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P300 Development from Infancy to Adolescence

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Abstract

This paper provides an overview of P300 research from infancy through adolescence. First, a brief historical overview is provided highlighting seminal studies that began exploration of the P300 component in developmental groups. Overall, these studies suggest that the P300 can be detected in children and appears to reflect similar cognitive processes to those in adults, however it is significantly delayed in its latency to peak. Second, two striking findings from developmental research are the lack of a clear P300 component in infancy and differential electrophysiological responses to novel, unexpected stimuli in children, adolescents and adults. Third, contemporary questions are described, which include: P300-like components in infancy, alteration of P300 in atypically developing groups, relations between P300 and behavior, individual differences of P300, and neural substrates of P300 across development. Finally, we conclude with comments regarding the power of a developmental perspective and suggestions for important issues that should be addressed in the *next* 50 years of P300 research.

Keywords: P300, development, P3a, P3b, infants, children, adolescents

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1. Introduction

The study of development is important both to understand how processes change over time as well as to uncover the foundations of adult abilities. The electroencephalogram (EEG) and more specifically, the event-related potential (ERP) are important methodological tools used in investigations of both adults and children. The P300 component, arguably the most studied component in human adult cognitive electrophysiology, has also been widely investigated in developmental populations. The following review provides an overview of P300 research in developmental groups, highlights foundational studies, summarizes contemporary questions and raises important questions for the field to address in the *next* 50 years.

The P300 is an event-related brain potential commonly elicited during tasks engaging attention, memory, and/or problem solving (Polich, 2007). Although the exact cognitive function(s) reflected by the P300 remain debated, there seems to be general agreement that the P300 reflects information processing and updating of working memory (Polich, 2012). In contemporary adult research, the P300 is often further subdivided into P3a and P3b subcomponents. The P3a, which is also referred to as the 'novelty P300,' has a fronto-central topography that is elicited in response to novel stimuli and does not require an active response from the participant. In contrast, the P3b has a parietal topography and is typically observed in tasks that involve intentional or conscious discrimination of novel stimuli.

Table 1 provides examples of studies in typically developing cross-sectional samples that report age-related differences in P300. Although there is considerable variability in the studies conducted, paradigms utilized, and analytic procedures applied, some consistencies in results are apparent. This is particularly the case for studies of auditory P3b using 2-stimuli of varying

frequencies, which are the most abundant in the literature, that show decreases in latencies and increases in amplitudes as a function of age (Downes, Bathelt, & de Haan, 2017; van Dinteren, Arns, Jongsma, & Kessles, 2014). In the following section we provide historical context for the study of P300 in development and describe several influential studies that laid the foundation of this field.

INSERT TABLE 1 ABOUT HERE

2. Historical Overview

Currently, a salient goal in the field of human developmental cognitive electrophysiology is to use ERPs to explore changes in brain function and associate them with cognitive development. However, this has not always been a primary concern. In the 1970s, when studies first began to emerge, a key interest was simply to determine if ERP components commonly found in adults, such as the P300[1], could be detected in younger individuals (Courchesne, 1983). As such, designs for very early "developmental" experiments were not derived from or for the developmental literature but instead were based on adult paradigms and findings and employed in children to determine if a P300 component was generated.

These initial studies were successful at recording a P300 (or P300-like) component in developmental groups, which lead to a dramatic increase both in the number and innovative-quality of empirical investigations. First, studies began to include a wider span of ages to document developmental differences across the lifespan. This lead to the striking discovery that the P300 component was difficult to detect, and potentially absent, in infants. Second, investigators began to examine whether the P300 recorded in children reflected similar cognitive processes to those in adults. These studies demonstrated that once an adult-like P300 was consistently detectable, it appeared to be influenced by similar factors, such as attention and

stimulus probability throughout development. Third, P300 brain potentials to a wider variety of stimuli, such as completely novel or unexpected stimuli, were examined. This led to a second remarkable discovery that ERPs to novel, unexpected stimuli differ dramatically across development and auditory versus visual modalities. Overall, these studies suggested that the P300 can be used as a general index of cognition in development starting around 5 years of age, but that the P300 component is also influenced by factors such as task demands, sensory modality, and participant age. Each of these advances represents an important step toward understanding the P300 and its development. In the following section we describe important studies from each of these lines of inquiry.

3. Seminal Studies

3.1 Earliest studies sought to identify the P300 component in children and adolescents

The earliest studies examining the P300 in children and adolescents emerged in the 1970s and were largely based on tasks and results from adult cognitive electrophysiology research. These cross-sectional investigations typically included a small number of school-aged children in a narrow age range and used simple discrimination tasks involving specific sets of stimuli, such as letters and sounds (e.g., Friedman, Vaughan, & Erlenmeyer-Kimling, 1978; Friedman, Vaughan, & Erlenmeyer-Kimling, 1981; Goodin, Squires, Henderson, & Starr, 1978; Grünewald, Grünewald-Zuberbier, & Netz, 1978; Kurtzberg, Vaughan, & Kreutzer, 1979; Shelburne, 1973). Consistent with studies in adults, stimulus presentation probabilities were often manipulated with one stimulus presented frequently (.80) and another presented infrequently (.20). Participants were typically asked to pay attention to the infrequent oddball/ target stimulus by keeping track of its occurrence or counting or responding with a button press. The ability to successfully complete the task was determined based on these behavioral responses.

3.1.1 P300 latency. Figure 1 illustrates P300 components recorded in school-aged children using oddball paradigms. Overall, early investigations reported that electrical brain responses to target stimuli were associated with positive-going waves peaking between 300-600 ms that were maximal over central or parietal leads. This pattern led to the conclusion that the ERP component recorded in developmental samples was analogous to the adult P300, specifically, the P3b. However, one major difference was that the latency to peak amplitude was delayed compared to adults. Age-related decreases in latency ranged from 3.6 to 18.4 ms/yr (Finley, Faux, Hutcheson, & Amstutz, 1985; Goodin et al., 1978). Variations in these rates were attributed to differences in paradigms, study design, and the age distribution of subjects included in the study (see Pearce, Crowell, Tokioka, & Pacheco, 1989). Age-related decreases in latency were also shown to be relevant to behavior (Fuchigami et al., 1993), as they correlated with decreases in reaction time (RT). Together these findings suggested that developmental differences in P300 latency reflected increases in information processing efficiency, which was hypothesized to be related to increased myelination and dendritic arborization during development (Kurtzberg et al., 1979; Pearce et al., 1989).[2]

INSERT FIGURE 1 ABOUT HERE

Age-related decreases in P300 latency could also be observed within the same individuals. Kurtzberg et al. (1979) published the first longitudinal study of the P300 using a simple visual discrimination task in children from 5- to 8-years of age. Each participant was tested three times at one year intervals. Consistent with the cross-sectional studies, a P300 component was observed and the latency of this component decreased across development along with corresponding decreases in RT. This study also reported that amplitude became more prominent over right scalp regions with age, suggesting age-related increases in functional specialization may also exist.

3.1.2 P300 amplitude. Age-related differences in P300 amplitude were reported in some cross-sectional studies, but were less consistent than findings of age-related decreases in latency. Some studies reported increases in amplitude from childhood to adulthood that were correlated with increases in information processing capacity (Polich, Ladish, & Burns, 1990). However, other studies reported variations in amplitude that were primarily influenced by stimulus characteristics, such as the number or saliency of stimuli (van Dinteren, Arns, Jongsma, & Kessels, 2014), or maturational factors such as skull thickness or brain-skull distance (Beauchamp et al., 2011; Frodl et al., 2001).

3.1.3 Summary and future directions. Findings of age-related differences in the P300 have endured over time. A systematic review and meta-analysis of 75 studies (n=2,811) and a massive cross-sectional dataset examining participants from ages 6-87 years (n=1,572) supports age-related differences in P300 latency and amplitude (van Dinteren et al., 2014). In addition, due to the scope of data included in this report, these authors were able to make novel claims about the sequence of development. Specifically, they noted that P300 amplitude reaches its maximum significantly earlier (16-21 years) than P300 latency reaches its trough (22-25 years), however, both latency and amplitude reach 'maturity' earlier than RTs (~32 years).[3]

Such differences in the developmental trajectories of latency and amplitude suggest these two measures may index different aspects of brain maturation. Latency changes may reflect variations in neural speed or brain efficiency (possibly linked to myelination), whereas amplitude changes may reflect variations in the magnitude of a neural or cognitive response (van Dinteren et al., 2014). However, other interpretations also exist. For example, it is also possible that within- and between-subjects variability in both latency and amplitude change with age and that more variable peaks across trials leads to decreased amplitude and depressed peaks with longer latencies.

Thus, although the traditional view is that age-related differences in latency and amplitude of the P300 component are due to specific maturational factors, differences in variability across age could also lead to similar outcomes. These possibilities generate interesting hypotheses that are ripe for investigation over the next 50 years of P300 research.

4. The first striking report of developmental differences: Studies of P300 in infancy

4.1 Visual paradigms. Early electrophysiological studies with infants immediately revealed that the morphology and timing of ERP responses in infants did not readily correspond to adult components. In a pioneering study, Schulman-Galambos and Galambos (1978) examined ERPs recorded from bilateral central scalp locations while adults and infants (ranging from 7 weeks to 12 months of age) viewed blurred (.50) or focused (.50) slides of characters, people, scenes, and artwork. They found that whereas adults exhibited 6 clear components (N1 through P4) between 140-600 ms after a visual stimulus was presented, the same stimuli only elicited 3 components in infants. These 3 components, called Pb or P2, Negative central component or Nc, and Positive component or Pc, were delayed in time, extending from 200 ms to 1000 ms after stimulus onset and were present under a variety of conditions (Courchesne, Ganz, & Norcia, 1981; Courchesne, 1983; Hofmann, Salapatek, & Kuskowski, 1981; Nelson & Salapatek, 1986). Results of this early work highlighted the utility of ERPs for studying infant cognitive development, but also began an ongoing debate about the interpretation of infant ERP results and the link between adult and infant components.

Courchesne and colleagues (1981) were one of the first to specifically probe for the P300 component in infants. In this study, ERPs were recorded in 4- to 7-month olds to frequently (.88) versus infrequently (.12) presented human faces. Results revealed no discernable P300 present at any age tested. Instead, waveforms were characterized by a frontally distributed Negative wave

around 700 ms, which is now called Nc, and a long-latency positive wave around 1300 ms, which is now called late slow wave or LSW. The infrequently presented face elicited a larger Nc that peaked later than the frequently presented face; however, the LSW did not vary based on stimulus frequency. The authors concluded that the infant Nc may be similar to the P300 as it appeared to be involved in the detection of, and attention to, infrequent stimuli.

Subsequent investigations challenged Courchesne et al.'s (1981) conclusion that the Nc was the only infant component sensitive to stimulus probability. The first of these investigations used images of visual gratings with 13-month-old infants (Hofmann et al., 1981) and the second tested 3-month-old infants using pure tones paired with visual gratings (Hofmann & Salapatek, 1981). In these studies, infants were pre-experimentally familiarized (for 40 trials) to the to-be-frequent (.80) stimulus condition in order to direct attention to the frequent event and provide infants with the equivalent of "instructions" typical in adult P300 investigations. Across both studies, a Pc, recorded over Oz, Pz, and Cz, between 300-600 ms differentiated frequently presented and recently familiarized stimuli from infrequently presented stimuli (Hofmann & Salapatek, 1981; Hofmann et al., 1981).

