

Asynchronies in the Development of Electrophysiological Responses to Motion and Color

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Abstract

■ Recent reports have documented greater plasticity in the dorsal visual stream as compared with the ventral visual stream. This study sought to test the hypothesis that this greater plasticity may be related to a more protracted period of development in the dorsal as compared with the ventral stream. Age-related effects on event-related potentials (ERPs) elicited by motion and color stimuli, designed to activate the two visual streams, were assessed in healthy individuals aged

6 years through adulthood. Although significant developmental effects were observed in amplitudes of ERPs to both color and motion stimuli, marked latency effects were observed only in response to motion. These results provide support for the hypothesis that the dorsal stream displays a longer developmental time course across the early school years than the ventral stream. Implications for neural and behavioral plasticity are discussed. ■

INTRODUCTION

Neural development is highly asynchronous across systems, and this asynchrony has important consequences for the behaviors and skills observed at each developmental age and stage. Anatomical work has shown that synaptic density varies across the human cerebral cortex, with frontal regions displaying the longest period of developmental change, stretching into the teens (Huttenlocher & Dabholkar, 1997; Huttenlocher, 1984, 1990). Similarly, myelination continues into early adulthood, with the longest period of myelination occurring in frontal and superior brain regions (Yakovlev & Lecours, 1967). Recent magnetic resonance imaging data has confirmed this result, showing that localized decreases in gray matter density accompanied by brain growth, signaling developmental processes such as myelination, continue into early adulthood in prefrontal and posterior temporo-occipital cortex (Sowell, Thompson, Tessner, & Toga, 2001; Sowell, Thompson, Holmes, Jernigan, & Toga, 1999).

Research has shown that the development of behavioral skills parallels these asynchronies in brain maturation. For example, primary visual cortex appears to achieve adult-like organization early in life and the sensitivity and binocularity skills associated with it similarly become adult-like within the first year or two of life (Skoczenski & Norcia, 1998; Hainline & Riddell, 1995). By contrast, the cognitive skills associated with prefrontal cortex, such as working memory, inhibition, and

attention, continue to develop well into early adulthood (Diamond, 2002; Kwon, Reiss, & Menon, 2002; Luna et al., 2001; Casey, Giedd, & Thomas, 2000).

Neurocognitive systems display not only varying rates of development, but also varying degrees of plasticity across the life span. For example, in language, those systems that are involved in syntactic processing appear to be fully developed by early puberty and are relatively fixed after this period, while those systems that are involved in semantic processing continue to develop across the life span and can be modified by the introduction of new languages even late in adulthood (Weber-Fox & Neville, 1996). Within the visual system, it has been posited that high-precision systems requiring high acuity reach maturity earlier and are less modifiable by input and experience than lower precision systems (Chalupa & Dreher, 1991). Thus, systems that undergo protracted periods of development may display a higher degree of plasticity and variability of function across individuals than systems that undergo shorter periods of development.

The asynchronies observed in typical development can be disrupted in atypical development, and these disruptions can have similarly important consequences for individual development. Recent research findings suggest that the dorsal or “where” visual stream is more affected by atypical experience and input than the ventral or “what” visual stream. Studies of patients with glaucoma report behavioral (Anderson & O’Brien, 1997) and anatomical (Quigley, Dunkelberger, & Green, 1989) evidence of deficits traceable to dorsal stream layers of the lateral geniculate nucleus. Many behavioral and physiological studies of individuals with dyslexia report

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deficits in dorsal stream functions, such as motion perception (Demb, Boynton, Best, & Heeger, 1998; Kubova, Kuba, Peregrin, & Novakova, 1995; Lovegrove, Garzia, & Nocholson, 1990; see Stein & Walsh, 1997, for a review), while functional magnetic resonance imaging data show that visual motion elicits reduced activation of area MT in adults with dyslexia (Demb, Boynton, & Heeger, 1998; Eden et al., 1996), although other studies do not report dorsal stream deficits in this population (Olson & Datta, 2002; Skottun, 1997; Johannes, Kussmaul, Munta, & Mangun, 1996). Psychophysical studies of adults with Williams syndrome also report spared functioning of ventral pathway functions, but deficits in tasks requiring dorsal pathway functions, such as motion coherence thresholds (Bellugi, Lichtenberger, Mills, Galaburda, & Korenberg, 1999; Atkinson et al., 1997), as do reports of individuals with autism (Spencer et al., 2000) and hemiplegia (Gunn et al., 2002). Therefore, available evidence is consistent with the idea that the dorsal visual pathway may be more modifiable by atypical input and/or experience than the ventral visual pathway.

Further evidence from deaf adults shows that dorsal stream functions are more plastic than ventral stream functions. Armstrong, Neville, Hillyard, and Mitchell (2002) presented sinusoidal gratings that varied in color and spatial frequency in the center and four corners of a computer screen. Event-related potentials (ERPs) were time locked to the apparent motion of grayscale gratings and color change of colored gratings. Results showed that centrally presented motion evoked a large N1 observed across the scalp and a highly focal positivity at the most posterior midline electrode (referred to as the P-INZ). Peripherally presented motion also evoked a prominent N1, but it was smaller than that evoked by central presentations. By contrast, color evoked a P1 that appeared in posterior lateral sites and a prominent N1 for all stimulus locations. These responses differed for adults who were born deaf. Deaf and hearing adults produced similar ERPs in response to color. However, the N1 evoked by motion in deaf individuals was larger in amplitude and was distributed more anteriorly and medially than in normally hearing adults. These results support the hypothesis that greater compensatory plasticity in this population occurs within the dorsal visual stream than the ventral (Spencer et al., 2000; Neville, 1990).

