HABITUATION AND THE DYANMIC ENCODING OF NOVELTY IN NEWBORN INFANTS: AN ERP STUDY

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Full-term neonates are capable of discriminating speech sounds and habituating to repeated auditory stimuli as soon as they are born. Differences in the electrophysiological waveform of neonates' response is interpreted as an index of their ability to discriminate speech sounds. In addition, the decrement in response amplitude to a repeated stimulus reflects habituation. However, little research examines the relationship of these measures to each other in early infancy.

Event-related potential (ERPs) were recorded from 35 full-term neonates in response to two different test paradigms, consonant discrimination and habituation/novelty detection. In response to the consonant discrimination task, neonates significantly discriminated natural speech sounds with /b/-/g/ and /b/-/d/ contrasts. For the habituation task, trial-by-trial analysis demonstrated that neonates habituate to a repeated sound quickly, showing amplitude attenuation over the first ten experimental trials. At the introduction of a novel stimulus, neonatal electrophysiological response amplitude recovered, demonstrating novelty detection.

Individual differences in the electrophysiological response to these two paradigms were compared to assess the relationship between speech sound discrimination and habituation/novelty detection in the first few days of life. Habituation speed, speech

sound discrimination, and response variability were estimated for each individual. A set of multilevel models indicated that each of these between-subjects predictors helped to describe the electrophysiological response to the novelty detection task. A model that includes all of these measures as predictors best characterized full-term neonatal electrophysiological responses. In addition, relationships between individual differences in speech sound discrimination, habituation, novelty detection, and response variability were described. Results indicated that some individual differences in the electrophysiological response map onto a general index of neonatal health / maturity. This research sheds light on the etiology of neonatal neurocognition and provides support for the validity of neonatal ERPs as predictive indicators of later development.

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CHAPTER 1: INTRODUCTION

For over 35 years, researchers have investigated how neonates discriminate auditory stimuli (Molfese, Fonaryova-Key, Maguire, Dove, & Molfese, 2005; Molfese & Molfese, 1979). The neural network for auditory processing is functional at birth, and differences in the ERP waveform morphology in the neonate's responses to speech sounds reflect their speech sound discrimination abilities. Speech sound discrimination skills are of particular interest to researchers as it is essential for the development of speech and language (Streri, Hevia, Izard, & Coubart, 2013). In addition, speech sound discrimination is predictive of risk for developmental disorders such as dyslexia (e.g. Leppänen et al., 2012), as well as projecting a range of normal abilities such as reading skill (e.g. Tsao, Liu, & Kuhl, 2004). Genetic information related to parental reading ability or family history of reading disability may influence speech sound discrimination at birth (e.g. Guttorm, Leppänen, Hämäläinen, Eklund, & Lyytinen, 2010).

In addition, research has investigated neonatal habituation to a repeated stimulus for over 50 years (e.g. Bridger, 1961) as it provides a window into neuropsychological and cognitive functioning in early infancy. As a neonate becomes familiar with a stimulus, the magnitude of response to that stimulus tends to decrease over repeated exposures, a process described as habituation. Based on the stimulus-comparator theory (Sokolov, 1963b; Kavšek, 2013), habituation is thought to index encoding of perceptual information. A large field of research shows infant habituation to predict later developmental outcomes including intelligence and information processing (e.g. Bornstein & Benasich, 1986; Kavšek, 2004). Therefore, habituation represents a functional adaptation to the environment, which is related to later learning outcomes.

Brain-imaging techniques such as event-related potentials (ERP) permit the examination of the ongoing patterns of activity, and are ideal for the measurement of neonatal cognitive function including speech sound discrimination and habituation. ERPs are a portion of the ongoing scalp recorded electroencephalograph (EEG) activity that is time-locked to the onset of a stimulus. ERP methods are optimal for neonatal populations, as ERPs are safe, painless, and do not require a behavioral response (Johnson et al., 2001; Picton & Taylor, 2007; Wolfe & Bell, 2007). EEG and ERP provide temporally precise information on a millisecond time scale, which allows for the examination of dynamic trial-by-trial changes in neural responses over time (Csibra, Kushnerenko, & Grossmann, 2008). Meaningful changes in the morphology of infant ERPs may occur from moment-to-moment or trial-to-trial as the infant encodes a repeating stimulus within a session.