Next, in an attempt to not only reconcile differences between Courchesne et al. (1981) and the two reports by Hofmann and colleagues (1981) but also examine the extent to which infant ERP components index an endogenous response to novelty/uncertainty, Nelson and Salapatek (1986) tested 6-month-old infant's ERPs to faces across three experiments. Similar to Courchesne et al. (1981) infants viewed faces across several conditions. In Experiment 1, one face was presented frequently and a second face presented infrequently. However, infants were first familiarized to the to-be-frequently presented face so that it was also more familiar. This manipulation was employed so that the resulting neural response would tap into a stored memory

representation. For Experiment 2, recently familiarized versus unfamiliar faces were presented with equal probability, and in Experiment 3 two unfamiliar faces were presented with equal probability.

Figure 2 illustrates the occipital P1-N2-P2 complex and Nc and LSW components recorded across experiments by Nelson and Salapatek (1986). The occipital components, which would now likely be called the P1, N290, and P400, did not differentiate between the conditions. However, both the central Nc (550-700 ms) and frontal LSW (850-1000 ms) were modulated by different conditions within the task. The Nc showed differences between familiar and unfamiliar stimuli regardless of familiarization, whereas the LSW only showed differences between the novel stimulus and the pre-exposed familiar stimulus. Based on these findings, Nelson and Salapatek (1986) hypothesized that the LSW indexed both recognition and the updating of working memory. Moreover, they also speculated that, despite differences in the latency and form of the components observed in infants, some commonalities between adult P300s and the infant LSW were apparent. Specifically, similar to adult reports (Donchin, 1981; Duncan-Johnson & Donchin, 1977), as the probability of an infrequent stimulus increased, component amplitudes also decreased. Moreover, both adult and infants exhibit similar topography, despite a low number of recording locations.

INSERT FIGURE 2 ABOUT HERE

The ground-breaking work by Nelson and Salapatek (1986) set the stage for over 30 years of infant research examining the Nc across a variety of tasks, condition manipulations, and ages (Ackles & Cook, 1998; deHaan & Nelson, 1997; 1999; Karrer & Ackles, 1987; Marinovic, Hoehl & Pauen, 2014; Nelson & Collins, 1991; Nelson, 1994; Pickron, Iyer, Fava & Scott, 2017; Reynolds, Guy, & Zhang, 2010; Reynolds & Richards, 2005; Richards, 2001) and LSW (de Haan & Nelson, 1999; de Haan, Johnson & Halit, 2003; Nelson, 1994; 1997; Pascalis et al., 1998;

Reynolds & Richards, 2017; Webb, Long & Nelson, 2005). However, whether there is a direct link between one of these components and the adult P300 is still debated.

4.2 Auditory paradigms. In parallel with studies using visual stimuli, Kurtzberg and her colleagues examined newborn and infant discrimination of auditory phonemes using a passive oddball task (Novak, Kurtzberg, Kreuzer, & Vaughan, 1989; for a review, see Kurtzberg, Vaughan, Courchesne, Friedman, Harter, & Putnam, 1984). Similar to studies in the visual domain, these authors reported two components, an Nc between 500-700 ms and a LSW between 1200-1400 ms that discriminated stimulus probability. Results from these studies, combined with work in the visual domain, suggested that the infant Nc and LSW were present across auditory and visual modalities and that both varied as a function of stimulus probability.

Very few studies have directly compared the P300 in infants and adults. The first investigation using the same task for all ages was not conducted until the early 1990's. McIsaac and Polich (1992) presented different auditory tones to 5- to 10-month-old infants and adults in the context of an auditory oddball task. In infants, the authors reported an ERP component peaking around 620 ms after stimulus onset that increased in amplitude from Fz to Cz and Pz. This wave was similar to the P300 component recorded in adults, but the peak was delayed relative to adults. Unlike the conclusions made by those examining ERPs in the visual modality, McIssac and Polich (1992) concluded that "the use of the P3 and other ERP components offers significant promise in providing a reliability and valid measure for assessing cognitive function in normal infants and especially those at risk for central nervous system disorders" (p. 125).

4.3 Summary and future directions. In sum, a "classic" or clear adult-like P300 has not been found in infants. Even when paradigms are consistent across ages, P300-like components are significantly delayed and may differ in topography and morphology. McIssac and Polich

(1992) provided the closest report of an adult-like auditory P300 in infants. However, no such report exists in the visual domain, though several infant ERP components exhibited P300-like characteristics, including distinguishing frequently presented and infrequently presented stimuli. Consistent with the development of the visual and auditory sensory systems, it is possible that the auditory P300 matures earlier than the visual P300, however, this question awaits examination in future research.

5. Does the P300 reflect similar cognitive processes in children and adults?

After it was established that a P300 could be recorded in children and adolescents, researchers began to investigate whether this component was influenced by factors similar to those reported in adults, including: (1) attention, (2) stimulus probability, (3) stimulus repetition, (4) the subjective importance of a stimulus, such as variations in assigned reward or monetary value, and (5) the amount of cognitive effort expended. In addition, studies explored whether, similar to adults, the P300 component was related to behavioral measures of cognitive ability.

Overall, studies have reported similarities between the above factors in children and adults. Attentional effects were similar, as both children and adults exhibited greater P300 amplitudes in response to "attend" compared to "ignore" conditions (e.g., Goodin et al., 1978). Stimulus probability effects were similar, as stimulus probability decreased, P300 amplitudes increased and latencies decreased (e.g., Ladish & Polich, 1989). Effects of stimulus repetition were similar, with decreased P300 amplitudes to repetition of novel, but not target, stimuli (e.g., Courchesne, 1979). P300 amplitudes also showed similar profiles across ages to subjective importance, such as rewards, with the greatest values eliciting the largest rewards (e.g., Hömberg, Grünewald, & Grünewald-Zuberbier, 1981). Processing demands, such as difficulty, were also shown to influence amplitude with more difficult tasks eliciting components with greater amplitudes (e.g.,

Friedman et al., 1978). Finally, P300 components in children were shown to correlate with behavior (e.g., Shelburne, 1973). For example, in individuals aged 5 to 87 years, P300 latencies in an auditory oddball task were shown to correlate with working memory ability as measured by digit span (Howard & Polich, 1985; Polich, Howard & Starr, 1983; Polich, 1992). Shorter latencies were associated with larger spans, even after controlling for age and head size (Howard & Polich, 1985; Polich, 1992).

6. The second striking report of developmental differences: ERPs to novel/unexpected stimuli

6.1 Visual paradigms. Despite the similarities between P300s in children and adults to frequent and infrequent *expected* stimuli, there are large differences across development in ERP components to infrequent yet *unexpected* stimuli. Figure 3 illustrates an example of these differences. In 1977 Courchesne examined P300s to visual stimuli in 6- to 8-year-old children and adults. Similar to previous studies, both frequent and infrequent letter stimuli were presented and participants were instructed to keep track of infrequent stimuli and disregard all other stimuli. P300/P3b ERPs were elicited to the infrequent target stimuli in children and adults, albeit at delayed latencies. However, Courchesne *also* presented equally infrequent but unexpected visual stimuli, such as quasi-random unrecognizable color patterns. These stimuli, called "novels," elicited different brain potentials in adults and children. At Fz, adults evidenced P300 (or P3a) waves, whereas children showed Nc and Pc waves. Based on this pattern of results, Courchesne (1977) suggested these differences reflected variations in the way children and adults spontaneously categorize events.

INSERT FIGURE 3 ABOUT HERE

In a subsequent study, Courchesne (1978) extended these findings by identifying that the transition from child- to adult-like P300/P3a components occurred in the mid-teens. Courchesne (1978) posited that this pattern of results reflected the development of a new neuro-cognitive system employed to process *novel* and perhaps unrecognizable events. However, once this system was established, it showed further development, similar to that observed for P300/P3b, as reflected by increases in speed of processing (Courchesne, 1978; 1979). Finally, he also speculated that the Nc may reflect the perception of events that were attention getting, but acknowledged it was unclear whether Nc disappeared with age because the neurocognitive processes were superseded by other systems or because they were simply obscured by changes in P300 waves morphology.

6.2 Visual vs. auditory paradigms. As illustrated in Figure 4, Courchesne (1983) went on to compare brain waves between children, adolescents and adults to novel, unexpected stimuli in *both* visual and auditory domains. Stimuli used in the visual paradigms, such as letters and colorful abstract patterns, are described above. Stimuli in the parallel auditory paradigms were words, such as "you" or "me", presented either frequently (.76) or infrequently (.12) and novels were 'bizarre never-heard-before sounds' that were presented infrequently (.12). ERPs to novel, unexpected stimuli changed substantially with age *and* differed between auditory and visual stimuli. In short, auditory novels elicited A/Pcz/300 (Auditory, Positive, maximal at Cz at 300 ms) and A/Ncz/800 (Auditory Negative maximal at Cz at 800 ms) components, but visual novels did not. Conversely, visual novels elicited the fronto-central P300/P3a component, whereas auditory novels did not. Although Nc and Pc were identified in both modalities, they differed in scalp distribution as both were more frontally distributed for auditory compared to visual paradigms. Taken together, these age- and modality-related differences led to the hypothesis that processing problems may be handled in different ways by the brain at various ages.

INSERT FIGURE 4 ABOUT HERE

6.3 Summary. Courchesne summarized his series of studies examining age- and modality-related differences in ERPs to multiple types of stimuli (1983) by arguing that many ERP components associated with cognitive processes are different in children and adults (although perhaps A/Pcz/300 is an exception). Further, he noted that these developmental differences were both quantitative and qualitative in nature. He also suggested that although the transition from 'child-like' to 'adult-like' components may appear to be gradual, the rate of change is not necessarily constant. For instance, components reach "maturity" at different ages; A/Pcz/300 appears to reach maturity in childhood, whereas P300/P3b reaches maturity in pre-adolescence/adolescence, and the visuo-central P300/P3a reaches maturity during young adulthood. In addition, some components were elicited by stimuli in only one modality, whereas others were elicited by both modalities. Finally, at all ages, different types of information elicit different patterns of ERPs. For example, in children, auditory targets elicit large P300/P3b, whereas auditory novels elicit small P300/P3bs but large A/Pcz/300 and A/Ncz/800 components. These conclusions spawned a wave of studies examining processing of novel stimuli.

7. Development of novelty processing and the P3a subcomponent

Results from Courchesne's early work on the processing of novel unexpected stimuli was consistent with research in adults suggesting the presence of two P300 components: A "traditional" P300 (P3b) associated with responding to infrequent target stimuli and a slightly earlier P300 (P3a) that was shorter in latency, more frontally distributed, associated with the relatively automatic processing of stimulus novelty (Snyder & Hillyard, 1976; Squires, Squires, & Hillyard, 1975). As described above, research on P300/P3b during development flourished and persisted throughout the 1990s and 2000s (e.g., Fuchigami et al., 1995; Oades, Dittmann-Balcar, & Zerbin, 1997;

Rozhkov, Sergeeva, & Soroko, 2009; Segalowitz & Davies, 2004; Stige, Fjell, Smith, Lindgren, & Walhovd, 2007; Thomas & Nelson, 1996; Yordanova & Kolev, 1997). In contrast, research on the development of P300/P3a has been sparse.

7.1 Auditory paradigms. Of the P300/P3a studies that exist, most have used auditory stimuli (Čeponiene et al., 2004; Fuchigami et al., 1995; Gumenyuk, Korzyukov, Alho, Escera, & Näätanen, 2004; Määttä, Pääkkönen, Saavalainen, & Partanen, 2005; Putkinen, Niinikuru, Lipsanen, Tervaniemi, & Huotilainen, 2012; Segalowitz & Davies, 2004). These studies have shown that P300/P3a to auditory stimuli can be elicited in children starting as early as 2 to 3 years of age using a variety of novel stimuli, and that latency of the auditory P300/P3a decreases with age and displays a more centrally dominant topography than in adults. Findings on age-related differences in P300/P3a amplitude are mixed (Čeponiene et al., 2004; Määttä et al., 2005), with some studies reporting no changes (e.g., Ceponienë et al., 2004), whereas others report decreases in amplitude as a function of age (e.g., Gumenyuk et al., 2004).