One mechanism by which the dorsal visual stream would be more modifiable by atypical experience and input would be if it undergoes a longer developmental time course than the ventral stream. A longer developmental time course would provide greater opportunity for atypical input or experience to affect the structure and function of this neurocognitive subsystem. The existing data on the development of dorsal and ventral streams in humans is equivocal. Anatomical data show that the layers of the human lateral geniculate nucleus

that are a part of the dorsal visual stream display a protracted postnatal developmental time course in comparison to the layers that are part of the ventral visual stream (Hickey, 1977). Results from behavioral studies of infant vision are mixed. Some reports suggest that dorsal stream functions may mature faster than ventral stream functions (Dobkins, Anderson, & Liab, 1999; Crognale, Kelly, Weiss, & Teller, 1998), while others document faster development of ventral stream functions (Atkinson & Braddick, 1992). In any case, both visual streams appear to develop well beyond infancy. Behavioral studies of school-aged children report that contour detection, a ventral pathway skill, continues to improve until age 14 (Kovacs, Kozma, Feher, & Benedek, 1999), whereas flicker contrast, a dorsal pathway skill, improves until age 10 (Barnard, Crewther, & Crewther, 1998). In studies directly comparing the two streams, motion coherence is slightly delayed in typical development and more variable as compared with form coherence (Gunn et al., 2002). Similarly, color-contrast thresholds reach adult levels at roughly 13 years of age, although the detection of motion-defined forms does not reach adult levels until after 16 years of age (Hollants-Gilhuijs, Ruijter, & Spekreijse, 1998a, 1998b). Results from studies employing the visual evoked potential technique are mixed as well. Some studies document earlier maturation of ventral stream functions than dorsal stream functions (Crewther, Crewther, Klistorner, & Kiely, 1999; Crewther, Crewther, Barnard, & Klistorner, 1996), while others find the reverse (Madrid & Crognale, 2000; Gordon & McCulloch, 1999). Additional developmental research is needed to establish whether, how, and at what level(s) the developmental timetables of these two visual streams differ.

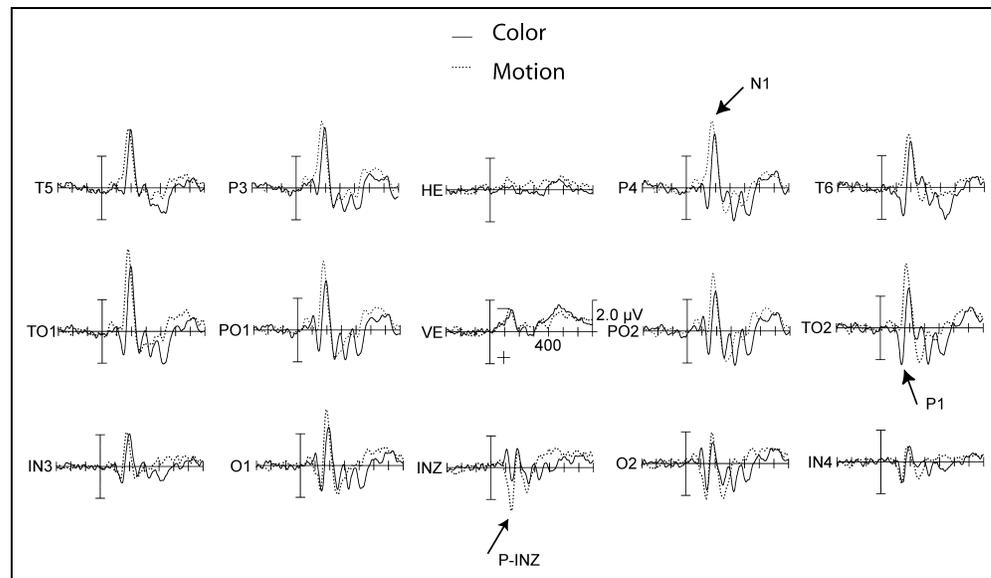
The current study was designed to test the hypothesis that motion processing, a skill associated with the dorsal visual stream, develops more slowly than color processing, a skill associated with the ventral visual stream. We assessed the development of electrophysiological responses to motion and color stimuli in a cross-sectional study. We predicted that ERPs evoked by motion stimuli, designed to stimulate the dorsal visual stream, would become adult-like at a later age than ERPs elicited by color stimuli, designed to stimulate the ventral visual stream.

RESULTS

ERPs to Standard Stimuli

Figure 1 presents the results from adult participants in response to CVF presentations of the color and motion stimuli. The positive and negative components analyzed in this experiment are noted in the figure. The first component analyzed was a positivity focal to electrode INZ, recorded in response only to centrally presented motion stimuli, hereafter called the P-INZ. Its peak

Figure 1. Average ERP waveforms for the 15 adult participants in response to CVF presentations. Color ERPs are shown in solid lines, motion ERPs are shown in dashed lines. All components analyzed in this study are shown in the tracings.



amplitude and latency were measured in response to centrally presented stimuli at INZ, between 95 and 185 msec. A second positive component, the P1, has been well characterized in ERP literature (Clark & Hillyard, 1996; Mangun, Hillyard, & Luck, 1993). Its peak amplitude and latency were measured at six lateral posterior sites between 100 and 180 msec poststimulus. Finally, a large negativity, the N1, peaked around 190 msec and could be observed across the scalp. This peak has also been well characterized in the ERP literature (Clark & Hillyard, 1996; Mangun et al., 1993). The peak amplitude and latency of the N1 were calculated between 150 and 270 msec poststimulus and analyzed across 12 posterior medial and lateral electrodes.

Figures 2 and 3 present ERP averages to CVF stimuli for 8- to 10-year-olds and 6- to 7-year-olds, respectively.

P-INZ Component

Overall amplitudes of the P-INZ were larger in response to motion than color stimuli, $F(2,42) = 12.37, p < .01$, and decreased with age, $F(2,42) = 8.53, p < .001$. Larger overall peak amplitudes were observed in 8- to 10-year-olds than both 6- to 7-year-olds and adults, $F(1,2) = 8.53, p < .01$. Analyses performed within each of the three age groups revealed that motion elicited a marginally larger P-INZ than color for 6- to 7-year-olds ($p = .058$), a significantly larger P-INZ for in adults, $F(1,14) = 22.96$,

Figure 2. Average ERP waveforms for the fifteen 8- to 10-year-old participants in response to CVF presentations. Color ERPs are shown in solid lines, motion ERPs are shown in dashed lines. All components analyzed in this study are shown in the tracings.

