect for the P2 component. Motion stimuli elicited a larger P2 in all three groups of children, while color stimuli elicited a larger P2 in adults.*

Mitchell & Neville, 2004) and children (as in Mitchell & Neville, 2004). As predicted, motion stimuli elicited an earlier N1 in adults. However, the opposite held true in children, and N1 latency to motion stimuli was shorter in adults than in children, consistent with an hypothesis of a longer developmental time course for motion processing.

P2

The P2 was larger to motion stimuli only in children, while the opposite held true in adults (condition × group, $F(3, 76) = 8.7$, $p < .001$; see Figure 9). In analyses by group, the larger P2 to motion stimuli was a marginal effect for 6-year-olds ($F(1, 19) = 4.0$, $p = .07$) but a stronger effect for 7-year-olds ($F(1, 20) = 5.7$, $p < .05$) and 8-year-olds ($F(1, 22) = 6.5$, $p < .05$), and the larger P2 to color stimuli was a substantial effect in adults ($F(1, 15) = 13.2$, $p < .01$).

Overall P2 latency was shorter to motion stimuli than to color stimuli (condition, $F(1, 76) = 32.8$, $p < .001$), but this varied by group (condition × group × medial/midline, $F(6, 152) = 2.9$, $p < .05$). In analyses by group, the main effect of condition was such that P2 was earlier to motion stimuli in 6-year-olds ($F(1, 19) = 11.4$, $p < .01$), 7-year-olds ($F(1, 20) = 15.2$, $p < .001$), and 8-year-olds ($F(1, 22) = 7.5$, $p < .05$), but not in adults ($p = .12$).

In summary, color stimuli elicited a larger P2 than motion stimuli in adults while the opposite pattern was observed in children. Moreover, motion stimuli elicited an earlier P2 than color stimuli only in children.

Discussion

In an ERP investigation of the development of the neural systems important in processing motion and color, adults and three groups of school-age children viewed stimuli designed to selectively activate processing in the dorsal (magnocellular; motion stimuli) and ventral (parvocellular; color stimuli) visual streams (cf. Armstrong *et al.*, 2002; Mitchell & Neville, 2004). A previous study using a similar paradigm reported that color stimuli elicited more similar ERPs in adults and children than did motion stimuli, indicating slower development of the dorsal as compared to the ventral stream (Mitchell & Neville, 2004). With a simplified version of the paradigm and participants more finely grouped by age, we found similar results and further evidence for a relatively more protracted time course of development for the motion processing system. Interestingly, we found little evidence of development from age 6 to age 8, suggesting both early development (before age 6) of aspects of the color processing system and quite protracted development (beyond age 8) for aspects of the motion processing system as indexed by the present paradigm.

Consistent with previous findings (Brecelj *et al.*, 2002; Buchsbaum *et al.*, 1974), the amplitude and latency of the N1 and P1 were greater in children than in adults.

These typical developmental changes suggest increasing speed and efficiency in early visual processing across childhood and may reflect increasing myelination in visual cortical areas (Yakovlev & Lecours, 1967). Remarkably, the P1 and N1 appeared similarly distributed in children and adults, suggesting similar orientation of extrastriate neural generators across ages. In contrast, amplitude and latency measures of the P2 did not show consistent developmental effects, although the distribution of the P2 shifted with age. Neither Armstrong *et al*. (2002) nor Mitchell and Neville (2004) measured a P2 in studies using a more complex version of the present paradigm and the functional significance and neural generators of the P2 remain unknown. There is some suggestion that the P2 indexes 'post-perceptual' processing (Wastell & Kleinmen, 1980); the present findings suggest that this component indexes processing within some aspect of the visual system, whether perceptual or higher-level, that is relatively mature early in development.