In addition, ERPs recorded from neonates are robust predictors of later language and cognitive developmental outcomes (Fellman et al., 2004; Molfese, 2000, Molfese & Molfese, 1985, Molfese, Molfese, & Modgline, 2001), as well as the development of learning disabilities and other cognitive impairments (Guttorm et al., 2010; Leppänen et al., 2012; Molfese, 2000). Therefore, ERPs provide a precise and robust method to assess neonatal mental processes. Electrophysiological methods may hold the key to a better understanding of the mechanism and mental processes underlying habituation on a micro time scale in neonates. However, a relatively small pool of research utilizes electrophysiological or neuroimaging methods to examine the neural mechanisms that underlie habituation processes in neonates.

Statement of the Problem

Approximately one in six children in the United States is diagnosed with some form of developmental disability, and the incidence of developmental disability diagnoses is increasing (Boyle et al., 2011). A growing field of literature demonstrates that some brain measures assessed at birth relate to later developmental outcomes (e.g. Fellman et al., 2004). However, much is still unknown about the mechanisms of neonatal cognition in healthy neonates. Therefore, interpretation of indicators of risk for later developmental disabilities is difficult. There is a critical need to identify indicators of risk as early as possible in order to detect maladaptive brain processing before it manifests via later developmental or intellectual disability. Successful identification of infants soon after birth who may be at risk for developmental disabilities requires a more nuanced understanding of the neonatal brain.

Several disparate fields of brain imaging research indicate predictive relationships between electrophysiological and/or neuroimaging measures in infancy and later developmental outcomes. In particular, a large field of research notes the predictive ability of speech sound discrimination tasks at birth, which relate to subsequent language disorders and reading difficulty later in development. Other investigators of cognitive measures in infancy such as habituation, novelty detection, and response variability note that these are also predictive of cognitive performance and information processing later in development. However, it is currently unclear how these measures of neonatal neurocognition relate to each other. In addition, it is unknown whether electrophysiological measures in early infancy map onto a single index of health / maturity, or whether there are distinct neural response profiles at birth which may relate

to differentiable developmental outcomes or perhaps predict specific developmental disorders. It is possible that many measures of brain functioning at birth map onto to a single construct of brain 'maturity' in early infancy.

In conclusion, speech sound discrimination, habituation, novelty detection, and response variability in the neonatal period are each predictive of later developmental outcomes. However, there is little research examining the relationship of these measures to each other in early infancy. More research is needed to elucidate the nature of neonatal ERPs as measures and whether or not individual differences in speech sound discrimination, habituation, novelty detection, and response variability all map onto a single index of cognitive 'maturity' soon after birth.

Research Question

This dissertation aims to assess measures of the neonatal electrophysiological response, and describe the relationship between four measures of individual difference in electrophysiological responses in healthy neonates. I will investigate healthy full-term neonates' electrophysiological responses to auditory tokens in relation to speech sound discrimination, habituation, novelty detection, and response variability. Together, these four measures represent a profile of individual differences that may relate to the maturity or health of the neonatal brain. These measures are selected because each are shown to be related to indices of maturity and health in developmental populations. Also, longitudinal research shows that each are predictive of later developmental outcomes of language and/or learning. This dissertation will address three primary aims. First, I will identify the neural correlates of habituation and novelty detection in the neonatal ERP response.

Second, I will develop a model to characterize the relationship between within-subject predictors of ERP response to the novelty detection task, and between-subjects predictors of habituation speed, speech sound discrimination and response variability. Finally, I will characterize patterns of relationship between between-subjects estimates of Novelty Detection, Habituation Speed, Speech Sound Discrimination, and Response Variability.

Definition of Terms

I provide the following definitions to ensure continuity throughout the study:

Habituation: decrements in the magnitude of response with stimulus repetition, or repetition attenuation.

Mental Representation: residual trace of a stimulus that persists beyond the duration of the sensory input (Haith, 1997).

Neurocognition: cognitive functions linked to activation of the neural substrate

Novelty detection: increase in magnitude of ERP response related to the detection of a stimulus change.