7.2 Visual paradigms. In contrast, only *one* study to date appears to have examined development of P300/P3a using visual stimuli in a 3-stimulus oddball task (Stige et al., 2007; but see Rojas-Benjumea, Sauqué-Poggio, Barriga-Paulino, Rodríguez-Martínez, & Gómez, 2015 who used a 2-stimulus task with visual stimuli). Stige et al. (2007) examined visual P3a and P3b in children (6–15 years) and adults. In this study, the standard stimulus was a small blue elliptical shape. The target stimulus was a larger blue elliptical shape. The novel stimulus, which the participant was told to ignore, was a large blue rectangle. Although this paradigm varied significantly from early work by Courchesne that used completely novel stimuli, research in adults suggested that such a manipulation yielded a similar novelty P3a component (e.g., Demiralp, Ademoglu, Comerchero, & Polich, 2001; Simons, Graham, Miles, & Chen, 2001). Contrary to

early findings by Courchesne (1978), in this study a P300/P3a was detected in children, and age-related differences were observed in both amplitude and topography but not latency. Specifically, P3a amplitude decreased with age and its topography was more fronto-central in younger compared to older children. Digit span was related to P3a, as well as P3b, in both children and adults, although these associations were noted to be weak. However, the variations in findings reported by Stige and colleagues (2007) and Courchesne (1978) are difficult to reconcile given that different quasi-novel stimuli were used to elicit the P3a. Further exploration of the development of visual P3a is clearly warranted.

8. Development of P3a vs. P3b subcomponents

Only a few studies have explicitly addressed the *relative* developmental trajectories of P3a versus P3b in either the auditory or visual domain. These suggest that the P3a matures earlier than P3b (Fuchigami et al., 1995; Stige et al., 2007), although not all studies report this difference (e.g., Rozhkov et al., 2009). The relative earlier development of P3a may reflect a greater reliance on 'automated' cognitive mechanisms that is more readily generated by immature frontal circuits as opposed to deeper processing associated with controlled attention (see Stige et al., 2007 for elaboration).

One study not only examined relative developmental trajectories of P3a and P3b, but did so in individuals ages 1-21 years (Fuchigami et al., 1995). This study is unique in that it attempted to address a methodological confound, namely that most studies in children and adults utilize instructions and require participants to respond to target stimuli, whereas studies in infants do not use instructions or require responses. To address this, a "passive" auditory oddball paradigm without instructions was used to examine the P300 component in individuals aged 1-21 years. In addition, an "active" or attend condition was also administered to individuals ages 4-21 years. A

P300-like component at Pz was generated in infants and in older participants, perhaps suggesting that P3a can be detected in infancy under certain circumstances. P300 latencies in the passive condition decreased between 1-12 years, and between 4-16 years in the active condition. Thus, the age at which P300 latency reached "adult levels" was earlier in the passive compared to the active condition, which suggests that task demands and the ability of the participant to achieve them may play a role. There was also greater variability in latencies and a greater difference between latencies for the active versus passive conditions in younger participants, suggesting greater within and between subject variability earlier in development, which can impact amplitude and latency measures as well.

9. Contemporary studies

The pioneering studies described above paved the way for modern day researchers in the field of human developmental cognitive electrophysiology. Contemporary studies have built on this foundational work by focusing on a variety of topics including: (1) P300-like components in infancy, (2) alteration of P300 in atypically developing or clinical groups, (3) relations between P300 and behavior, (4) P300 and individual differences, and (5) neural substrates associated with P300. Below we highlight a few studies in each of these domains.

9.1 P300-like components/ P300 precursors in infancy

Figure 5 shows the morphology and topographic distribution of several commonly recorded ERP components in infants. A review of the infant ERP literature to date suggests that the last 30 years of research has not produced a robust and reliable infant P300 across modalities. However, several infant ERP components are modulated by factors that have been shown to influence P300 in adults and children, including: attention, novelty, stimulus probability and working memory. Of these components, the frontal-central distributed Nc, the frontally and/or

temporally distributed Late Slow Wave, also previously called the Pc, Positive Slow Wave (PSW) or Negative Slow Wave (NSW), and the posterior P400 component have all been found to exhibit P300-like qualities. Each of these components may be "precursor" to the adult-P300 as they exhibit similar response properties as the adult-P300.

INSERT FIGURE 5 ABOUT HERE

9.1.1 Nc. Early studies suggested the Nc is sensitive to stimulus probability (Ackles & Cook, 1998; 2009; Courchesne et al., 1981; Karrer & Ackles, 1987; Karrer et al., 1995), is often greater during periods of increased attention (Reynolds & Richards, 2005; 2009; Richards, 2003; Webb et al., 2005), and is also larger in response to preferred stimuli, such as the mother's face (de Haan & Nelson, 1999; Snyder, Webb, & Nelson, 2002). Due to its similar properties, the Nc is a candidate precursor to the adult P300. In an elegant series of studies that incorporated measures of heart rate, ERP source localization, and behavioral measures of visual preference, the infant Nc was directly linked to orienting that occurs during periods of sustained attention (Reynolds & Richards, 2005; Reynolds, Courage & Richards, 2013; Reynolds, Guy, & Zhang, 2013; Reynolds & Richards, 2017; Richards, 2003; for review: Reynolds, Courage, & Richards, 2010), and has been consistently localized to the anterior cingulate and basomedial/basolateral prefrontal cortex (Reynolds & Richards, 2005; Reynolds et al., 2010). These anterior regions are somewhat consistent with previously proposed adult P3a neural generators in adults (Polich, 2012). In a recent investigation that followed infants from 6 to 9 months, the Nc discriminated frequently and infrequently presented novel object stimuli, but only after a learning period during which objects were paired with individual-level names (Pickron, Iyer, Fava & Scott, 2017). Thus, results from these investigations suggest that the Nc indexes attention and is sensitive to probability after a familiarization/learning period.

9.1.2 LSW. The infant LSW component begins approximately 800-1000 ms after stimulus onset, lasts about 1000 ms, and has been recorded over both frontal/anterior and temporal scalp locations. Following research described previously (Nelson & Salapatek, 1986), Nelson and Collins (1991) hypothesized that the infant LSW component varied depending on the extent to which stimuli have been fully encoded in memory, similar to the adult P300. A negative slow wave (NSW) was found to index novelty detection, a positive slow wave (PSW) was found to reflect updating of working memory for a partially encoded stimulus, and a return to baseline (i.e., no slow wave response) was observed when stimuli were fully encoded or not encoded at all. Nelson and Collins (1992) compared 4- and 8-month-old ERPs to (1) a frequently presented recently familiarized face, (2) an infrequently presented recently familiarized face, and (3) an infrequently presented novel/unfamiliar face (called a "three stimulus oddball task" similar to Nelson and Salapatek, 1986). Whereas 4-month-old infants did not appear to exhibit a LSW that distinguished between these three conditions, the 8-month old LSW distinguished the two familiarized faces from the novel face and showed a NSW to the novel stimuli and a return to baseline for the frequently and infrequently presented familiar faces. Unlike the P300, these findings suggest a link between the LSW and stimulus familiarity that is not sensitive to stimulus probability.

Similarly, de Haan and Nelson (1999) reported that the PSW component may reflect memory encoding of new stimuli or updating of known stimuli, and Nelson (1997) postulated that the PSW component was generated by mnemonic, temporal lobe, structures in the brain. This hypothesis was later supported by source localization findings that link the PSW source to right temporal regions (Reynolds & Richards, 2005). However, Reynolds and Richards (2005) localized the NSW to frontal regions, suggesting that although the timing of LSW components are similar,

two separate but possibly overlapping neural generators are likely. These results somewhat align with the hypothesized different neural generators that produce the P3a and P3b components in adults (Polich, 2012) and suggest that the LSW is sensitive to similar manipulations as the adult P300. More specifically, the NSW may be generated by anterior neural regions, similar to the P3a, and the PSW may be generated by temporal lobe structures, somewhat similar with the adult P3b.

9.1.3 P400. Finally, the P400 component has been primarily measured as an index of face processing (for review see: de Haan, Johnson, & Halit, 2003; Scott & Nelson, 2004). However, despite being recorded over posterior brain regions, source analyses of the infant P400 indicate anterior sources associated with attention (Guy, Zieber, & Richards, 2016; Barry-Anwar, Hadley & Scott, 2018). Guy and colleagues (2016) suggest that the early part of the P400 may arise from posterior perceptual regions whereas the sustained response after the initial rise is likely a result of attention and the positive expression of the Nc. The P400 has not been systematically examined as a P300 precursor, but the morphology, topography, and timing of the component is somewhat similar to the adult P3b and certainly warrants further investigation.

9.2 P300 and atypical developmental outcomes

Research examining the impact of atypical development on the P300 emerged at nearly the same time as the first reports that P300 components could be recorded in children. The earliest studies examined P300s with traditional oddball paradigms and documented variations in P300 amplitude and/or latency across a variety of atypical developmental groups (Prichep, Sutton & Hakerem, 1976; Satterfield & Braley, 1977; Grünewald et al., 1978).

Tables 2 and 3 summarize contemporary areas of P300 research with atypical populations and the direction of the effects on the P300 component. Over time, both the quantity and quality of studies examining atypical developmental outcomes using P300 has increased. Studies with the

strongest implications have built upon previous research in which the typical developmental trajectory of the P300 was well-characterized and utilized traditional auditory oddball paradigms, well-thought out control or comparison groups, and measures of behaviors/symptoms. A summary of findings across multiple atypical groups is beyond the scope of this paper; however, as summarized in Tables 1 and 2, variations in P300 amplitude, latency and topography have been noted across a wide variety of conditions.

INSERT TABLES 2 AND 3 ABOUT HERE

Conclusions from studies with special populations have added valuable insight into atypical development. First, ERP studies have helped address whether development is abnormal or simply delayed in some groups. For example, ERP research on attention-deficit hyperactivity disorder (ADHD) suggests multiple neural processing deficits contribute to this condition: abnormalities in P300 that become undetectable in adulthood, due to the resolution of a developmental delay in inhibitory brain processes, as well as abnormalities that persist across development, as reflected by persistent differences in contingent negative variation or CNV, which reflects other aspects of attentional processing (Doehnert, Brandeis, Imhof, Drechsler, & Steinhausen, 2010). Second, some ERP studies have used differences in P300 components to more accurately characterize the nature of the disorder or developmental outcome. For example, ERP research on autism suggests that differences arise in some experimental conditions, such as those that require active attention, but not others such as passive attention tasks (Courchesne et al., 1984). Moreover, the differences in the active condition were determined to be quantitative in nature (i.e., shifted in time), rather than qualitative (i.e., dissimilar components; Courchesne et al., 1984).

Some clinicians have suggested that because ERPs do not require a physical or verbal response, ERP paradigms, such as versions of the oddball task, may eventually be a useful tool in

clinical settings for selected pediatric populations, such as those whose expressive language and motor skills are notably impaired, such as cerebral palsy (Byrne, Hurley, Daly, & Cunningham, 2001), or non-responsive patients (Brinkman & Stauder, 2008). Regardless of whether children are capable of responding, ERPs may prove useful in measuring attention or lapses in attention in both typically and atypically developing children (e.g., Gumenyuk et al., 2001; 2004). Finally, ERPs may help disentangle cognitive markers of disorders such as autism spectrum disorders and ADHD as well as individual differences within disorders to further elucidate the basis of co-occurring diagnoses and guide clinical assessment (Tye et al., 2013). Exploring these avenues will be beneficial during the next 50 years of electrophysiological research.