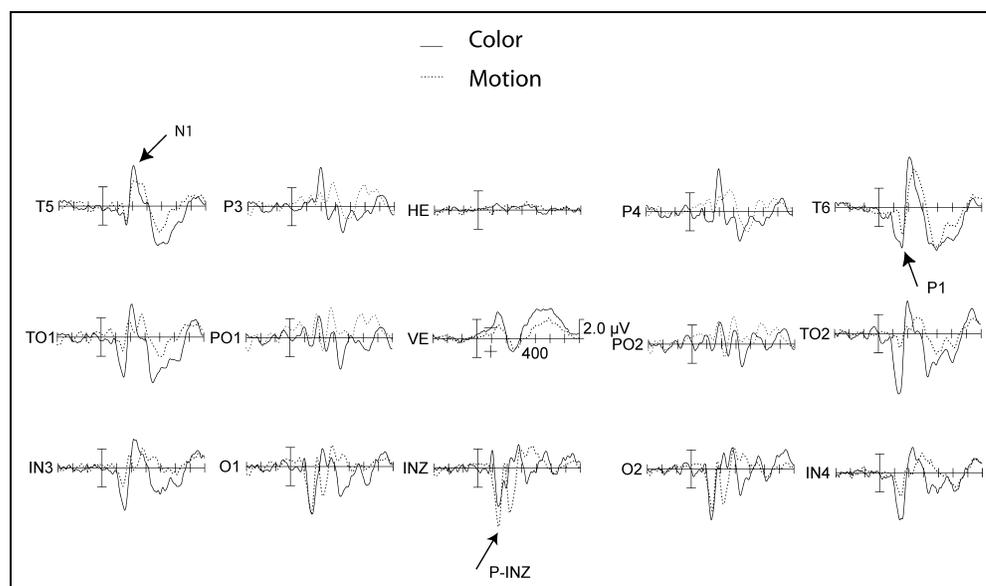
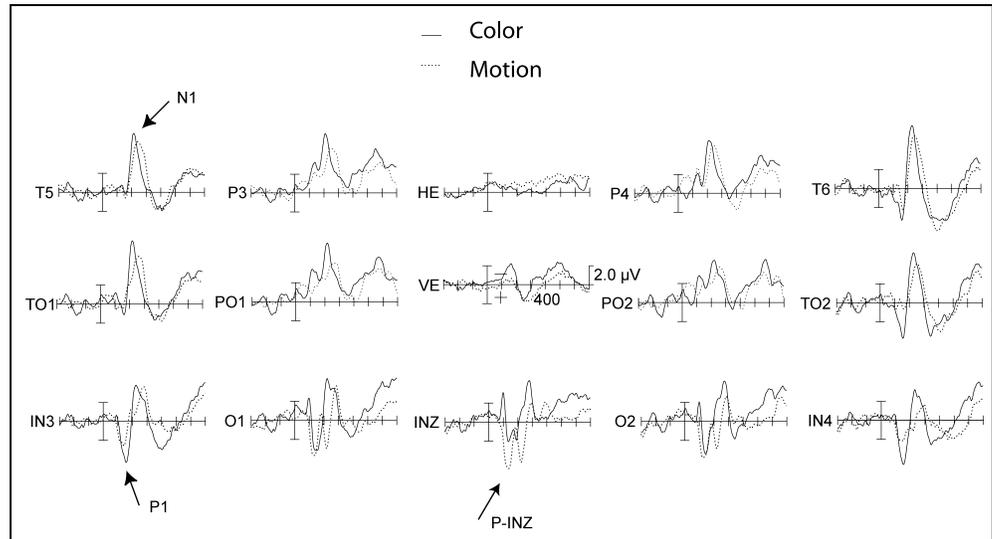


Figure 3. Average ERP waveforms for the fifteen 6- to 7-year-old participants in response to CVF presentations. Color ERPs are shown in solid lines, motion ERPs are shown in dashed lines. All components analyzed in this study are shown in the tracings.



$p < .001$, but no stimulus difference for 8- to 10-year-olds (see Figure 4). No latency effects were observed at any age level.

P1 Component

Central Visual Field Presentations

Overall amplitudes of the P1 were larger in response to color than motion stimuli, $F(1,42) = 14.99$, $p < .001$, and decreased with age, $F(2,42) = 13.3$, $p < .0001$. Latencies of the P1 varied across age and stimulus. Overall latencies decreased with age, $F(2,42) = 5.21$, $p < .01$, and a stimulus by age interaction, $F(2,42) = 3.41$, $p = .04$, shown in Figure 5, indicated that motion elicited shorter latencies than color for adult participants, $F(1,14) = 21.4$, $p < .001$, but not for 6- to 7-year-olds or 8- to 10-year-olds. Analyses conducted separately for each stimulus type revealed a significant reduction in latency across age groups for motion stimuli, $F(2,42) = 7.92$, $p = .0012$, but a marginal age effect for color ($p = .0542$).

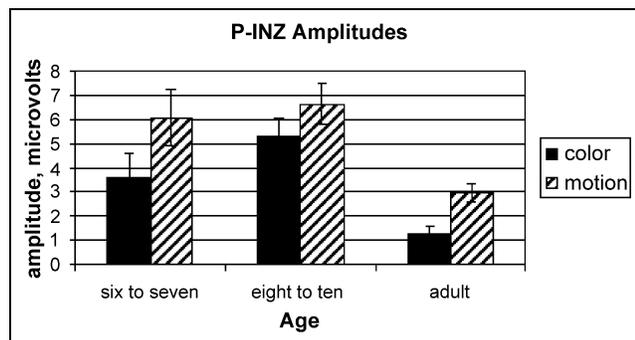


Figure 4. Averaged amplitudes of the P-INZ component, plotted by age and stimulus. Error bars are standard errors.