Response variability: amount of variance in response magnitude across experimental trials, measured within-subject.

Speech sound discrimination: difference in magnitude or latency of response to stimuli that differ on acoustic properties characteristic of human speech.

Organization of the Remainder of the Study

Chapter 1 presented an introduction, statement of the problem, research aims, and definitions of terms to be used in this study. Next, Chapter 2 will present a

comprehensive review of the the background literature relevant to the research aims outlined above. Chapter 2 begins by describing the functional neural network for auditory processing at birth, in order to establish justification for using an auditory task with neonates. I also provide insight into the underlying neural activations plausibly responsible for the neonatal response to each task. Next, an overview of the literature examines speech sound discrimination as measured by ERP, and describes how speech sound discrimination in early infancy is related to developmental outcomes later in life. Next, I present literature examining mechanisms of habituation and novelty detection, followed by literature specifically utilizing electrophysiology and neuroimaging to investigate habituation and novelty detection. I discuss how measures of habituation and novelty detection are related to later developmental outcomes. Finally, Chapter 2 concludes with a discussion of response variability, and outlines how response variability in early infancy may relate to later developmental outcomes.

Chapter 3 outlines the aims and specific hypotheses of this study. In addition, I describe the methodology for participant selection, materials, data collection procedures, and data processing.

The analytic rationale and results of analyses are presented in Chapter 4, for each of the three aims. A summary of findings, as well as a discussion of the results in light of previous research, alternative hypotheses, and limitations is presented in Chapter 5. This study concludes with tables and figures illustrating the results.

In conclusion, speech sound discrimination, habituation, novelty detection, and response variability can each be measured using ERPs, and are shown to sensitively predict later developmental language and learning outcomes. This study aims to describe

the relationship between four measures of individual difference in the electrophysiological response of healthy neonates. Future implications of this research include contribution to the basic scientific understanding of neonatal neurocognition. Information about the relationship between electrophysiological measures soon after birth may serve as a blueprint for guiding successful strategies for the identification of and intervention with neonates who may be at risk for language or learning disabilities later in life. Understanding the relationships between neurocognitive measures in early infancy will inform future research with the long-term goal of providing timely identification and effective intervention for infants who may be at risk for language or learning disabilities.

CHAPTER 2: BACKGROUND

Auditory Discrimination

Human language processing begins even before birth, supported by an emerging network of neural circuits responsible for auditory perception (Eggermont, 1985). Although research has investigated the neural systems of language since the time of Broca and Wernicke (Binder et al., 1997), the functional neuroanatomical specification of speech sound perception remains highly complex, difficult to characterize, and replete with paradoxical research evidence (Hickok & Poeppel, 2007). However, it is essential to understand the underlying neural foundation of auditory discrimination in order to properly interpret the results of auditory ERP studies with neonates. The interpolation of cortical sources from scalp recorded ERP can be difficult, especially for very young infants with highly variable neuroanatomical structure (Nunez, 1990; Reynolds & Richards, 2009). In addition, structural MRI is cost and time prohibitive, and not plausible for healthy neonates within 1-3 days of birth. Although this study cannot propose direct measurement of cortical sources of neonatal ERPs, a body of extant literature points to the continuity of the neural mechanisms of auditory processing throughout the lifespan (e.g. Dehaene-Lambertz, 2000). Therefore, the interpretation of infant auditory ERP may be informed by the known functional mechanisms of auditory processing in adults.

Generally, it is agreed that regions of the superior temporal sulcus, transverse temporal gyrus, arcuate fasciculus, planum temporale, and posterior-inferior frontal regions are all cooperatively involved in language processing, both in infancy and adulthood (Belin, Zatorre, Lafaille, Ahad, & Pike, 2000; Dubois et al., 2009; Leroy et al.,

2011). Functional neuroimaging studies, both Magnetic Resonance Imaging (MRI) and ERP source analyses, show a correlation between these auditory processing neural network streams throughout infancy, measured between 2.6 – 16.3 weeks old, and in adulthood (Dehaene-Lambertz, 2000; Leroy et al., 2011). However, there are significant maturational changes that occur in the connectivity, myelination, and lateralization of functional brain activity between infancy and adulthood (Eggermont, 1985; Perani et al., 2011). Neonatal auditory ERP research must take into account differences in evoked potential latency and scalp distribution specific to the developing neonatal auditory system.