9.3 P300 and behavior

Measures of P300 latency and amplitude have been shown to relate to specific and general measures of cognitive ability, including "real-world" measures of cognition, such as academic success. For example, as described above, shorter P300/P3b latency during auditory oddball tasks is related to faster reaction times and larger digit spans (Fuchigami et al., 1993; Polich et al., 1983; Polich et al., 1990). The P300 has also been related to school-aged children's performance on assessments of cognitive development, such as the Figural Intersection Test (Travis, 1998), Piagetian liquid conservation tasks (Stauder, Molenaar, & van der Molen, 1993), and both Stroop and memory assessments (Boucher, Bastien, Muckle, Saint-Amour, Jacobson, & Jacobson, 2010). Finally, in a sample of socioeconomically disadvantaged kindergarteners, Willner and colleagues (2015) found that greater P300/P3b target amplitudes were associated with more adaptive learning-related behaviors, suggesting educational applications for P300 research (Willner, Gatzke-Kopp, Bierman, Greenberg, & Segalowitz, 2015).

9.4 P300 and individual differences (gender, traits, states, and genetics)

Similar to studies linking P300 to individual differences in cognitive abilities, relations between the P300 and other traits (e.g., sex, shyness/sociability) and states (e.g., pubertal stage) have also been examined during development (Brumback, Arbel, Donchin, & Goldman, 2012; Sumich et al., 2012; Tang, Santesso, Segalowitz, & Schmidt, 2016). Brumback and colleagues (2012) examined the influence of age, sex, and pubertal development on the P300 during a visual oddball task in a sample of 99 8-13 year olds. Their results indicated that P300 latency and amplitude decreased as age and pubertal status increased in both males and females. This correlation is consistent with previous work suggesting developmental improvements in information processing with age (e.g., Fuchigami et al., 1993; Polich et al., 1983; Polich et al., 1992). However, girls also exhibited shorter P300 latencies and smaller P300 amplitudes, which the authors suggest should be considered in future studies (Brumback et al., 2012).

Studies also suggest that P300 amplitude is heritable and that common genetic factors may influence P300 parameters at multiple points in development (Burns & Polich, 1987; Carlson & Iacono, 2006; Van Baal, De Geus, & Boomsma, 1998;Van Beijsterveldt, van Baal, Molenaar, Boomsma, & de Geus, 2001). For example, one study reported that differences in the developmental course of P300 amplitude during adolescence were associated with a specific dopamine receptor (DRD2) polymorphism (Berman, Noble, Antolin, Sheen, Conner, & Ritchie, 2006). Studies such as this point to the possibility of genetic variation, particularly within the dopaminergic system, for understanding individual differences in the P300 component.

9.5 Neural sources associated with P300 in development

Despite many papers claiming that age-related differences in P300 reflect brain development, only a few have actually directly examined differences in the neural source(s) of P300 as a function of age. Overall, findings from these studies suggest the neural source(s) of the

P300 are not consistent across development; however, given the different paradigms and methods used across these studies, more research is needed on this topic.

One study used magnetoencephalography (MEG) to examine the source of P300 activity to target stimuli during a visual oddball paradigm. Source estimation was successfully localized to the vicinity of the thalamus and the cingulate gyrus in adults, but was less stable in children and appeared to be distributed in more anterior temporal regions (Horiguchi, Ohta, & Nishikawa, 2003). Another study used standardized low-resolution brain electromagnetic tomography (sLORETA) to analyze activity during a visual working memory task. Results again revealed differences between adults and children. However, in this study, anterior regions appeared more involved than posterior regions in adults compared to the opposite pattern in young children (Barriga-Paulino et al., 2015). Yet another study used time-frequency analyses to examine sources of change in the P300 component during an auditory oddball paradigm (Yordanova & Kolev, 1997). Specifically, this study examined latency of the maximal theta response, which is thought to be related to higher cognitive and associative brain processes in adults. Results suggested that the maximal theta response latency was shorter in children than adults. Additionally, within children, theta response latency was strongly associated with the latency of the P300/P3b component, suggesting that the developmental latency decrease in P300 may originate from a decrease in theta-related processes, and ultimately, a speeding of cognitive stimulus evaluation. In summary, although these three studies all report differences in neural sources of the P300 in adults and children, more work in this area is needed.

10. The power of a developmental perspective

Understanding the developmental profile of ERPs such as the P300 is not just important for developmentalists, but also for the field in general, as knowledge regarding development can

inform understanding of components in adults (Courchesne, 1983). For example, if two ERP components have different developmental trajectories, they likely have different neural generators as well. Such an effect has been observed in auditory and visual P300/P3bs, which follow different developmental time courses, and has added to accumulating evidence suggesting reliance on different neural generators (Courchesne, 1979; Courchesne, 1983; Courchesne, 1990; Thomas & Nelson, 1996).

However, developmental ERP work can also inform our understanding of cognitive development. For example, in the 1970s, it was widely held, based on work by Piaget, that cognitive development occurred in stages and that developmental change was qualitative. Findings from early P300 studies suggested developmental change could also be characterized as quantitative in nature. These ERP studies showed that the sequence of ERP components was similar across ages, suggesting that the order and relative timing of different stages of cognitive processing was consistent across development (Courchesne, 1983). Additionally, because ERPs do not rely on behavioral output but provide a direct index of central nervous system functioning, they have been used to uncover and dissociate the source(s) of developmental changes, such as performance changes due to cognitive development versus the development of motor coordination (Courchesne, 1983; Kurtzberg et al., 1984).

Despite the similarities in P300 components in children and adults, differences are detectable under some circumstances. These differences may shed light on variations in cognitive processing or neural representations that extend beyond simple variations in timing or speed of processing. Specifically, one study examining sequence effects on P300 reported that when target stimuli were preceded by a large number of standard stimuli, P300s were about twice as large, had significantly shorter latencies, a more widespread distribution, and an earlier positivity in the

frontal area (Kilpeläinen et al., 1999). These effects were especially true in children, suggesting that more resources may be required to update neural representations in children compared to adults. Another study reported that decreases in P300 amplitude between trial blocks, due to habituation, was greater in children compared to that in adolescents or adults (Pfueller et al., 2011). Stronger habituation effects in children may arise because they activate a larger neuronal pool from which unnecessary neurons can be excluded during short-term learning. In contrast, these neurons in adolescents may have already been eliminated as a consequence of pruning, thus reducing habituation effects. Finally, studies using single trial analyses of the P300 suggest the detection ratio shows significant differences between children and adults (Miyazaki et al., 1994). The most likely reason for this is that background EEG in childhood contains frequencies similar to those generating the P300, making it more difficult to discriminate the P300 signal from the background noise. However, the mechanism or consequences of such a finding remain unexplored.

Finally, researchers have begun to utilize the P300 to gain insight into (1) the neural processing of novel types of stimuli and (2) cognitive tasks known to show developmental changes. In terms of the former, studies have used the P300 to investigate processing of novel kinds of stimuli, such as 3-D auditory stimuli (Fuchigami et al., 2009) or novel experimental conditions, such as noisy versus non-noisy environments (Ubiali, Sanfins, Borges, Colella-Santos, 2016; Zenker & Barajas, 1999) during development. In terms of the latter, studies have created novel paradigms adapted from behavioral tasks used in infants or children that elicit a P300-like component. These include a cross-modal cueing paradigm to probe infants' understanding of predictive violations (Kouider et al., 2015), a novel predictor-target paradigm to examine the development of implicit statistical learning (Jost, Conway, Purdy, Walk & Hendricks, 2015), decision making tasks (e.g., Carlson, Zayas, & Guthormsen, 2009), face processing tasks (Dai et

al., 2014), sustained attention and prediction tasks (Thillay et al., 2015), spatial cueing of attention (Flores, Gomez, & Meneres, 2010), response preparation (Killikelly & Szűcs, 2013), and emotion processing tasks (Anokhin, Golosheykin, & Heath, 2010; Kujawa, Klein & Proudfit, 2013).

11. Conclusions

The last 50 years have yielded an impressive amount of information regarding the development of the P300. Although, a simple summary of developmental findings in typically developing groups is not currently possible, some consistencies begin to emerge when results are grouped according to (1) the subcomponent recorded, (2) the sensory modality probed (3) paradigms utilized and (4) the age ranges included (see Table 1).

P3b components recorded from children during auditory tasks with 2 stimuli appear to reflect similar cognitive processes as P3bs recorded in adults from about 5 years of age onward (van Dinteren et al., 2014) and possibly earlier given the similar auditory P300 findings reported in infants (McIsaac & Polich, 1992). However, with age, there are notable decreases in latency and increases in amplitude that persist until the mid-20s. Within the visual domain, fewer studies have explored developmental differences in P3b. Findings that do exist suggest that this component can also be detected during childhood and that latencies decrease with age in a manner similar to auditory P3bs. However, in contrast to findings in auditory P3b studies, amplitude of P3b in visual paradigms appear to decrease with age. In both auditory and visual domains, the cognitive or neural source underlying age-related differences in P3b remains unclear, but studies suggest differences in these components are related to behavioral responses reflecting delayed and immature information processing and working memory capacity in younger age groups (Howard & Polich, 1985; Polich, 1992).

In contrast to the relative similarities between P3bs in children and adults, there are large differences across development in the P3a component generated by novel stimuli (Courchesne, 1978). The auditory P3a can be elicited in children using 3-stimulus paradigms starting as early as 2 to 3 years of age, however, latency of this component decreases with age and exhibits a more centrally dominant topography than in adults (Fuchigami et al., 1995). Findings regarding developmental differences in P3a amplitude during auditory 3-stimulus paradigms are mixed. Very few studies have examined P3a in the visual domain (Stige et al., 2007). Those that have been conducted also seem to suggest that once the component can be detected, it shows age-related decreases in amplitude and differences in topography, but more research is needed.

In infants, summarizing research on the P300 or its subcomponents is complicated by dramatic differences in timing and morphology of the ERP response. Moreover, paradigms used in infant research often differ dramatically from those used in children and adults. Despite these differences, there is some evidence that a delayed P300 can be detected in auditory oddball paradigms (McIsaac & Polich, 1992), but the same is not true in visual domain. Instead, within the visual domain, several infant ERP components, such as the Nc, LSW and posterior P400, appear to exhibit P300-like characteristics, including distinguishing frequently presented and infrequently presented stimuli.

12. Remaining questions for the next 50 years

In the previous sections, we pointed out several areas of inquiry that would benefit from continued exploration. These include: (1) the hypothesis by van Dinteren et al. (2014) that latency and amplitude index different aspects of brain maturation, (2) the search of an infant P300 and/or infant precursors to adult-like P300 components, (3) the development of P3a, particularly in the visual domain, (4) differences between P3a in auditory and visual modalities across development,

(5) improving clinical utility of developmental P300 studies, and (6) more research on the neural generators of P300 during development.

In addition, the infant and child ERP literature is in need of large scale studies using similar methods and study designs. The field is plagued by small sample sizes and wide variations in recording montage, reference, and data collection and processing procedures (Table 1). Moreover, very little is known about how ERPs change within participants across age or how both within- and between-subject variability impacts the latency and amplitude of infant ERP components. Many authors have previously interpreted both amplitude and latency differences between developmental populations and adults as reflecting underlying neural differences in myelination or synaptic integrity. However, it is also possible that decreased amplitudes or latencies in infants and children simply reflect increased within- and between-subject variability. One study has examined the contribution of variability within subjects over the course of a single recording session and found individual differences in the number of trials an infant completes in an ERP session were associated with differences in the amplitude and latency of the Nc (Snyder et al., 2002).