Peripheral Visual Field Presentations

As with CVF presentations, peripherally presented color elicited larger overall P1 amplitudes than motion, $F(1,42) = 38.34$, $p < .0001$, and overall amplitudes decreased with age, $F(2,42) = 8.91$, $p = .0006$. Within-age group analyses showed that no stimulus effect was observed in either 6- to 7-year-olds or 8- to 10-year-olds, but motion elicited significantly faster latencies than color for adults, $F(1,14) = 21.38$, $p < .001$. Overall latencies also decreased with age, $F(2,42) = 3.89$, $p = .0283$. This was true for within-stimulus analysis of motion, $F(2,42) = 3.28$, $p = .0473$, but not for color ($p = .18$). A contralateral latency effect emerged across age groups [age by hemifield by hemisphere, $F(2,42) = 9.75$, $p = .0003$]. Although faster latencies were observed in scalp sites contralateral to stimulus presentation for adults, $F(1,14) = 28.1$, $p = .0001$, this effect was not observed in child participants. This contralateral effect was observed in both within-stimulus analyses

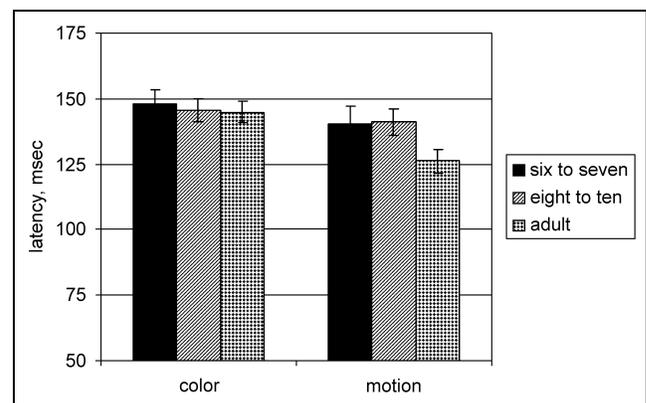


Figure 5. Latencies of the P1, averaged across all electrode sites, recorded in response to CVF presentations and plotted by age and stimulus. Error bars are standard errors.

[color, $F(2,42) = 4.67, p = .0148$; motion, $F(2,42) = 8.51, p = .0008$].

N1 Component

Central Visual Field Presentations

Overall amplitudes decreased significantly with age, $F(2,42) = 6.9, p < .01$; this was observed in separate analyses of both stimulus types (color, $p = .001$; motion, $p = .04$). An age by stimulus interaction, $F(2,42) = 3.73, p < .05$, was further explored in analyses within each age group. As shown in Figures 6A and 7, color evoked larger amplitudes than motion for 6- to 7-year-olds, $F(1,14) = 5.1, p < .05$, and 8- to 10-year-olds, $F(1,14) = 14.8, p < .01$, whereas the two stimuli evoked similar amplitudes for adults.

Overall latencies decreased with age, $F(2,42) = 22, p < .0001$, and, as shown in Figures 6B and 7, there was a larger decrease in latencies with age in response to motion than color [age by stimulus, $F(2,42) = 9.73, p < .001$]. Analyses within each age group showed that no stimulus effect was observed for child participants, while motion elicited faster latencies than color for adults, $F(1,14) = 21.5, p < .001$.

Peripheral Visual Field

Overall N1 amplitudes were larger to color than to motion stimuli, $F(1,42) = 103.8, p < .0001$; this was true for all age groups (6- to 7-year-olds, $p < .001$; 8- to 10-year-olds, $p < .0001$; adults, $p < .0001$). Larger amplitudes were observed in electrodes contralateral to stimulus presentation in adults, but not in child participants [age by hemisphere by left/right visual field, $F(2,42) = 3.65, p < .05$]. Within-age group analyses supported this result, with larger amplitudes observed contralateral to stimulus presentation only for adult participants, $F(1,14) = 20.2, p < .001$. Within-stimulus analyses showed that the emergence of this contralateral

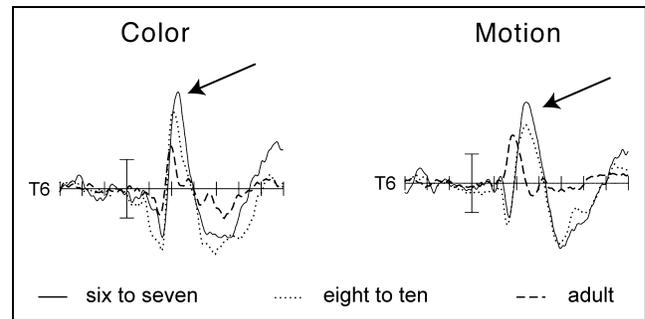


Figure 7. Averaged ERPs recorded in response to CVF stimulus presentations at a representative electrode, T6. Each age group is represented by a separate trace and the arrow indicates the N1 component.

effect was observed in response to motion stimuli ($p = .0001$) but not color.

Multiple latency effects were observed. Overall latencies decreased with age, $F(1,42) = 24.36, p < .0001$, and were faster to motion than color stimuli, $F(1,42) = 4.73, p < .05$. Analyses within each age group revealed that this stimulus effect was observed primarily in posterior electrode locations (stimulus by anterior/posterior; adults, $p < .001$, 8- to 10-year-olds, $p < .0001$, 6- to 7-year-olds, $p < .001$). A contralateral effect also emerged in latency analyses. An age by hemisphere by visual field interaction, $F(2,42) = 3.65, p < .05$, was explored in within-age analyses. Faster latencies were observed contralateral to stimulus presentations only in adult participants, $F(1,14) = 13.8, p < .01$. This contralateral effect was elicited primarily by motion, as shown in Figure 8 [stimulus by hemisphere by left/right visual field, $F(1,42) = 6.5, p < .01$; within-motion, $p < .001$] and not color.

Behavioral Responses to Target Stimuli

Participants performed a basic target detection task during ERP recording to ensure that all five stimulus

