

The Development of Attention Systems and Working Memory in Infancy

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1 Running Title: Infant attention and working memory

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4 **The Development of Attention Systems and Working Memory in**
5 **Infancy**

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46 **Abstract**

47
48 In this paper, we review research and theory on the development of attention and working
49 memory in infancy using a developmental cognitive neuroscience framework. We begin with a
50 review of studies examining the influence of attention on neural and behavioral correlates of an
51 earlier developing and closely related form of memory (i.e., recognition memory). Findings
52 from studies measuring attention utilizing looking measures, heart rate, and event-related
53 potentials (ERPs) indicate significant developmental change in sustained and selective attention
54 across the infancy period. For example, infants show gains in the magnitude of the attention
55 related response and spend a greater proportion of time engaged in attention with increasing age
56 (Richards & Turner, 2001). Throughout infancy, attention has a significant impact on infant
57 performance on a variety of tasks tapping into recognition memory; however, this approach to
58 examining the influence of infant attention on memory performance has yet to be utilized in
59 research on working memory. In the second half of the paper, we review research on working
60 memory in infancy focusing on studies that provide insight into the developmental timing of
61 significant gains in working memory as well as research and theory related to neural systems
62 potentially involved in working memory in early development. We also examine issues related
63 to measuring and distinguishing between working memory and recognition memory in infancy.
64 To conclude, we discuss relations between the development of attention systems and working
65 memory.

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The Development of Attention Systems and Working Memory in Infancy

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74 What are the mechanisms that support the ability to retain information for a period of time before
75 acting on it? When does this ability emerge in human development? What role does the
76 development of attention play in this process? Answers to these questions are not only important
77 for furthering our understanding of working memory, but are also fundamental to understanding
78 cognitive development at a broader level. We delve into these questions from a developmental
79 cognitive neuroscience perspective with a particular focus on the impact of the development of
80 attention systems on recognition memory and working memory. In the sections that follow, we
81 present a selective review of research in which psychophysiological and neuroscience techniques
82 have been combined with behavioral tasks to provide insight into the effects of infant attention
83 on performance on recognition memory tasks. We begin our review with a focus on infant
84 attention and recognition memory because the combined measures used in this line of work
85 provide unique insight into the influence of sustained attention on memory. To date, this
86 approach has yet to be utilized to examine relations between attention and working memory in
87 early development. In the second half of the paper, we review research on working memory in
88 infancy with a focus on studies utilizing behavioral and neuroscience measures (for more
89 exhaustive reviews, see: Bauer, 2009; Cowan, 1995; Nelson, 1995; Pelphrey & Reznick, 2003;
90 Rose, Feldman, & Jankowski, 2004; Rovee-Collier & Cuevas, 2009). We also focus on recent
91 research findings that shed light on neural systems potentially involved in attention and working
92 memory in infancy (for excellent reviews on attention and working memory relations in
93 childhood, see: Astle & Scerif, 2011; Amso & Scerif, 2015). Because the human infant is
94 incapable of producing verbal or complex behavioral responses and also cannot be given
95 instructions on how to perform a given task, by necessity, many of the existing behavioral
96 studies on infant working memory have been built upon look duration or preferential looking
97 tasks traditionally used to tap into infant visual attention and recognition memory. Thus, it is
98 difficult to draw distinct lines when determining the relative contribution of these cognitive
99 processes to performance on these tasks in the infancy period (but see, Perone & Spencer, 2013a,
100 2013b). We conclude with a section examining potential relations between attention and
101 working memory and propose that the development of attention systems plays a key role in the
102 timing of significant gains in working memory observed in the second half of the first postnatal
103 year.

Infant Visual Attention and Recognition Memory

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105
106
107 Much of what we know about the early development of visual attention comes from a large body
108 of research on recognition memory in infancy. Because the defining feature of recognition
109 memory is differential responsiveness to novel stimuli in comparison to familiar (or previously
110 viewed) stimuli (Rose et al., 2004), the majority of behavioral research in the area has utilized
111 the visual paired comparison (VPC) task. This task involves the simultaneous presentation of
112 two visual stimuli. Look duration to each stimulus during the paired comparison is measured.
113 Under the framework of Sokolov's (1963) comparator model, longer looking to a novel stimulus
114 in comparison to a familiar stimulus (i.e., a novelty preference) is indicative of recognition of a
115 fully encoded familiar stimulus. In contrast, familiarity preferences are indicative of incomplete
116 processing and continued encoding of the familiar stimulus. The underlying assumption is that

117 infants will continue to look at a stimulus until it is fully encoded, at which point attention will
118 be shifted toward novel information in the surrounding environment.

119
120 Thus, infant look duration has been a widely used and highly informative behavioral measure of
121 infant attention that also provides insight into memory in early development. Findings from these
122 studies indicate that older infants require less familiarization time to demonstrate novelty
123 preferences than younger infants; and within age groups, increasing the amount of
124 familiarization results in a shift from familiarity preferences to novelty preferences (Freese-
125 man, Colombo, & Coldren, 1993; Hunter & Ames, 1988; Rose et al., 1982). Older infants also show
126 evidence of recognition with longer delays between familiarization and testing. For example,
127 Diamond (1990) found that 4-month-olds demonstrate recognition with up to 10 s delays
128 between familiarization and testing, 6-month-olds demonstrate recognition with up to 1 min
129 delays, and 9-month-olds demonstrate recognition with up to 10 min delays. These findings
130 indicate that with increasing age, infants are able to process visual stimuli more efficiently and
131 subsequently recognize those stimuli after longer delays. Unfortunately for infancy researchers,
132 look duration and attention are not isomorphic. For example, it is not uncommon for infants to
133 continue looking at a stimulus when they are no longer actively paying attention; therefore,
134 looking measures alone do not provide a particularly accurate measure of infant attention. This
135 phenomenon is most prevalent in early infancy and has been referred to as attention capture,
136 obligatory attention, and sticky-fixation (Hood, 1995; Ruff & Rothbart, 2001).