Another methodological decision that contributes to variability in developmental ERP studies is grouping broad ranges of ages together, such as 5-10 months or 8-10 years. Due to increased variability between subjects, these groupings may result in less prominent (smaller amplitude) ERP components, increased latency of components, and a more diffuse topographic distribution. Moving forward it will be important for developmental researchers to examine these factors empirically and strive toward increasing the internal consistency of voltage measurements and the distribution of these components across time and the scalp.

Finally, when age-related differences are observed in components such as the P300, sources of these effects should be systematically probed. For example, effects of age and performance and are often confounded and efforts should be made to tease these apart. Similarly, oscillations at different frequencies may contribute to the observed effects in the time domain; it would be worthwhile to examine these across development. The use of multi-method approaches to combine ERP with fMRI or MEG to explore neural sources of change should be pursued as well. Research examining specific neural sources contributing to observed differences in P300 components will shed additional light on mechanisms underlying change. These suggestions are just a few of the challenges that can be addressed in the *next* 50 years of P300 research.

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Footnotes

[1]Many different terms have been used in the literature to identify this component. For the sake of simplicity, in this paper, P300 will be used in this paper to refer to any P3-like component. When possible or appropriate, we will also try to clarify whether this was thought to be a P3a- or P3b-component.

[2]Not all studies showed latency decreases across age, especially if they used narrow age ranges. For example, Friedman, Vaughan, and Erlenmeyer-Kimling (1981) studied children between 12 and 17 years using a visual Continuous Performance Task. Although this study elicited P300 (P3b) responses, no latency differences were observed. Similarly, Friedman et al. (1981) used auditory oddball stimulus change task in 11-18 year olds and showed no systematic age effects on P300 (P3b).

[3]See their paper for discussion of why amplitude matures earlier than latency.

Table 1

Examples of studies in typically developing cross-sectional samples reporting age-related differences in P300.

Modality	**Paradigm**	**Stimuli**	**Ages**	**n**	**Time Window**	**Mean or max amp-litude**	**Leads analyzed**	**Developmental differences in latency**	**Developmental differences in amplitude**	**Developmental differences in topography**	**Reference**
auditory	2-stimulus oddball	standard tones = 500 Hz; targets = 1000 Hz; ratio 82.4-17.6	4-95y (review); 6-87y	2811 (review of 75 studies); 1572	250-500 ms	mean	Pz	P3b ↓ until ~22-25y, ↑ in later adulthood	P3b ↑ until ~16-21y, ↓ in later adulthood	n/a	van Dinteren et al., 2014
auditory	3-stimulus oddball	.8, 1.4, 2.0 kHz tones; ratio 70-15-15	8-22y	44	240-540 ms	mean	F7, F3, Fz, F4, F8, C3, Cz, C4, P3 Pz, P4, T3, T4, T5, T6	P300 ↓	P300 ↑	compared to other groups, the youngest group had lowest P300 amplitude in frontal regions and highest at posterior regions	Oades, Dittmann-Balcar, & Zerbin 1997

auditory	3-stimulus oddball	target = high-pitched tone; novel = 300 Hz of tone gliding; ratio 78-11-11	7-17y and 19-25y	77	324 ms for P3a; 526 ms for P3b	max	29 electrode sites, none below the scalp line	not reported	less variation in amplitude with age for P3a	P3b in younger children was similar to adults topographically, with larger posterior amplitudes, whereas P3a only emerged as adult-like (larger frontal amplitudes) around age 13	Segalowitz & Davies, 2004 - a preliminary data analysis
auditory	3-stimulus oddball	standard = /ka/; target= /ta/; novel = salient clicks, chirps, other syllables, etc.; ratio 80-10-10	9-13y	11	150-280 ms, 280-420 ms	mean centered on peak	F3, Fz, F4, C3, Cz, C4, P3, Pz, P4, Oz, mastoids	comparable to adults	no age-related analyses	looked at early and late P3a; early P3a showed ↑ amplitude in frontal and central regions than in parietal regions, and late P3a ↑ centrally than frontally or parietally; eP3a ↑ than lP3a in frontal regions, but ↓ than lP3a in parietal regions	Cepioniene et al 2004

visual	2- and 3-stimulus oddball	standard = "A"; target = "B"; novel = any other letter OR quasi-random color pattern (2 conditions); ratio 88-12 for 2-stimulus; ratio 76-12-12 for 3-stimulus	6-36y	60	maximum peak at Pz between 300-340ms and 1200 ms in 2-stim	max	Pz, Fz, Cz with results maximal at Pz for all ages in 2-stim condition; maximal at Fz and Cz in adults in novel 3-stim condition	P3a ↓ by 300 ms in adults in 2-stimulus paradigm; ↓ in 3-stimulus paradigm	P3a ↓ in 2-stim	n/a	Courchesne, 1978
visual	2-stimulus oddball; infrequent stimuli were novel	cartoon images; standard = picture of bee; target = any other novel cartoon image; ratio 75-25	6-26y	127	P3a: 340-380 ms in adults, 490-530 ms in pre-adolescents; P3b: 380-500ms in adults, 530-700 ms in pre-adolescents	mean	Fp1, Fpz, Fp2, F7, F3, Fz, F4, F8, FC5, FC1, FC2, FC6, M1, T7, C3, Cz, C4, T8, M2, CP5, CP1, CP2, CP6, P7, P3, Pz, P4, P8, POz, O1, Oz, O2, mastoids; P3a: F3, Fz F4, FC1, FC2;	P3b ↓, P3a no difference	P3b ↓	P3a more frontal than parietal in adults; P3b primarily in posterior regions that becomes more posterior with age	Rojas-Benjumea, Saque-Poggio, Barriga-Paulino, Rodriguez-Martinez, & Gomez 2015

							P3b: P3, Pz, P4, POz, O1, Oz, O2				
visual	3-stimulus oddball with shapes	standard = blue ellipse; target = larger blue ellipse; deviant = blue rectangle; ratio 80-10-10	6.8-15.8y; 20.0-88.8y	155	250-650ms	P300 determined by max; P3a mean for distractors; P3b mean for targets	Fz, Cz, Pz, Oz	P3b ↓ in older children compared to younger children; P3a ↑, no change for P3b in full life-span sample	P3a and P3b ↓ in older children compared to younger, especially in frontal leads; P3a ↓ and P3b nonlinear ↓ for full life-span sample	P3a more fronto-central in younger compared to older children	Stige et al., 2007
visual	3-stimulus oddball with faces and photos	standard = female face with neutral expression; target = different female face with neutral expression; novel = non-face images like animals, food, scenery, abstract patterns,	8y and 20-30y	29	220-690 ms	max	Fz, Cz, Pz, Fpl, Fp2, F7, F8, F3, F4, C3, C4, T3, T4, P3, P4, and mastoids	↓ for adults than children for both P3a and P3b at midline leads, especially in frontal regions	↓ at lateral leads for P3a	↑ amplitude in frontal regions compared to posterior regions for P3b in both adults and children	Thomas & Nelson 1996

		etc.; ratio 60-20-20									

y=years of age; ms=milliseconds; eP3a=early P3a; lP3a=late P3a

Table 2

Examples of P300 studies using the oddball paradigm in atypical developmental samples.

Atypical Group	Modality of oddball paradigm	Study Group(s)	Age(s)	Reference	P300 finding(s) compared to typicals[unless otherwise noted]
ADHD	auditory	ADHD	7-14yrs	Janssen et al., 2016	↓ amplitude for targets, esp. in frontal and temporoparietal left hemisphere
	auditory	ADHD	6-13yrs	Johnstone et al., 1996	↓ amplitude in posterior, ↑ amplitude in frontal regions
	auditory	ADHD	6-12yrs	Senderecka et al., 2012	↓ difference in amplitude between targets and standards
	auditory	ADHD, LD, CD, LD+ADHD	8-18+yrs	Frank et al., 1998	no age differences; ↑ latency, ↓ amplitude, ↓ amplitude difference between targets and non-targets for LD+ADHD
	auditory	LD, LD+ADHD	~7-14yrs	Frank et al., 1994	↓ amplitude, ↑ latency for both clinical groups
	visual	ADHD, ADD, reading disorder	8-11yrs (males)	Holcomb et al., 1985	↓ amplitude in all clinical groups
Alcoholism/ Risk for alcoholism	auditory	familial alcoholism risk*	8-18yrs	Steinhauer et al., 1993	↓ amplitude for higher-risk children, esp. for older males
	auditory	familial alcoholism risk, paternal delinquency	8yrs	Viana-Wackermann et al., 2007	↓ amplitude in frontal regions only when paternal delinquency co-occurred with paternal alcoholism
	visual	familial alcoholism risk, paternal psychopathy	17-23yrs, longitudinal	Carlson et al., 2008	↓ amplitude and less change over time
	visual	familial alcoholism risk	8-18+yrs, longitudinal	Hill et al., 2002	↓ amplitude related to high risk of psychopathy/alcoholism in boys, and in girls with childhood diagnosis
	visual	familial alcoholism risk, parental externalizing disorders	17-20yrs, longitudinal	Iacono et al., 2002	↓ amplitude with ↑ paternal risk for disorders predicted development of substance use disorders at 20
	visual	familial alcoholism risk, externalizing disorders	11yrs and 17yrs	Iacono et al., 2003	↓ amplitude related to parental alcoholism and childhood disruptive disorders/antisocial behavior
	visual	familial alcoholism risk	18y	Perlman et al., 2009	↓ amplitude predicted alcoholism risk independent of adolescent alcohol use
	visual	familial alcoholism risk	14-17yrs	Rangaswamy et al., 2007	↓ amplitude in parietal regions

Autism	auditory	ASD	13-21yrs	Courchesne et al., 1984	↓ amplitude to targets and novels
	auditory	ASD	13-25yrs	Courchesne et al., 1985	↓ amplitude to visual and auditory novels and to auditory targets
	auditory	ASD	8-20yrs	Magliaro et al., 2010	absence of P300 more common
	auditory, visual	ASD, RDLD	8-14yrs	Lincoln et al., 1993	↓ amplitude for ASD group, not for RDLD group
	visual	ASD	6-14yrs	Pritchard et al., 1987	no typical increase in task vs. no task conditions
	visual	ASD	9-27yrs	Sokhadze et al., 2009	↑ latency to novels, esp. in right hemisphere
	visual	ASD	5-15yrs	Kemner et al., 1999	↓ or ↑ in amplitude depending on electrode location
Childhood Epilepsy	auditory	childhood epilepsy	8-14yrs	Boscariol et al., 2015	no difference in amplitude or latency
	auditory	childhood epilepsy, TLE	9-14yrs	Casali et al., 2016	↑ latency for children with TLE only
	auditory	childhood epilepsy	5-20yrs	Konishi et al., 1995	↑ latency, less typical latency ↓ with age
	auditory	childhood epilepsy	5-16yrs	Naganuma et al., 1997	↑ latency, some differences between epilepsy sub-types
	auditory	febrile seizures	6-15yrs	Tsai et al., 2015	↓ amplitude, ↑ latency for children who developed afebrile seizures after febrile seizures
	auditory	infantile spasm	5-11mo	Fosi et al., 2017	↓ amplitude
Environmental exposure	auditory	cannabis use	8-18+yrs, longitudinal	Hill et al., 2016	↓ amplitude trajectories over time
	auditory	insecticide poisoning	14-56yrs	Dassanayake et al., 2008	↑ latency even 6mo. after recovery
	visual	dioxin exposure	7-18yrs, longitudinal	Ten Tusscher et al., 2014	no typical controls; ↑ latency, ↑ amplitude for higher levels of dioxin exposure than lower
Externalizing disorders	auditory	CD	~14-17yrs	Kim et al., 2001	↓ amplitude, ↑ latency
	auditory	schizophrenia, siblings of schizophrenia patients, ADHD	14-21yrs	Groom et al., 2008	↓ amplitude for schizophrenia and sibling groups, but not for ADHD group
	visual	BPD	14-19yrs (females)	Houston et al., 2005	no typical ↓ in amplitude with ↑ in age
	visual	BPD, CD, CD+BPD	14-19yrs	Ceballos et al., 2006	no typical age-related ↓ in amplitude for CD/CD+BPD groups only
	visual	CD, parental alcohol use	15-20yrs	Bauer et al., 1999	↓ amplitude with more conduct problems; regions with ↓ amplitude vary based on age
Internalizing	auditory	anxiety	10-14yrs	Hogan et al., 2007	no difference in amplitude or latency