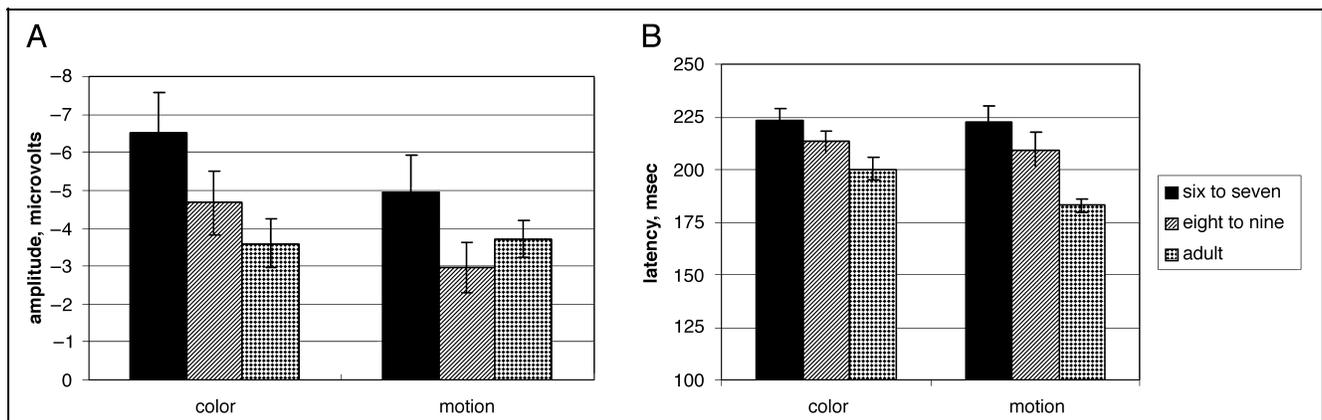


Figure 6. Age by stimulus interactions for the N1 component, averaged per age group across all electrodes and recorded in response to CVF presentations: (A) N1 amplitudes; (B) N1 latencies. Error bars are standard errors.

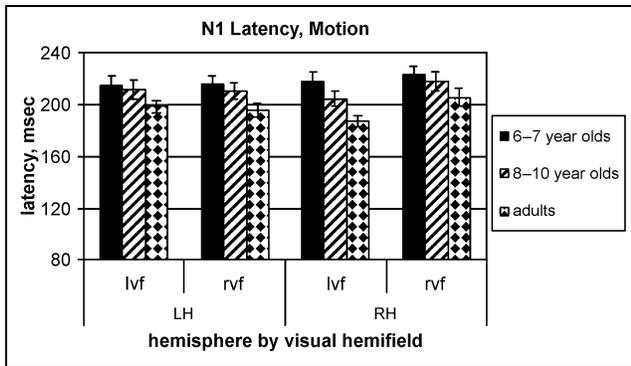


Figure 8. Averaged latencies of the N1 elicited by peripheral motion stimuli, plotted by age, hemisphere, and visual hemifield. Faster latencies were observed in electrodes contralateral to stimulus presentation only for adult participants.

locations were attended simultaneously throughout each stimulus block. Reaction times (RTs) were recorded to button presses made in response to detection of target black square stimuli in any of the five stimulus locations. RTs faster than 200 msec or longer than 1500 msec were excluded from the analysis. This resulted in average losses between 14% and 0% per age/condition. Fewer trials were dropped with age, $F(2,42) = 3.0, p < .06$, and fewer trials were dropped for the motion task than the color task, $F(1,42) = 8.1, p < .006$.

RTs and percent of correct responses to centrally presented targets were each analyzed in a mixed two-way (age by task) repeated measures analysis of variance (ANOVA). As shown in Figure 9A, there was a significant overall decrease in RTs with age, $F(2,42) = 9.9, p < .001$, and overall RTs to targets in the motion task were significantly faster than to targets in the color task, $F(1,42) = 4.6, p < .05$. Accuracy also increased significantly with age, $F(2,42) = 3.5, p < .05$. No other effects were observed.

RTs and percent of correct responses to peripheral targets were each analyzed in a mixed four-way (age by

stimulus by upper/lower and left/right visual fields) repeated measures ANOVA. As shown in Figure 9B, overall RTs decreased with age, $F(2,42) = 28.35, p < .0001$, and participants were faster to respond to targets when viewing the motion stimuli as compared to the color stimuli, $F(1,42) = 39.82, p < .0001$. Responses were faster to targets in the upper visual field than the lower visual field, $F(1,42) = 11.16, p < .0005$. No other latency effects were observed. Overall accuracy increased with age, $F(2,42) = 4.78, p < .05$, and was higher for the motion than the color task, $F(1,42) = 8.85, p < .005$. Overall accuracy was higher for upper than lower visual field presentations, $F(1,42) = 4.66, p < .05$, an effect that emerged with age, $F(2,42) = 3.64, p < .05$.

All participants responded faster and more accurately to centrally than peripherally presented targets [RT, $F(1,42) = 9.58, p < .005$; accuracy, $F(1,42) = 4.31, p < .05$]. There was a marginal stimulus by location interaction, $F(1,42) = 3.73, p = .06$, with responses during the motion task more accurate for central than peripheral target locations.

DISCUSSION

The current study was designed to test the hypothesis that motion processing, a skill associated with the dorsal visual stream, develops more slowly than color processing, a skill associated with the ventral visual stream. We assessed the development of electrophysiological responses to motion and color stimuli in a cross-sectional study. We predicted that ERPs evoked by motion stimuli, designed to stimulate the dorsal visual stream, would become adult-like at a later age than ERPs evoked by color stimuli, designed to stimulate the ventral visual stream.

The overall stimulus effects observed in the ERPs recorded to color and motion stimuli in this study replicated past research (Armstrong et al., 2002). The P-INZ was observed primarily in response to centrally

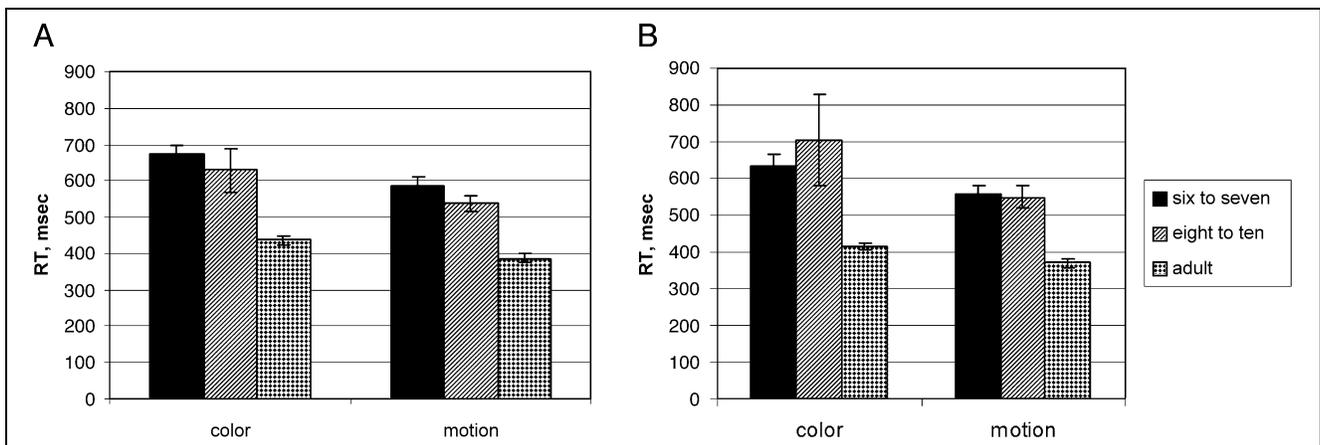


Figure 9. RTs (in milliseconds) recorded to target stimuli presented in the CVF (A), and the PVF (B). Graphs depict significant main effects of age and stimulus type. Error bars are standard errors.