In addition to these maturational effects for the ERP components of interest, there were clear developmental differences in the processing of color and motion stimuli. On the one hand, color stimuli elicited relatively similar ERPs across the four age groups. Color stimuli elicited a larger P1 than motion stimuli in both adults and children, consistent with previous findings (Armstrong *et al*., 2002; Mitchell & Neville, 2004) and studies that have linked the P1 to ventral stream processing (Heinze, Mangun, Burchert, Hinrichs, Scholz, Münte, Gös, Scherg, Johannes, Hundeshagen, Gazzaniga & Hillyard, 1994; Kubovà *et al*., 1995; Mangun *et al*., 1993). Color stimuli also elicited a larger N1 than motion stimuli across groups, consistent with previous findings from children (Mitchell & Neville, 2004).[2] Moreover, the latency of both the P1 and N1 to color stimuli did not vary across groups. Overall, these consistent results indicating relatively adult-like responses to color stimuli in children suggest that aspects of the ventral visual system indexed by the P1 and N1 elicited by color stimuli in this paradigm are comparatively mature by the age of 6.

On the other hand, ERPs to motion stimuli were relatively dissimilar across groups. Motion stimuli elicited a markedly larger P-INZ than color stimuli in adults (Armstrong *et al*., 2002), while motion and color stimuli elicited equivalent P-INZ responses in children (Mitchell & Neville, 2004). Motion stimuli elicited an earlier P1 and N1 than color stimuli in adults, but the opposite pattern was observed in children. Mitchell and Neville (2004) reported an N1 similarly earlier to motion stimuli in adults but of equivalent latency to motion and color stimuli in children. The present study used a greater number of younger children, which may have revealed a developmental progression (from an N1 earlier to color stimuli to an N1 earlier to motion stimuli with age) unseen in the previous report combining 6- and 7-year-olds and 8- to 10-year-olds. Further, N1 latency to motion (but not to color) stimuli was shorter in adults than in children in the present study. Previous studies with adults have linked the N1 with magnocellular (dorsal) processing (Kubovà *et al*., 1995; Mangun *et al*., 1993) and high-density electrical mapping has shown that activation in dorsal stream areas precedes activity in ventral stream areas (Foxe & Simpson, 2002). Across the P1, N1 and P-INZ, the present findings suggest that aspects of fast dorsal stream processing indexed by the motion stimuli in the present paradigm are not mature by the age of 8, consistent with an hypothesis of a longer maturational time course for some dorsal as compared to ventral stream functions.

Interestingly, a contrasting developmental pattern was observed for the P2 component. This component was not analyzed in previous similar studies, perhaps because it was not particularly prominent in the adult waveforms (cf. Armstrong *et al.*, 2002; Mitchell & Neville, 2004). In the present study, motion stimuli elicited a larger and earlier P2 than color stimuli only in children, while color stimuli elicited a larger P2 in adults. To our knowledge, there is no precedent for a sensitivity to motion stimuli for the P2 in children. It might be speculated that the faster response to motion stimuli observed in adults (but not children) in terms of the P1 and N1 is shifted to a later time window in children, and appears as a P2 effect. This speculation is consistent with the finding that the P2 component itself, in contrast to the P1 and N1, showed little developmental change in the present paradigm. Further studies are under way to investigate this hypothesis.

Findings related to the P-INZ component not only indicated lagging development for the motion processing system, but also suggested that aspects of *both* the color and motion processing systems continue to develop throughout childhood: analyses showed that the amplitude of the P-INZ to both color and motion stimuli changed over time. This finding is difficult to interpret because the functional significance of the P-INZ is unknown. Armstrong *et al*. (2002) first used the label

[2] Previous studies with adults have reported a larger N1 to motion stimuli (Armstrong *et al*., 2002) or a similar N1 to motion and color stimuli (Mitchell & Neville, 2004); given the known sensitivity of the N1 to attentional manipulations (e.g. Luck, 1998), it is likely that the discrepancy between previous and current findings is due to different attentional requirements across paradigms. Interestingly, children appear to be less affected by the attention manipulation, perhaps because attention skills develop throughout childhood (e.g. Rueda, Fan, McCandliss, Halparin, Gruber, Lercari & Posner, 2004). In any case, with focused central attention as was required here, color stimuli evoked a larger N1 than motion stimuli in both children and adults.

