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Physiological correlates of memory recall in infancy: Vagal tone, cortisol, and imitation in preterm and full-term infants at 6 months

David W. Haley[a,*], Ruth E. Grunau[b,c], Joanne Weinberg[b,d], Adi Keidar[b], Tim F. Oberlander[b,c]

[a] Department of Psychology, University of Toronto, 1265 Military Trail, M1C 1A4 Canada
[b] Centre for Community Child Health Research, Child and Family Research Institute, University of British Columbia, Canada
[c] Department of Pediatrics, University of British Columbia, Canada
[d] Department of Cellular & Physiological Sciences, University of British Columbia, Canada

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ABSTRACT

We examined the role of physiological regulation (heart rate, vagal tone, and salivary cortisol) in short-term memory in preterm and full-term 6-month-old infants. Using a deferred imitation task to evaluate social learning and memory recall, an experimenter modeled three novel behaviors (removing, shaking, and replacing a glove) on a puppet. Infants were tested immediately after being shown the behaviors as well as following a 10-min delay. We found that greater suppression of vagal tone was related to better memory recall in full-term infants tested immediately after the demonstration as well as in preterm infants tested later after a 10-min delay. We also found that preterm infants showed greater coordination of physiology (i.e., tighter coupling of vagal tone, heart rate, and cortisol) at rest and during retrieval than full-term infants. These findings provide new evidence of the important links between changes in autonomic activity and memory recall in infancy. They also raise the intriguing possibility that social learning, imitation behavior, and the formation of new memories are modulated by autonomic activity that is coordinated differently in preterm and full-term infants.

1. Introduction

Preterm infants show poorer habituation to sensory stimulation and require longer exposure to test stimuli before demonstrating learning and memory compared to full-term children starting in the neonatal period (e.g., Howard, Parmelee, Kopp, & Littman, 1976; Sigman & Parmelee, 1974), and extending into infancy (e.g., Rose, Feldman, & Jankowski, 2001; Rose, Feldman, & Wallace, 1988) and childhood (e.g., Rose & Feldman, 1996). Moreover, preterm infants display memory difficulties involving recognition (e.g., Gekoski, Fagen, & Pearlman, 1984; Haley, Weinberg, & Grunau, 2006; Heathcock, Bhat, Lobo, & Galloway, 2004) and recall (De Haan, Bauer, Georgieff, & Nelson, 2000; Rose, Feldman, & Jankowski, 2005). Poorer habituation has been related to alterations in physiological response systems in preterm neonates (e.g., Field, Dempsey, Hatch, Ting, & Clifton, 1979; Gardner & Karmel, 1983; Krafchuk, Tronick, & Clifton, 1983; Rose, Schmidt, & Bridger, 1976). Paradoxically, preterm infants exhibit both hypo- and hypercardiac responses to test stimuli during habituation tasks compared to full-term infants (Rose et al., 1976; Field et al., 1979; Krafchuk et al., 1983). This response pattern contributes to the widely held view that preterm infants tend to be physiologically dysregulated or disorganized, which is thought to compromise their

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* Corresponding author. Tel.: +1 416 208 4896.
E-mail address: d.haley@utoronto.ca (D.W. Haley).

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ability to attend to and process new information (Field, 1981; Mayes, 2000; Tronick, Scanlon, & Scanlon, 1990). Beyond the neonatal period, however, it has remained unclear whether learning and memory performance is attributed to physiological differences in preterm and full-term infants.

1.1. Memory

Several important differences in cognitive processing have been observed in preterm infants. First, they tend to process novel information more slowly than full-term infants (e.g., Sigman & Parmelee, 1974). This observation is well established and has systematically been demonstrated using experimental designs that independently evaluate encoding speed and habituation performance (e.g., Rose et al., 2001). Second, preterm infants show specific types of memory processing difficulties involving encoding, consolidation, and retrieval (Gekoski et al., 1984; Haley et al., 2006; Heathcock et al., 2004). For example, Gekoski et al. (1984) demonstrated that while 3-month-old preterm infants eventually learned to associate foot kicking with a movement of a mobile after 2 days of training, they failed to remember the kick–mobile association when tested a week later, unlike full-term infants. This work demonstrates that even when encoding speed is controlled by repeated days of exposure and training, the memory trace formed during encoding is not sufficiently stable to be consolidated for later retrieval. A third difference is that preterm infants have difficulty recalling action sequences after brief delays, particularly multiple actions sequences that require encoding of temporal order (de Haan et al., 2000; Rose et al., 2005)—a difference that persists into childhood (e.g., Luciana, Lindeke, Georgieff, Mills, & Nelson, 1999).