presented motion. For all participants, color elicited a larger P1 and motion elicited faster P1 latencies in adults. Similarly, color tended to elicit larger N1 amplitudes than motion, and motion elicited faster N1 latencies than color.

Significant developmental changes were observed in ERP components elicited by both color and motion stimuli. Reductions in overall amplitudes with age were observed for all three ERP components and conditions, except for the N1 recorded in response to peripheral stimuli. Similarly, significant reductions in overall latencies were observed for all components and conditions except the P-INZ. These large-scale developmental changes may be driven, in part, by factors such as skull growth and myelination (Yakovlev & Lecours, 1967), as well as by perceptual and cognitive development.

Developmental changes in lateralization of components were also observed. Peripherally presented stimuli elicited larger amplitudes and/or faster latencies in the contralateral hemisphere in adult participants, but elicited similar ERPs across hemispheres in young children. The emergence of contralateral latency effects may be due to the protracted period of myelination in human development and may also be due to the development of the corpus callosum. These changes in transmission times may, in turn, contribute to the stronger, more efficient processing that is indexed by contralateral amplitude distributions. The development of the contralateral effects documented in this study is similar to the development of hemispheric advantages in other perceptual and cognitive processes. For example, in face processing, the Nc component is right lateralized in response to faces but not objects as early as 6 months (de Haan & Nelson, 1999), whereas the N170, the face-specific component observed in adults, is bilaterally distributed in early childhood with a right hemisphere advantage not observed until puberty (Taylor, Edmonds, McCarthy, & Allison, 2001; Taylor, McCarthy, Saliba, & Degiovanni, 1999). In language processing, ERPs elicited by single words are bimodally distributed in young toddlers and the left hemisphere advantage emerges slowly and appears to be driven in part by vocabulary growth, not simply age (Neville & Mills, 1997; Mills, Coffey-Corina, & Neville, 1993, 1997). Thus, the emergence of laterality effects appears to be an important developmental marker and future research should focus on how it is affected by behavioral and experiential variables.

The behavioral task provided a gross measure of subjects' simultaneous attention across the five stimulus locations. Participants of all ages were able to respond to black target stimuli and significant improvements in RT and accuracy were observed across the three age groups. All participants were faster and more accurate to respond to target stimuli during the motion task than the color task. Perhaps detection of target stimuli was easier when they were presented amidst the motion stimuli than the color stimuli because the difference

between a black square and moving gratings is more visually salient than the difference between a black square and a flash of red. Responses were also faster and more accurate for central than peripheral target locations, particularly during the motion task. These behavioral measures tap into several processes at once, including detection, response preparation, and response execution. These processes are likely to differ in development across the age range in this study and, most importantly, from the early sensory and perceptual processes indexed by the ERPs, which occurred hundreds of milliseconds faster and were recorded in response to the color changes and apparent motion of the grating stimuli. Although the results of the behavioral task do not directly test our hypothesis, they provide a measure of attention to the five stimuli and this improved across the age range studied.

In line with our hypothesis, we observed dissimilar developmental trends in the ERPs elicited by the two stimulus types. Color stimuli evoked similar wave shapes across the three age groups but significant changes in amplitude. P-INZ amplitudes in response to color were small and decreased across the three age groups. Amplitudes of the P1 in response to color decreased significantly with age, but little to no change was observed in latencies. Both amplitudes and latencies of the N1 in response to color decreased with age. Thus, ERPs evoked by color stimuli displayed relative stability in wave shape and latency across the age range studied, but significant changes in amplitude.

A different pattern of development was observed for ERPs to motion stimuli. The overall wave shape of the ERPs elicited by motion in child participants was unorganized in comparison to motion ERPs in adult participants and significant age effects were observed in both amplitudes and latencies. The amplitude of the P-INZ elicited by centrally presented motion decreased with age, with no accompanying change in latencies. By contrast, both amplitudes and latencies of the P1 in response to motion decreased with age; this decrease in latencies was not observed in the P1 response to color stimuli. Amplitudes of the N1 decreased with age in response to all stimulus presentations. Latencies also decreased with age, with this age effect being larger in motion ERPs than the complementary effect in color ERPs. Finally, the laterality by age interaction effect in N1 amplitudes and latencies was specifically observed in response to motion stimuli. These results correspond well to the development of motion coherence thresholds across a similar age range (Gunn et al., 2002). In sum, age effects in responses to motion included both large changes in amplitude and marked decreases in latencies that were significantly larger than latency decreases in response to color stimuli.