'P-INZ' to describe a focal positivity observed only at site INZ and elicited almost exclusively by motion stimuli; Mitchell and Neville (2004) reported a similar component. Given the similarities in polarity and timing, it might be hypothesized that the P-INZ is actually a midline P1. However, in both of these previous studies, centrally presented motion stimuli elicited a marked P-INZ and a minimal P1, while color stimuli elicited a prominent P1 and little P-INZ activity. This double dissociation was replicated in the present experiment and strongly suggests that P1 and P-INZ are indeed two separate components. Corroborating the separability of these posterior positivities, Mitchell and Neville (2004) first reported and we have also found that the latency of the P-INZ shows no change with age, while the latency of the P1 decreases with age. With different distribution, condition, and developmental effects, it is unlikely that the P-INZ and P1 are indexing activity within the same neural generator. From the pattern of results across studies, a dorsal stream source for the P-INZ might be predicted; Armstrong *et al*. (2002) suggested a visual occipital pole source for the P-INZ, in contrast to the reported ventrolateral occipital source for the P1 (Clark & Hillyard, 1996; Heinze *et al*., 1994).

Eventually, data such as the present ERP findings should be able to be linked with neuroanatomical and behavioral perceptual data to construct a causal theory of visual perceptual development across the childhood years (cf. Stanley, 1991; Van Sluyters, Atkinson, Banks, Held, Hoffmann & Shatz, 1990, for work in infancy). However, currently, both the brain and behavioral data from school-age children are too sparse and varied to draw many meaningful connections or conclusions. It is likely that decreases in early visual component amplitudes and latencies across childhood are related to physical brain maturation in visual cortex such as increases in myelination (Yakovlev & Lecours, 1967) or pruning or synaptogenesis (Huttenlocher, de Courten, Garey & van der Loos, 1982), as well as to improvements in visual skills. Behavioral, psychometric studies with school-age children have documented decreases in various visual thresholds across childhood and reported longer maturation for dorsal (motion) as compared to ventral (color, form) functions (Barnard *et al*., 1998; Gunn *et al*., 2002; Hollants-Gilhuijs *et al*., 1998a, 1998b; Schrauf, Wist & Ehrenstein, 1999). Decreasing thresholds may be related to increasingly efficient neural processing reflected in decreasing visual component amplitudes and latencies, while the longer time course of maturation for tasks tapping dorsal stream processing is consistent with the less adult-like ERP responses to motion stimuli observed here. Further speculation might relate a recent report of maturation of visual contrast sensitivity across childhood, noting more pronounced development at low spatial frequencies (Benedek, Benedek, Kéri & Janáky, 2003), to the present ERP findings of longer maturation for responses to motion (low spatial frequency) than color (high spatial frequency) stimuli. However, only future empirical investigations employing multiple measures will reveal specific meaningful relations between behavioral and brain findings.

In summary, our results relatively consistently show development of ERP responses to both motion and color stimuli from middle childhood to adulthood, but a longer developmental time course for aspects of dorsal stream motion processing as compared to ventral stream color processing in terms of the present tasks and stimuli. These findings are in accord with anatomical reports of a longer maturational timetable for the dorsal or magnocellular stream (Hickey, 1977; Sherman, 1985), are consistent with behavioral findings of more extended development for the motion processing system (Gunn *et al*., 2002; Hollants-Gilhuijs *et al*., 1998a, 1998b), are in agreement with previous studies indicating a more protracted period of development for magnocellular aspects of the visual evoked potential (Crewther *et al*., 1996, 1999; Klistorner *et al*., 1996), and are consonant with results from a more complex version of the paradigm (Mitchell & Neville, 2004). Across populations, tasks, and methodologies, evidence is accumulating for extended maturation of aspects of the dorsal as compared to the ventral visual processing stream, confirming asynchronies in basic visual development during childhood. How such asynchronies might be related to the relative plasticity and vulnerability of the two streams remains for further investigation.

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