disorders	auditory	anxiety, BI	13-16yrs	Reeb-Sutherland et al., 2009	BI participants with ↑ amplitude more likely to to have anxiety disorders
	auditory	depression	14-20yrs (females)	Houston et al., 2004	did not show typical amplitude reduction for harder condition vs. easier
	auditory	depression	10-12yrs	Lepistö et al., 2004	↑ amplitude
	visual	depression	14-20yrs (females)	Houston et al., 2003	↓ amplitude
Language	auditory	dyslexia	7-18yrs	Maciejewska et al., 2014	↑ latency; P300 frequently absent esp. in younger children; no typical ↓ latency with age
	auditory	dyslexia	9-12yrs	Oliviera et al., 2013	no difference in amplitude or latency
	auditory	phonological disorders	8-11yrs	Leite et al., 2014	↑ latency initially, latency ↓ after speech therapy
	auditory	SLI	4-6yrs	Shaheen et al., 2011	↑ latency, ↓ amplitude
	auditory	SLI	14-18yrs	Weber-Fox et al., 2010	↓ amplitude
Pervasive developmental disorders	auditory	Downs syndrome	7-15yrs	Medeiros Kazan et al., 2016	no difference in amplitude or latency
	auditory, visual	PDD	8-13, 15-24yrs	Hoeksma et al., 2006	↓ amplitude for younger group, but not older, in auditory and visual conditions
	visual	ASD, MCDD, ADD, dyslexia, PDD	5-15y	Kemner et al., 1999	no typical controls; ↓ amplitude for MCDD in non-frontal regions compared to most groups; ↓ central/occipital amplitude in ASD than MCDD children
Physical health	auditory	CPB, transcatheter closure	6-13yrs	Guan et al., 2011	↑ latency
	auditory	malnutrition	7-12yrs	Parente De Almeida et al., 2013	↑ latency
	auditory	prenatal polychlorinated biphenyl exposure; breastfed and formula-fed	9yrs	Vreugdenhill et al., 2004	↑ latency with higher exposure; ↓ latency with longer breastfeeding
	auditory	pre-term infants	40 gestational wks-15mos, longitudinal	Fellman et al., 2004	no difference from newborns at 40 gestational wks; mixed results after
	auditory, mechanical	migraine	10-15yrs	Zohsel et al., 2008	↑ amplitude, ↓ latency

Sensory problems	auditory	middle ear infections	22-26mos	Haapala et al., 2016	↓ difference in amplitude between frontal and central/parietal regions
	auditory	sensorineural hearing loss	11-42yrs	Reis et al., 2015	no typical controls; ↓ or absent P300 in patients who primarly use signed over spoken language

ADD = attention deficit disorder; ADHD = attention deficit hyperactivity disorder; ASD = autism spectrum disorder; BI = behavioral inhibition; BP = behavioral inhibition; BPD = borderline personality disorder; CD = conduct disorder; LD = learning disorder; MCDD = multiple complex developmental disorder; PDD = pervasive developmental disorder; RDLD = receptive developmental language disorder; SLI = specific language impairment; TLE = temporal lobe epilepsy

*This term encompasses parental alcoholism and substance abuse as well as genetic risk for alcoholism.

Table 3

Examples of P300 studies using non-oddball paradigms in atypical developmental samples.

Atypical Group	**Modality**	**Paradigm(s)**	**Study Group(s)**	**Age(s)**	**Reference**	**P300 finding(s) compared to typicals[unless otherwise noted]**
ADHD	auditory	listening	hyperactivity	6-12yrs (males)	Satterfield et al., 1977	↓ amplitude in younger children, ↑ in older children
	auditory	selective attention/vigilance	hyperactivity	12-14yrs	Loiselle et al., 1980	↓ amplitude and latencies
	auditory	single/double click guessing	hyperkinesis	8-11yrs	Prichep et al., 1976	↓ amplitude in uncertainty condition, no difference in certain condition
	auditory	stop signal task	ADHD	9-11yrs (males)	Liotti et al., 2005	↓ amplitude on successful trials
	visual	cued CPT and nogo	ADHD	9-13yrs	Doehnert et al., 2010	↓ GFP in CPT and NoGo
	visual	cued CPT and nogo	ADHD	10-21yrs, longitudinal	Doehnert et al., 2013	↓ GFP in CPT, no difference in developmental trajectories
	visual	warned reaction time	ADD	11yrs	Grünewald et al., 1978	↑ latencies
Alcoholism/ Risk for alcoholism	visual	go-nogo	offspring of alcoholics	18-25yrs	Kamarajan et al., 2005	↓ amplitude to nogo trials
	visual	go-nogo	offspring of alcoholics	18-25yrs	Kamarajan et al., 2006	↓ delta, theta, alpha to nogo trials, ↓ delta and theta to go trials
Autism	visual	face recognition	ASD	6-10yrs (males)	Gunji et al., 2013	no typical controls
	visual	face/name recognition	ASD	18-24yrs	Cygan et al., 2014	showed different pattern of amplitude changes across conditions
	visual	flanker-CPT-OX	ASD, ADHD	8-13yrs (males)	Tye et al., 2014	no P300 difference for ASD-only participants; ↓ amplitude for ADHD and ASD+ADHD
	visual	statistical learning	ASD	2-6yrs	Jeste et al., 2015	↓ amplitude
Childhood Epilepsy	visual	working memory (1- and 2-back)	childhood epilepsy	6-16yrs	Myatchin et al., 2011	↑ amplitude, esp. in frontal regions
Environmental exposures	visual	continuous recognition memory	early institutional care	9-11yrs	Güler et al., 2012	↓ amplitude difference between old and new items

	visual	emotional face processing	maltreatment	7-11yrs	Pollak et al., 1997	↑ amplitude to angry targets over happy
	visual	go-nogo	early institutional care	8yrs	McDermott et al., 2012	↓ amplitude to nogo trials
Externalizing disorders	auditory	contingent negative variation	Psychopathy, criminal behavior	14-16yrs (males)	Raine et al., 1990	↓ latencies predicted later criminal record
	auditory	receptive vocabulary	risk for psychosis, schizophrenia	10-13yrs	Murphy et al., 2012	↓ amplitude on difficult trials
	auditory	task-switching	CD	14-19yrs	Bauer et al., 2003	no typical age-related ↑ in amplitude
	visual	single-outcome gambling task	CD, parental alcohol use	13-17yrs (males)	Gao et al., 2016	↓ amplitude
	visual	Sternberg-type working memory	risk for schizophrenia	11-13yrs	Rawdon et al., 2013	↓ amplitude in posterior regions
Internalizing disorders	auditory	go-nogo	anxiety	10-11yrs	Éismont et al., 2009	↓ amplitude
	visual, auditory	mother's speech/face	physical abuse, anxiety	7-12yrs	Shackman et al., 2007	↑ amplitude to angry faces and voices in abused children
	visual	cued CPT and nogo	anxiety	11yrs	Baving et al., 2004	no P300 difference
	visual	picture presentation	phobia	8-12yrs	Leutgeb et al., 2010	↑ amplitude
	visual	spatial cuing task for facial affect	children of depressed mothers	9-17yrs	Gibb et al., 2016	↓ amplitude to sad faces
Language	auditory	incongruous sentence pitch	dyslexia	9-12yrs	Santos et al., 2007	no typical P300 in response to pitch incongruity before training; P300 resembled controls after training
	visual, auditory	working memory (1- and 2-back)	SLI	11-14yrs	Evans et al., 2011	↓ amplitude for 2-back auditory and both visual conditions
	visual	habituation	familial dyslexia risk	5-8yrs, longitudinal	Regtvoort et al., 2006	↑ latency at 5yrs predicted both poor readers and at-risk normal readers at 8 yrs
	visual	rhyme discrimination	reading disability	~7-8yrs	Molfese et al., 2013	↓ amplitude
Pervasive developmental disorders	visual	face recognition	PDD	8-13yrs	Gunji et al., 2009	no P300 differences
	visual, auditory	decision task with probes	PDD	4-17yrs (males)	Hoeksma et al., 2004	↓ amplitude
Physical health	visual	go-nogo	obesity	10yrs	Reyes et al., 2015	↓ amplitude
	visual	old/new word recognition	iron deficiency	10yrs	Congdon et al., 2012	↓ amplitude

	visual	old/new word recognition (food)	anorexia	22 yrs	Nikendei et al., 2012	↓ amplitude, especially at parietal midline
	visual	Sternberg-type working memory	iron deficiency	8-10yrs	Otero et al., 2008	↓ amplitude; no differences after iron supplements
Sensory problems	auditory	pitch-change detection	amusia	10-13yrs	Mignault et al., 2012	↓ amplitude
	auditory	sensory registration	sensory processing disorder	5-10yrs	Gavin et al., 2011	↓ amplitude

ADD = attention deficit disorder; ADHD = attention deficit hyperactivity disorder; ASD = autism spectrum disorder; CD = conduct disorder; CPT = continuous performance task; GFP = global field power; PDD = pervasive developmental disorder

Figure Captions

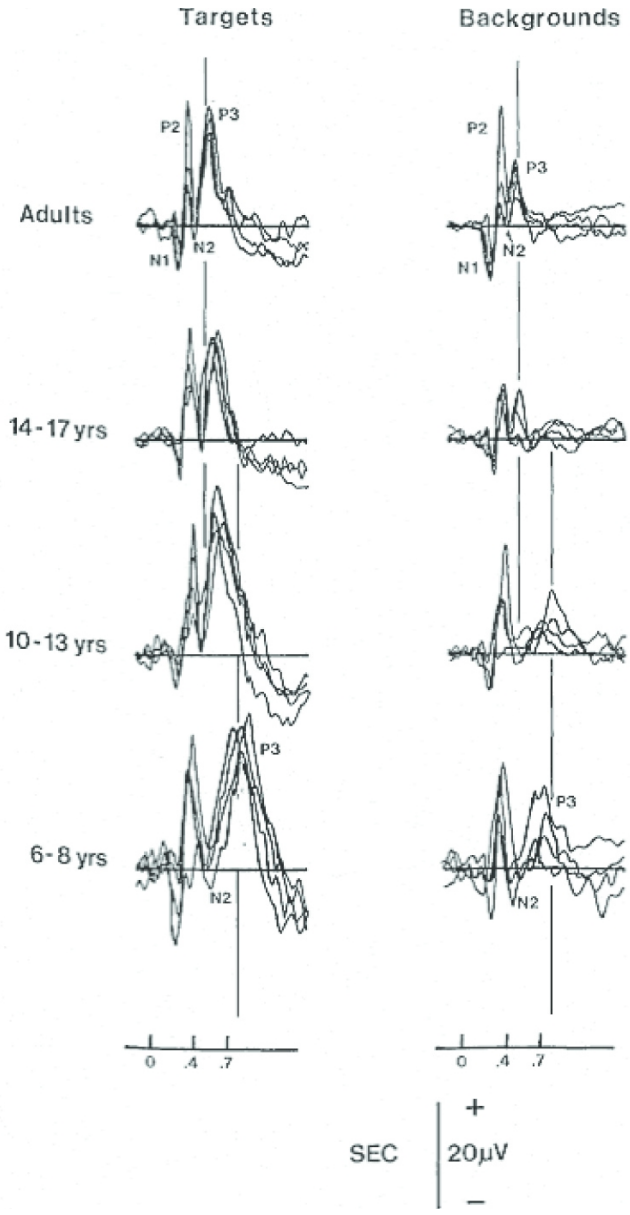
Figure 1. P300s can be elicited in school-aged children using oddball paradigms. However, latency to peak of the P300 decreases with age between 7-25 years of age. Panel A illustrates similarities in the morphology of P300 responses across ages. Panel B illustrates age-related decreases in latency of P300 to targets (but not P2 or N1). Panel C illustrates decreases in P300 latency during childhood (top) and modest increases in P300 amplitude (bottom) from 6-87 years of age. Adapted from Courchesne, 1978 and van Dinteren et al. 2014.