The question of whether the dorsal visual stream matures earlier or later than the ventral stream is complex. The disagreement that exists in the literature

stems from differences in ages of participants (exclusively infants or children), methodology (behavior, electrophysiology), and visual process assessed (contrast sensitivity, contour integration, motion detection), and few reports directly compare ventral and dorsal stream functions within the same individuals. Furthermore, both streams are made up of multiple connected “nodes” (e.g., layers of the LGN, blobs in V1, areas MT and V4), each of which may develop at different rates and may be differentially tapped by the various methodologies. Thus, results from some studies may reflect activity in early nodes of these pathways, such as the LGN, which may develop at a different rate than cortical nodes. Overall, it does appear that activity within the two pathways continues to develop beyond infancy into early childhood. This study reports the brain’s responses to color and motion stimuli across the early school years and adulthood. The neural generators of the P1 and N1, the major components analyzed in these articles, have been localized to ventral extrastriate regions and to multiple sources in dorsal extrastriate/parietal regions, respectively (Clark & Hillyard, 1996; Mangun et al., 1993). Neural development in these regions is likely to be beyond the early school years (Sowell et al., 1999, 2001; Huttenlocher & Dabholkar, 1997; Huttenlocher, 1984, 1990). Thus, the stimulus and developmental effects documented in this study are likely to occur in ventral and dorsal extrastriate visual regions and possibly parietal regions. The results of this study support the hypothesis that dorsal visual stream functions, such as motion processing, develop more slowly across early childhood than ventral visual stream functions, such as color processing. Previous research directly comparing the two streams has similarly reported that form coherence thresholds, a measure of ventral stream functioning, reach adult-like levels earlier and are less variable than motion coherence thresholds, a measure of dorsal stream functioning (Gunn et al., 2002). Continued research is needed to understand the nature and extent of the developmental differences that appear to exist between the two streams.

The current study was motivated by previous research in which we reported that color changes elicited similar ERPs in deaf and hearing adults while motion elicited larger and more anteriorly distributed ERPs in deaf than hearing adults (Armstrong et al., 2002). We hypothesized that one of several possible mechanisms for this particular instance of plasticity may be a longer developmental time course for the neural substrates of motion versus color responses. If the neural substrates involved in motion processing mature relatively late in development, then a lifetime of auditory deprivation would have greater opportunity to affect its developmental outcome than to affect the earlier-developing substrates of color processing. In this study, we limited our assessment to motion and color processing as representing dorsal and ventral activities, respectively. Although motion stimuli

generally produce little activity along the ventral stream, color stimuli have been shown to produce activity within the dorsal stream (Dobkins & Albright, 1994; Gegenfurtner et al., 1994). Because we did not control for all possible luminance contributions to our color stimuli, they may have evoked activity in both ventral and dorsal regions. We note that these contributions could work against our hypothesis by rendering the color ERPs more similar to the ERPs recorded in response to motion stimuli. Thus, the differences we observed may be smaller than if all luminance contributions to color responses had been controlled for. The important result is that motion processing—the same visual process that was enhanced in deaf adults over hearing adults (Armstrong et al., 2002)—differed the most between children and adults, while our measure of color processing was similar between deaf and hearing adults as well as more similar between children and adults. These findings suggest that slowly developing skills and systems may be more plastic than other faster developing ones in the face of atypical input and experience. An important aim for future research will be to understand the interactions between developmental timetables and functional and structural plasticity both across and within neurocognitive systems.

METHODS

Subjects

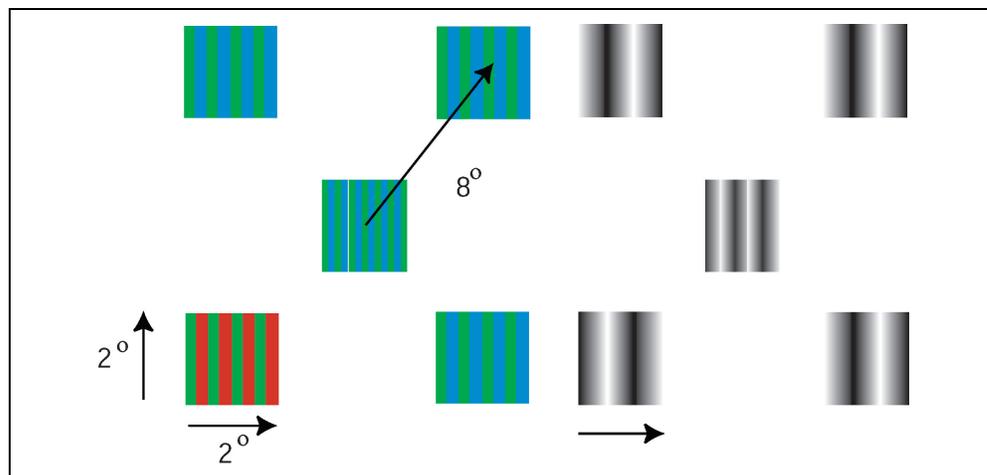
Forty-five participants volunteered for this experiment and were paid for their participation. There were 15 participants in each of three age groups: 6- to 7-year-olds (10 girls, average age 6 years, 8 months), 8- to 10-year-olds (8 girls, average age 8 years, 5 months), adults 18 years and older (10 women, average age 21 years). All were neurologically normal, native English speakers. All had normal (or corrected-to-normal) vision as assessed by Snellen charts and normal color vision as assessed by Ishihara tests.

Stimuli and Tasks

The stimuli and tasks used in this study are nearly identical to those used in previous research (Armstrong et al., 2002). All stimuli were vertically oriented, sinusoidal spatial frequency gratings presented on a gray background. Each stimulus was approximately $2^\circ \times 2^\circ$ and the edges were filtered with a ramp function to reduce high frequency artifacts. Stimuli were presented in the upper left, upper right, center, lower left, and lower right of a 21-in. diagonal color CRT monitor. A fixation point in the center of the monitor was presented at the beginning of each block. Centers of the four peripheral stimuli were located 8° diagonally from this fixation point.

There were two types of stimuli, as shown in Figure 10. The “color” stimulus, designed to activate the ventral pathway, was an isoluminant blue and green high spatial

Figure 10. Experimental stimuli. The leftward panel depicts the color stimuli, with the upper left stimulus illustrating a color standard in which the blue bars become red. The rightward panel depicts the motion stimuli, with the lower left stimulus illustrating a motion standard in which the bars translate rightward. Each stimulus subtended $2^\circ \times 2^\circ$ visual angle. The midpoint of each stimulus was 8° from the midpoint of neighboring stimuli.



frequency grating. The “motion” stimulus, designed to activate the dorsal pathway, was a low spatial frequency grayscale grating with a low luminance contrast of 4%. The motion and color stimuli and gray background all had a mean luminance of 8.5 cd/m^2 .

The spatial frequency of the peripheral stimuli was decreased in relation to central stimuli to obtain the same contrast sensitivity function for all retinal locations (see Rovamo & Virsu, 1979, for function). The central color stimulus had a spatial frequency of 10.5 cycles/deg and the peripheral color stimuli were at 3.5 cycles/deg. The central motion stimulus had a spatial frequency of 1.5 cycles/deg and the peripheral motion stimuli were scaled to 0.5 cycle/deg.