Bilateral temporal regions are connected to the inferior frontal regions where auditory and sensorimotor information are integrated for speech production in adults (Hickok & Poeppel, 2007). Although frontal regions of the brain are shown to have protracted development compared to other primary cortices (Sowell et al., 2003), research on speech perception in infants supports a functional role of the frontal lobe in neonatal speech perception (Leroy et al., 2011). Leroy and colleagues (2011) find greater maturational indices for inferior frontal sulci and planum temporale compared to temporal regions such as the superior temporal sulcus. The relative maturity of these regions lends support to a functionally complex network of language processing regions, even during early infancy. This evidence of frontal lobe activation to speech perception in neonates may help direct the interpretation of underlying neural mechanisms.

In addition, contrary to the popular assumption of left-hemisphere dominance for all language-related tasks, evidence suggests bilateral neural activation (Hickok, 2009). This bilateral activation may be particularly pronounced early in development. Leroy and

colleagues (2011) recorded T2 weighted MRI on sleeping neonates, and calculated a maturation index based on grey matter density. They report greater maturation in the right superior temporal sulcus compared to the left, which follows an age-related right-to-left pattern of maturational development. Another neonatal fMRI study shows that the network of activation to native-language speech in 2-day-olds is quite similar, but more bilaterally activated, compared to the language network in older children and adults (Perani et al., 2011). Specifically, the auditory cortices (bilateral transverse temporal gyri, superior temporal gyri, and planum temporale) and the hippocampus demonstrated greater activation during speech processing as compared to silence in 2-day-old neonates (Perani et al., 2011). In addition, 2-month-old infants show greater activation to speech as compared to music in the bilateral planum temporale (Dehaene-Lambertz et al., 2010). These networks align with the networks of activation for adults partaking in similar language-listening tasks (Hickok, 2009). Thus, language processing in infancy and adulthood may have similar neural bases (Dehaene-Lambertz & Gliga, 2004), perhaps with greater bilateral activation.

The consistency of auditory networks across development may enhance the ability to interpret plausible cortical sources for neonatal auditory ERP recorded at the scalp, even without direct measurement of source interpolation. However, neonatal auditory ERPs are likely to look dissimilar to adult ERPs in several ways. First, auditory networks may be more bilaterally activated in neonates. Research indicates that left-lateralization of language processing may be a result of specialization which occurs with experience (Perani et al., 2011). Second, neonatal auditory ERPs may have longer latencies and less well-defined component peaks than adults (Kushnerenko et al., 2002a; Wunderlich,

Cone-Wesson, & Shepherd, 2006). These maturational ERP differences may be attributed to age-related increases in myelination and processing speeds (Eggermont, 1985). Interpretation of auditory ERPs in neonates should take into account these maturational differences in the appearance of ERP waveforms.

Neonatal Speech Sound Discrimination

Although still immature, the neonatal brain is capable of differentiating complex auditory contrasts. Differential responding (whether behavioral or physiological) to two different stimuli is interpreted to indicate that the neonate is capable of detecting the sensory differences between the stimuli. EEG, MEG, and NIRS studies indicate that neonates are able to discriminate pitch change (Alho, Sainio, Sajaniemi, Reinikainen, & Näätänen, 1990), vowel sound and voice intonation (Kujala et al., 2004), consonant sounds (Molfese, Burger-Judisch, & Hans, 1991), temporal modulations in non-speech sounds (Telkemeyer et al., 2009), and sound frequency and duration (Ceponiene et al., 2002), among others (see Näätänen, Tervaniemi, Sussman, Paavilainen, & Winkler, 2001 for a review). Differences in brain responses to speech sounds are thought to reflect auditory discrimination abilities, and indicate successful sensory perception, as well as some differential activation of the neural substrate in response to differences in the auditory features of the stimuli.