Imitation of novel behaviors after a delay is considered to be a test of memory recall (McDonough, Mandler, McKee, & Squire, 1995). Memory recall has been demonstrated in full-term infants in the first year of life using the deferred imitation paradigm (Barr, Dowden, & Hayne, 1996; Hayne, Boniface, & Barr, 2000; Herbert, Gross, & Hayne, 2006), in which novel actions or sequences of actions are enacted with props by an experimenter and the infant is expected to imitate those actions after a delay. While premature birth did not affect memory recall for individual target actions at 19 months of age, preterm infants did show poorer memory for ordered actions—specifically, the temporal pairing of actions—compared to full-term infants (de Haan et al., 2000). In another study, using a similar memory task but with a larger longitudinal sample, Rose et al. (2005) found that preterm infants showed difficulties recalling both individual actions and order of actions at 12, 20, and 24 months compared to full-term infants. Interestingly, memory performance was highly stable across age, suggesting that important individual differences in how preterm and full-term infants recall events appear to be established in the first year of life.

1.2. Physiology and memory

Individual differences in physiology have been linked to individual differences in cognition and emotion. The parasympathetic branch of the autonomic nervous system has been widely studied in infants as a measurement of these differences. In polyvagal theory, Porges (1995) proposes that parasympathetic activity plays an important role in the coordination of physiological and behavioral response systems, which are needed to maintain homeostasis and enhance growth as well as mobilize energy needed to respond to changes in the environment. At rest, when no immediate challenge is present, greater parasympathetic activity supports growth, slows metabolic activity, and inhibits sympathetic activity. A rapid decrease in parasympathetic activity inhibits the expression of growth factors, speeds up metabolic activity, and increases sympathetic activity (e.g., greater blood flow, faster hear rate, and greater secretion of stress hormones). The capacity to withdraw parasympathetic activity in response to a challenge is thought to be adaptive and has been linked to cognitive performance (e.g., Bornstein & Suess, 2000; Richards, 1987), emotion regulation (e.g., Bazhenova, Plonskaia, & Porges, 2001; Stifter, Spinrad, & Braungart-Rieker, 1999), and temperament (e.g., Huffman et al., 1998).

Vagal tone is an established autonomic index of parasympathetic activity that reflects respiratory sinus arrhythmia (RSA), which is assumed to be regulated by the nucleus ambiguus in the brain stem. Studies on human infants have examined basal vagal tone and changes in vagal tone during cognitive tasks in relation to attention (DeGangi, DiPietro, Greenspan, & Porges, 1991; Huffman et al., 1998), habituation (Bornstein & Suess, 2000), memory recognition (Linnemeyer & Porges, 1986), play exploration (DiPietro, Porges, & Uhly, 1992), and contingency learning (Haley, Grunau, Oberlander, & Weinberg, 2008). These studies indicate that higher basal tone and greater suppression of vagal tone during a challenge facilitate cognitive performance.

There is a growing body of work suggesting that vagal activity plays a specific role in memory consolidation (Clark, Naritoku, Smith, Browning, & Jensen, 1999; Flood, Smith, & Morley, 1987). Several recent studies have shown that greater vagal tone suppression during encoding is related to better short-term memory recall in adults (Johnsen et al., 2003). This relationship is thought to be mediated by neurochemical pathways (e.g., Flood et al., 1987), in which activation of the vagus nerve releases catecholamines (Hassert, Miyashita, & Williams, 2004) such as norepinephrine (NE) and stress hormones, which modulate memory consolidation (Cahill & Alkire, 2003; McGaugh, 1966, 2000).

The effects of premature birth on infant autonomic activity are mixed. There is some evidence that the heart rate patterns in preterm infants differ from those of full-term infants in the neonatal period (e.g., Field et al., 1979; Rose et al., 1976) and in the first year of life (Coles, Bard, Platzman, & Lynch, 1999; Haley et al., 2008). For example, preterm infants at 3 months (age adjusted for preterm birth) show higher resting heart rates and greater reactivity to novel stimulation (Coles et al., 1999; Haley et al., 2008) than full-term infants. This pattern of greater sympathetic activity (i.e., faster heart rates) suggests