The color and motion stimuli were presented in separate blocks to control for ordering effects. Stimuli were continuously, binocularly visible at the five locations on the screen and at a randomly varying time interval (between 150 and 450 msec), the stimulus at one location would change—these changes were “standards.” A color block “standard” consisted of the blue bars of a particular stimulus changing to red for 100 msec, then changing back to blue. This created the perception of a flash of red at that location, with no transverse movement. A motion block “standard” consisted of the bars of one stimulus moving transversely to the right at a velocity of $13.7^\circ/\text{sec}$ for 100 msec. Across both the color and motion blocks, a “target” consisted of any of the five stimuli being replaced with a black square for 100 msec.

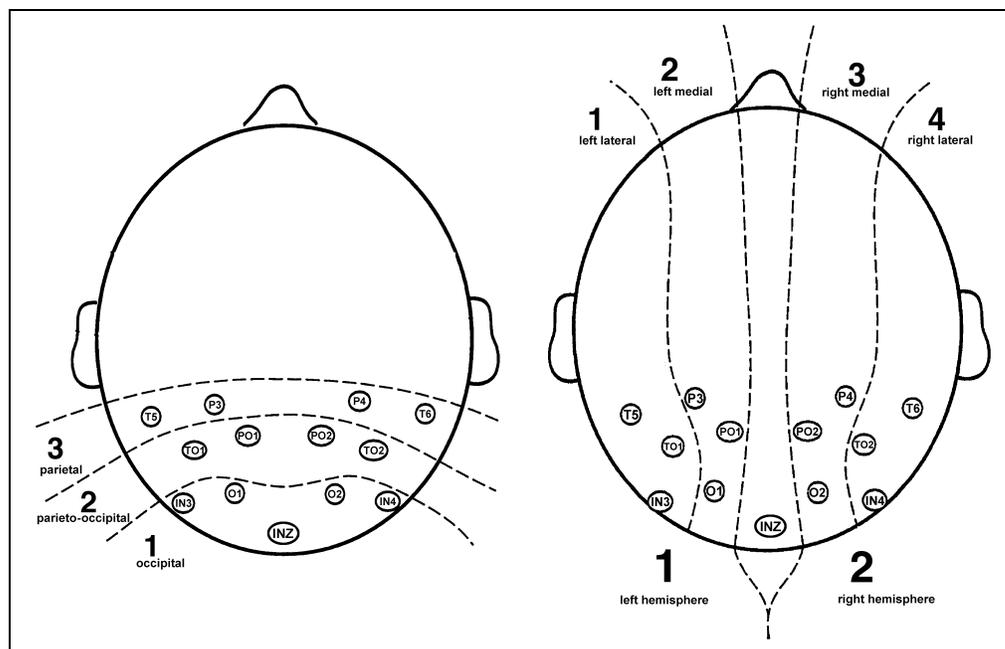
The recording room was darkened and sound attenuated. Participants were seated in a comfortable upright chair, at a distance of 46 in. from nasion to monitor, with a response box held on the lap. They fixated on a central cue provided before each block of trials and responded with a button press upon detection of a black “target” stimulus at any of the five stimulus locations. This task was designed to maintain diffuse attention across all stimuli and was not related to the stimulus manipulation. Participants switched response hand halfway

through each block. Each block consisted of 175 standards (stimulus changes) and 17 targets (black squares) at each of the 5 locations. Targets and standards were randomly interleaved and the location of stimulus occurrence was randomized. Small breaks were given between every 10- to 12-sec block of trials to allow subjects to rest and blink their eyes, and longer breaks were provided every 10 min or upon request. Participants were instructed to move their eyes or blink only during breaks, not during blocks of trials. Participants were allowed to practice the task before recording to become comfortable with the setup and participants made few errors.

ERP Recording and Analysis

Each participant’s brain activity was recorded from 29 scalp sites using an elastic cap (Electrocap) embedded with nonpolarizable tin electrodes. The array included 10 sites from the international 10–20 system plus an additional 19 sites interspersed between these to form a regular grid covering mostly the posterior portion of the head. Five additional electrodes were used to record horizontal and vertical eye movements and the left and right mastoids. All channels were referenced to the right mastoid during recording, except for the horizontal eye channel, which was a bipolar recording between the left and right outer canthi. Signals were amplified by a Grass Model 12 polygraph with a bandpass of 0.01–100 Hz and then digitized at 250 Hz. Digitized data were time-locked to stimulus presentations so that they could be averaged off-line to produce ERPs. Data were low-pass filtered at 60 Hz and trials that included blinks, eye movements, amplifier blocking, target presentations, and/or behavioral responses were rejected during averaging by software algorithms. The ERP data were also algebraically re-referenced off-line to the average of the left and right mastoids for waveform plotting and statistical analysis. Figure 11 represents the 13 electrodes that contributed to the statistical analyses in this report.

Figure 11. Electrode configuration and analysis factors. The left image represents the three possible levels of the anterior/posterior factor. The right image represents the combination of the two levels of the hemisphere factor and the two levels of the medial/lateral factor. Data from electrode INZ were analyzed separately.



Poststimulus voltage fluctuations were measured against the mean voltage of a 300-msec presampling baseline. Several consistent positive or negative peaks could be identified in the averaged ERP waveforms, thus, amplitude and latency measurements were performed on time windows that surrounded these primary components (see Results). Waveforms from each subject were examined to ensure that their peaks fell within the specified time windows.

The ERPs were analyzed with mixed-design repeated measures ANOVAs, with the Greenhouse–Geisser epsilon correction for nonsphericity (Jennings & Wood, 1976). Separate analyses were conducted on each of three components of interest (see Results), according to age (6–7 and 8–10 years old, adult), stimulus type (color vs. motion), stimulus location (upper/lower, left/right, center), and electrode location [collapsed across three major dimensions: anterior/posterior (three possible levels), left/right hemisphere, medial/lateral; see Figure 11]. Results from electrode INZ were analyzed separately. Additional ANOVAs were performed within each stimulus type and age group to further clarify results.

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