Figure 2. Adapted from from Nelson and Salapatek (1986). These figures were among the first reported infant ERP studies using a modified oddball paradigm. Panel A shows the P400 component at Oz. Panel B shows the Nc and LSW at Cz.

Figure 3. Differences in ERPs to novel, unexpected infrequent events in children and adults. At Fz (left panel), adults evidenced P300 (or P3a) waves, whereas children showed Nc and Pc waves; from Courchesne (1978).

Figure 4. ERPs to infrequent, unexpected stimuli (i.e., novels) in auditory and visual domains for 5 different age groups; from Courchesne (1983).

Figure 5: Adapted with permission from Reynolds Guy and Zhang (2011). This image shows the morphology and topographic distribution of the infant Nc, PSW, P400 and NSW. Waveforms are averaged across electrodes within each group and depict response to novel (bold line) and recently familiarized (thin line) object stimuli in 6- to 7.5 month olds infants.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Backgrounds
Adults
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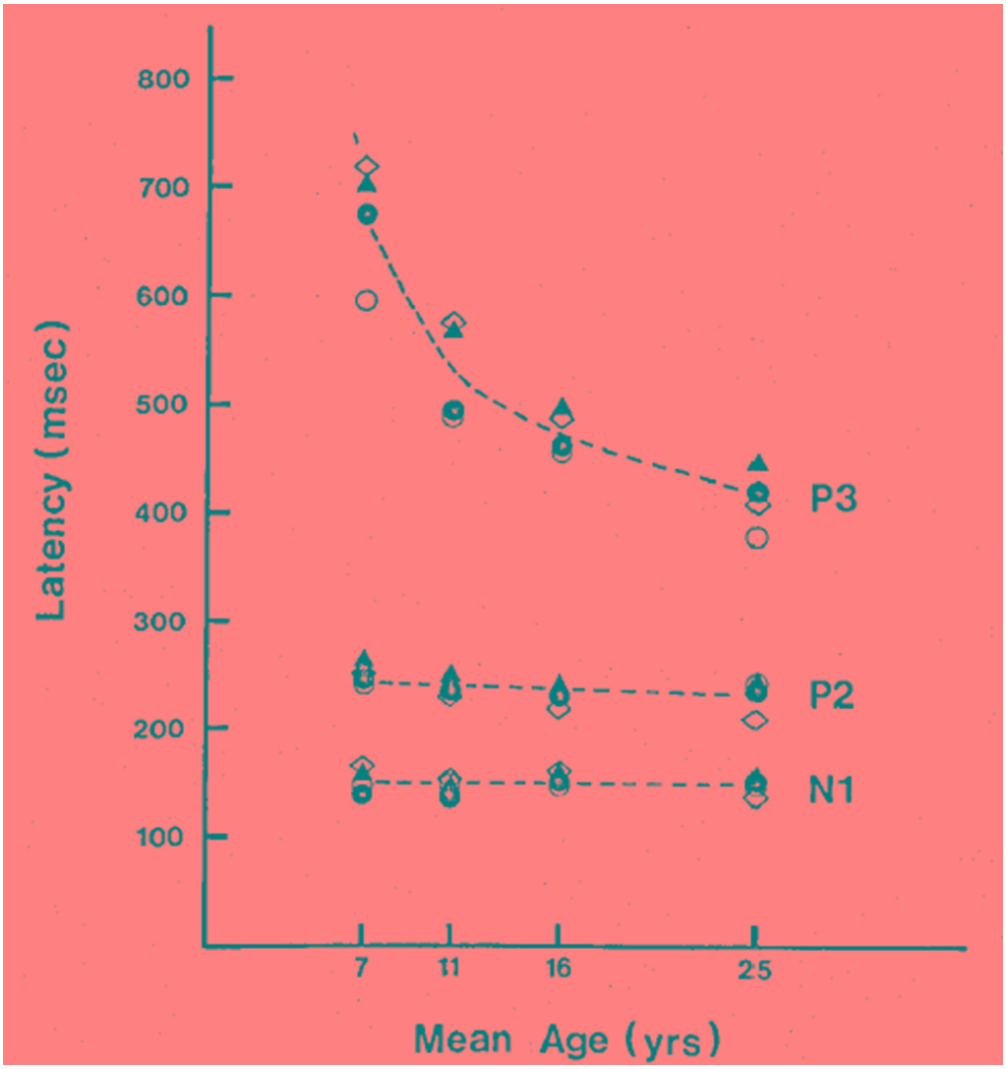
10-13 yrs
6-8 yrs
P2
P3
N1
N2
0
.4
.7
SEC
+
20μV
−



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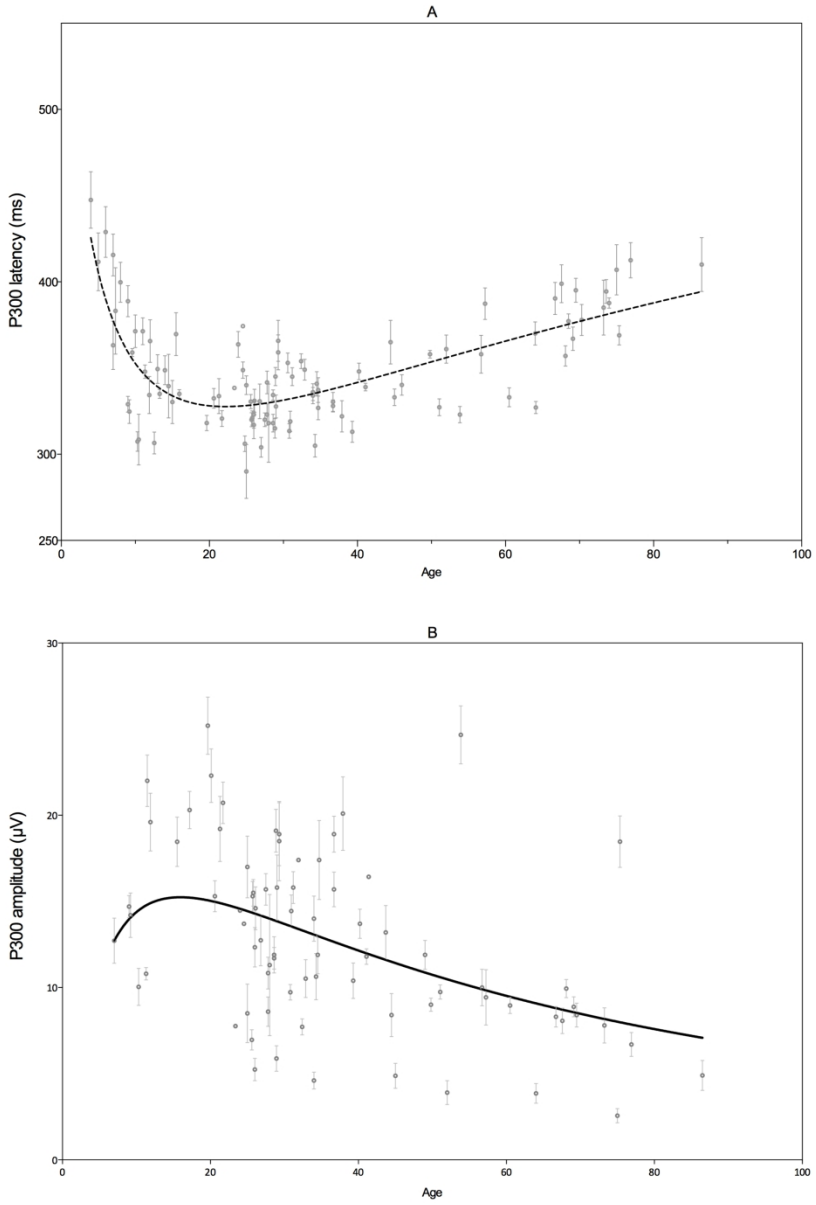

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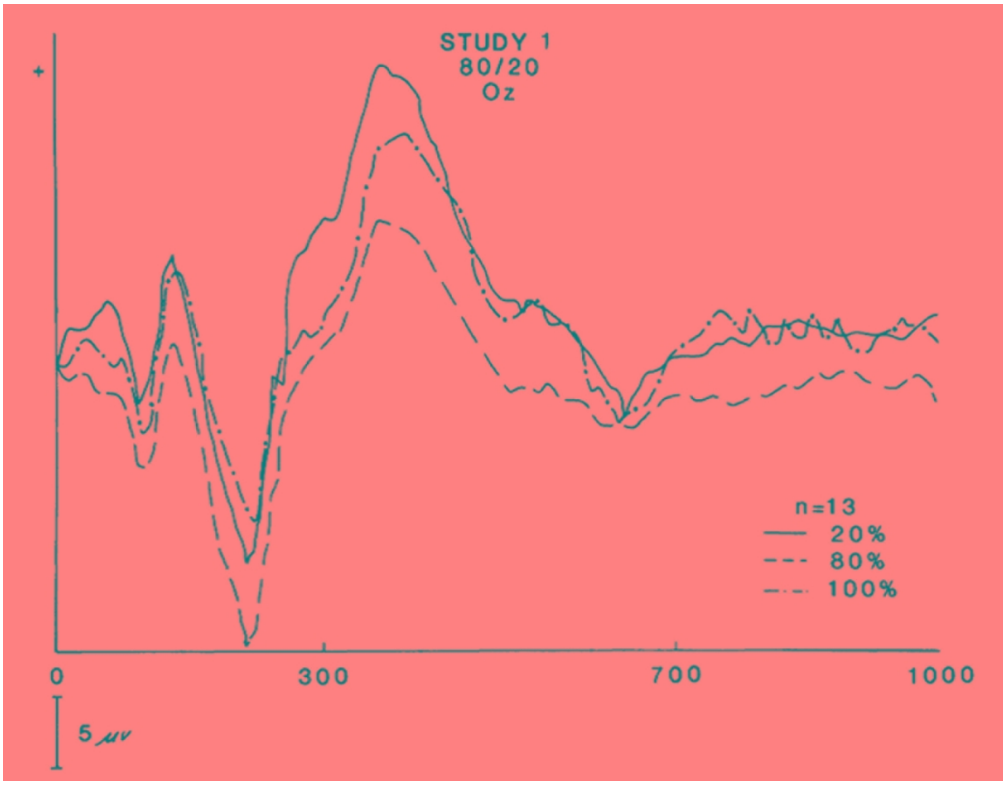