Two primary methods of stimulus presentation are used to examine auditory discrimination. First, the mismatched negativity (MMN) paradigm utilizes a frequent (or standard) stimulus paired with an infrequent (or deviant) stimulus to assess pre-attentive change detection in sensory memory (Ceponiene et al., 2002; Näätänen, 1990; 2001).

However, an alternative explanation of the MMN posits a frequency-based refractory response that may or may not involve an additional memory component (May & Tiitinen, 2010). Second, programmatic research demonstrates that equiprobable stimulus presentation paradigms are a well-validated method for assessing speech sound discrimination in adults (e.g. Molfese, 1978; 1980), children (e.g. Key, Molfese, O'Brien, & Gozal, 2009; Molfese & Molfese, 1988), and neonates (Molfese & Molfese, 1979; 1997). In addition, equiprobable paradigms may be advantageous for neonatal populations because they require fewer stimulus presentations in order to detect discrimination effects (Key & Yoder, 2103).

Speech sound discrimination, whether equiprobable or MMN, provides evidence for discriminative cognitive responses at the earliest developmental time points. Many ERP studies demonstrate neonates' ability to discriminate speech sounds or tones within the first few days of birth (Guttorm et al., 2005; Guttorm et al., 2010; Molfese & Molfese, 1985, 1997; Molfese, Molfese, & Espy, 1999; Thomas, Shucard, Shucard, & Campos, 1989). Other studies demonstrate similar discriminatory abilities in preterm infants as early as 30-35 weeks post-conceptual age (Cheour-Luhtanen et al., 1996), and as young as 29 weeks gestational age (Mahmoudzadeha et al., 2013).

ERPs to speech sound discrimination tasks are found to be associated with the maturational state of neonates. In general, with increasing infant age, ERP components tend to decrease in latency and increase in amplitude (e.g. Choudhury & Benasich, 2010). This association between waveform morphology and age may indicate that certain waveform patterns, such as longer-than-average latencies and smaller-than-average amplitudes, may serve as an indicator of cognitive immaturity.

Previous research also finds a relationship between ERP amplitude and other health indices in neonates such as gestational age, post-conceptual age, post-natal age, and birth weight (Guzzetta, 2011). For example, Fellman and colleagues (2004) find smaller amplitude peaks for preterm infants who were small for gestational age compared to preterms who were appropriate weight for gestational age. In addition, Therien, Worwa, Mattia, and deRegnier (2005) find that preterm infants perform poorly on a voice discrimination task compared to full-term infants, even at comparable post-conceptual ages. Key, Lambert, Aschner, and Maitre (2012) find a positive relationship between speech sound discrimination and gestational age, as well as with post-natal age for preterm infants. However, this study also found that gestational age interacts with post-natal age such that young gestational age (less than 30 weeks) is not associated with an increase in speech sound discrimination with increasing post-natal age (Key et al., 2012). Key and colleagues (2012) find that both gestational age and post-natal age are important factors in the maturation of the neonatal brain's speech processing abilities, both independently and in interaction with each other. In addition, by 12 months of age, a MMN response occurred only for full-term infants, and not for small- or appropriate-weight preterm infants, indicating less-mature ERP discrimination for preterm infants, with additional effects of low birth-weight that persists over the first year of life (Fellman et al., 2004).Together, these results suggest that speech sound discrimination ERPs in the neonatal period relate to measures of neonatal health and maturity, even when measured at comparable post-conceptual ages.

These maturity-related differences in ERPs to auditory discrimination tasks are similar to the differences in results seen in term infants tested with both easy and difficult

sound discrimination tasks (Kushnerenko, Ceponiene, Balan, Fellman, & Näätänen, 2002b). When comparing results from two different studies, one of full-term infants completing easy and difficult tasks (Kushnerenko et al., 2002b), and the other of preterm infants (Therien et al., 2004), discriminatory ERPs recorded from full-term infants during a difficult task appear less mature, more akin to the preterm infants of the previous study (Therien et al., 2004). The developmental changes in ERP morphology might be best characterized as continuous changes in speed and efficiency, modulated by the relative difficulty of the task, rather than mechanistic changes in the underlying functional neural networks with increasing age.