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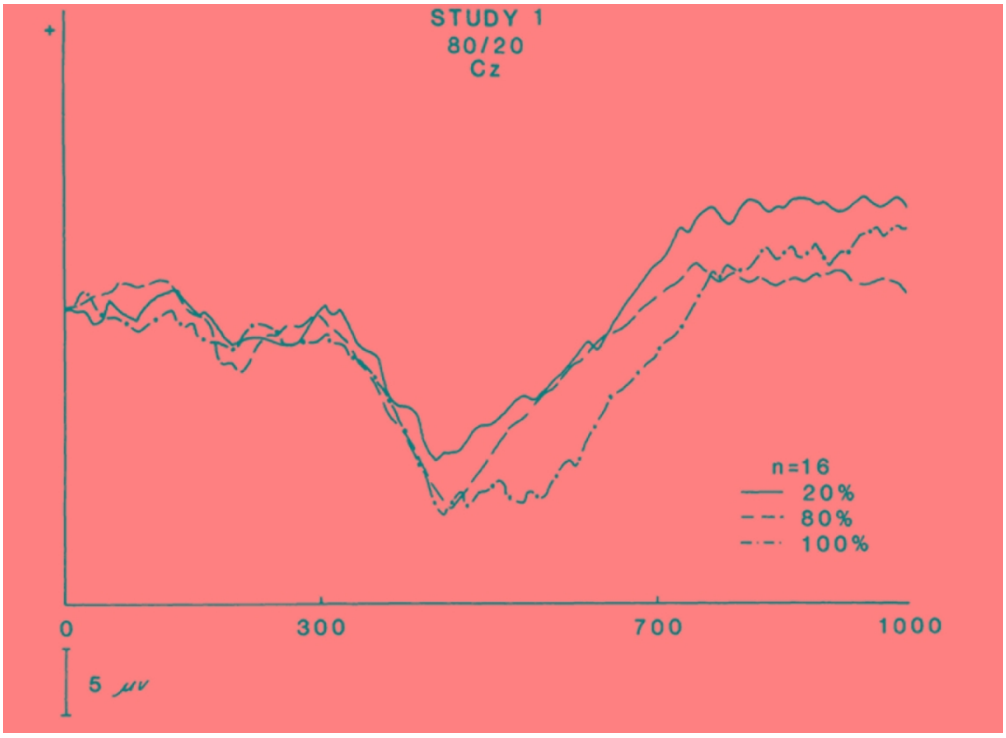

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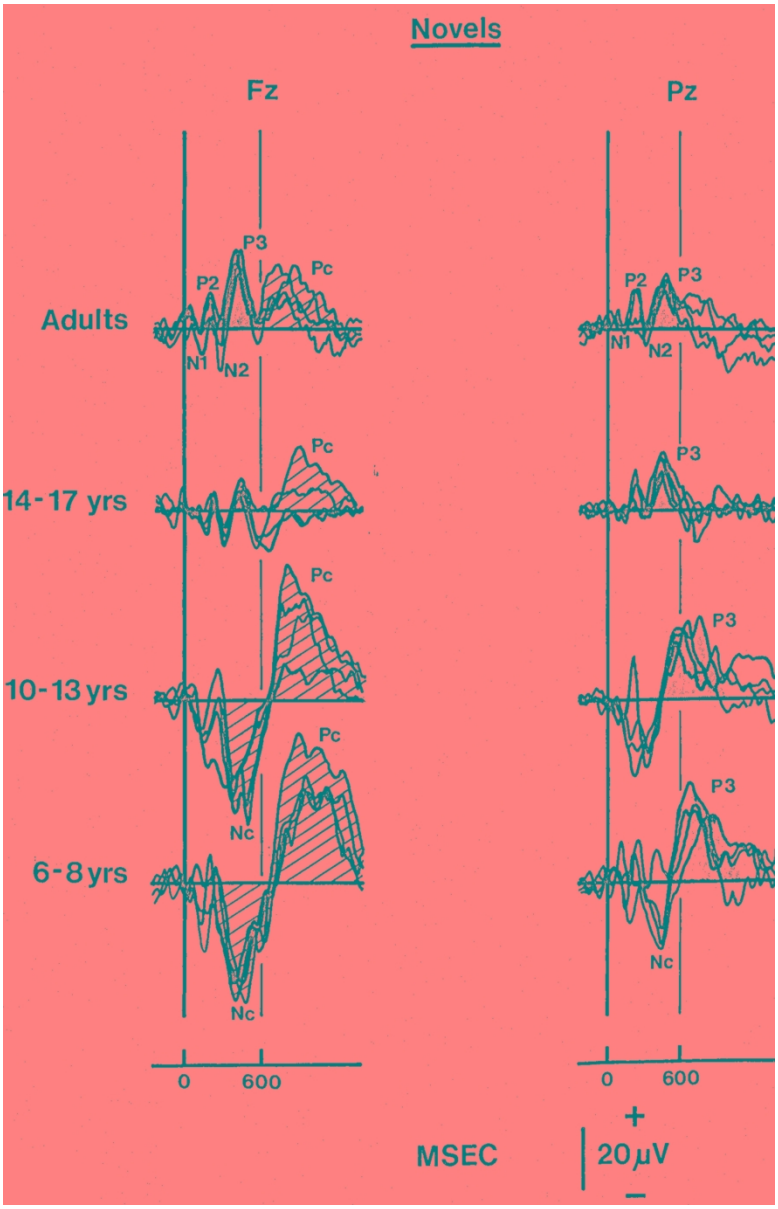

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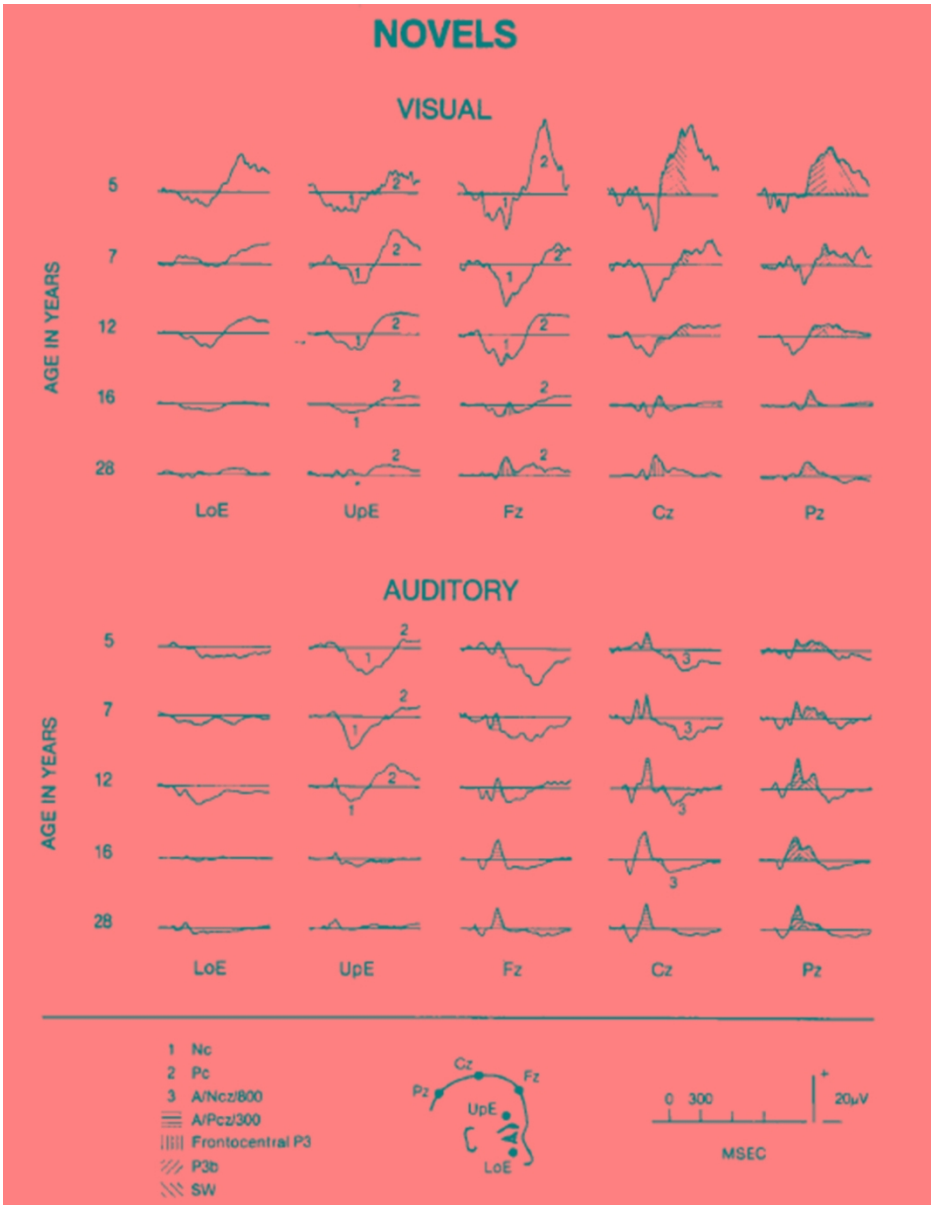

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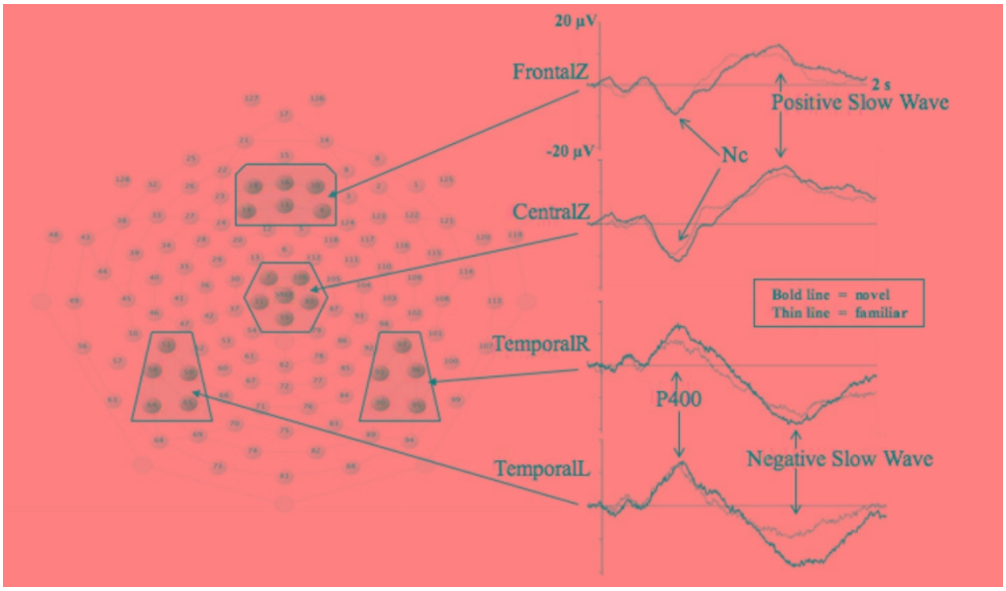
20 μV
FrontalZ
2 s
Positive Slow Wave
-20 μV
Nc
CentralZ
Bold line = novel
Thin line = familiar
TemporalR
P400
Negative Slow Wave
TemporalL

Impact statement

This paper is the first to provide an overview of P300 research from infancy through adolescence. Given the vast amount of research on P300 during typical and atypical development, this paper will serve as a useful summary of previous work and guide for future investigations. It includes a brief historical review of seminal studies and a summary of the most striking findings from developmental research. Contemporary questions are described and suggestions for future research are highlighted.