Speech Sound Discrimination Predicts Developmental Outcomes

ERPs recorded to speech sound discrimination tasks are related to various developmental disorders in adulthood including dyslexia (Guttorm, Leppänen, Richardson, & Lyytinen, 2001; Molfese, 2000; Stoodley, Hill, Stein, & Bishop, 2006), autism (Bomba & Pang, 2004; Ceponiene et al., 2003; Ferri et al., 2003; Whitehouse & Bishop, 2008), and specific language impairment (SLI) (Bishop & McArthur, 2004; McArthur, Atkinson, & Ellis, 2010). These differences are sensitively correlated with the degree of severity of the disability, such that literacy skills correlate with the amount of amplitude reduction of the mismatched negativity for individuals with severe dyslexia and mild subtle literacy deficits alike, compared to healthy controls (Stoodley et al., 2006).

Fellman and colleagues (2004) followed up with their cohort of infants at 2-years of age, and found a positive correlation between neonatal ERP discrimination abilities

and Bayley Scales of Infant Development scores. Similarly, a study by Mikkola and colleagues (2007) finds reduced P1 amplitudes at five years of age for children born preterm compared to healthy controls, as well as a relationship between lower P1 amplitudes and lower verbal IQ scores at five years of age. This suggests that neonatal maturity indices such as preterm birth (Mikkola et al., 2007) and neonatal ERPs (Fellman et al., 2004) are each predictive of future developmental outcomes through at least five years of age.

In addition, neonatal ERPs to speech sound discrimination are related to familial risk for learning disabilities or cognitive impairments (deRegnier, 2005; Guttorm et al., 2010; Guttorm et al., 2001; Leppänen, Pihko, Eklund, & Lyytinen, 1999; Leppänen et al., 2002; Molfese, 2000; Molfese, Molfese, & Espy, 1999). Neonatal speech sound discrimination is also an important predictor of later language and cognitive developmental outcomes within normative developmental ranges, for healthy infants with no known risk (Fellman et al., 2004; Molfese & Molfese, 1994; Molfese et al., 2001; Molfese, Tan, Sarkari, & Gill, 1997; Siddappa et al., 2004; Tsao et al., 2004). In addition, a recent study illustrated that infant ERPs are able to differentiate children with familial risk for dyslexia who go on to become good readers from those who go on to become poor readers (van Zuijen, Plakas, Maassen, Maurits, & van der Leij, 2013). Thus, ERPs are correlated with degree of disability, both concurrently when measured in adulthood, and as predictive of future disability and ability level when measured in infancy.

ERPs for individuals with language and learning disabilities tend to reflect similar morphological differences as age- and maturity-related changes. In general, language and learning disabled individuals often generate smaller amplitude ERPs (Kraus et al., 1996;

Kujala et al., 2000; Leppänen et al., 2002; Schulte-Körne, Deimel, Bartling, & Remschmidt, 1998; Uwer, Albrecht, & von Suchodoletz, 2002). The smaller amplitudes could be interpreted to suggest that ERPs recorded from individuals with developmental disabilities are less mature than those from healthy control counterparts. Consequently, the apparent immaturity of the ERP morphology in infancy may indicate potential risk for later disability.

Neonate Habituation & Novelty Detection

For over 50 years, researchers studied human infants' mental processes by examining their habituation, or decrease in response to a repeated stimulus (Bridger, 1961; Fantz, 1964). Similar patterns of decreased response with repeated exposure are found in simple animal models including mollusks or worms, but these models typically involve fatigue of the sensory receptors (Sirois & Mareschal, 2004). In contrast, researchers of human habituation are more interested in investigating the cognitive processing or encoding underlying habituation. In this case, the individual not only habituates to a stimulus, but remembers a familiar stimulus over intervals of time, as well as discriminates between a familiar and a novel stimulus that differ on certain dimensions (Thompson & Spencer, 1966).

The ability to encode information about and become familiar with a stimulus in the environment is likely a highly conserved behavior that is evolutionarily advantageous for neonates. For instance, the human fetus responds differentially to the familiar sound of their mother's voice compared to other voices (Kisilevsky et al., 2009), and neonates show a preference for the familiar mother's voice as compared to a female stranger's