137
138 Richards and colleagues (Courage, Reynolds, & Richards, 2006; Richards, 1985, 1997; Richards
139 & Casey, 1992; for review, Reynolds & Richards, 2008) have utilized the electrocardiogram to
140 identify changes in heart rate that coincide with different phases of infant attention. During the
141 course of a single look, infants will cycle through four phases of attention – stimulus orienting,
142 sustained attention, pre-attention termination, and attention termination. The most relevant of
143 these phases are sustained attention and attention termination. Sustained attention is manifested
144 as a significant and sustained decrease in heart rate from prestimulus levels that occurs when
145 infants are actively engaged in an attentive state. Attention termination follows sustained
146 attention and is manifested as a return of heart rate to prestimulus levels. Although the infant is
147 still looking at the stimulus during attention termination, she/he is no longer engaged in an
148 attentive state. Infants require significantly less time to process a visual stimulus if heart rate is
149 measured online and initial exposure is given during sustained attention (Frick and Richards,
150 2001; Richards, 1997). In stark contrast, infants given initial exposure to a stimulus during
151 attention termination do not demonstrate evidence of recognition of the stimulus in subsequent
152 testing (Richards, 1997).

153 154 **The General Arousal/Attention System**

155
156 Richards (2008, 2010) has proposed that sustained attention is a component of a general arousal
157 system involved in attention. Areas of the brain involved in this general arousal/attention system
158 include, the reticular activating system and other brainstem areas, thalamus, and cardio-
159 inhibitory centers in frontal cortex (Reynolds, Courage, & Richards, 2013). Cholinergic inputs
160 to cortical areas originating in the basal forebrain are also involved in this system (Sarter,
161 Givens, & Bruno, 2001). Activation of this system triggers cascading effects on the overall state
162 of the organism which foster an optimal range of arousal for attention and learning. These

163 effects include: decreased heart rate (i.e., sustained attention), motor quieting, and release of
164 acetylcholine (ACh) via corticopetal projections. Ruff's (Ruff & Capazzoli, 2003; Ruff &
165 Rothbart, 2001) description of "focused attention" in children engaged in toy play as being
166 characterized by motor quieting, decreased distractibility, and intense concentration coupled with
167 manipulation/exploration would be considered a behavioral manifestation of this general
168 arousal/attention system.

169
170 The general arousal/attention system is functional in early infancy but shows considerable
171 development across infancy and early childhood with increased magnitude of the HR response,
172 increased periods of sustained attention, and decreased distractibility occurring with increasing
173 age (Reynolds & Richards, 2008; Richards & Cronise, 2000; Richards & Turner, 2001). These
174 developmental changes most likely have a direct influence on performance on working memory
175 tasks. The general arousal/attention system is non-specific in that it functions to modulate
176 arousal regardless of the specific task or function the organism is engaged in. The effects of the
177 system on arousal and attention are also general and do not vary in a qualitative manner
178 depending on cognitive task, thus sustained attention would be expected to influence recognition
179 memory and working memory in a similar manner. This non-specific attention system directly
180 influences functioning of three specific visual attention systems that also show considerable
181 development in the infancy period. These specific attention systems are: the reflexive system,
182 the posterior orienting system, and the anterior attention system (Colombo, 2001; Johnson,
183 Posner, & Rothbart, 1991; Posner & Peterson, 1990; Schiller, 1985).

184 185 **The Development of Attention Systems in the Brain**

186
187 At birth, newborn visual fixation is believed to be primarily involuntary, exogenously driven,
188 and exclusively under the control of a reflexive system (Schiller, 1985). This reflexive system
189 includes the superior colliculus, the lateral geniculate nucleus of the thalamus, and the primary
190 visual cortex. Many newborn fixations are reflexively driven by direct pathways from the retina
191 to the superior colliculus (Johnson et al., 1991). Infant looking is attracted by basic but salient
192 stimulus features processed via the magnocellular pathway that can generally be discriminated in
193 the peripheral visual field, such as high-contrast borders, motion, and size.

194
195 Looking and visual fixation stays primarily reflexive for the first two months until the end of the
196 newborn period when the posterior orienting system reaches functional onset. The posterior
197 orienting system is involved in the voluntary control of eye movements, and shows considerable
198 development from 3 – 6 months of age. Areas of the brain involved in the posterior orienting
199 system include: posterior parietal areas, pulvinar, and frontal eye-fields (Johnson et al., 1991;
200 Posner & Petersen, 1990). The posterior parietal areas are believed to be involved in
201 disengaging fixation and the frontal eye-fields are key for initiating voluntary saccades. In
202 support of the view that the ability to voluntarily disengage and shift fixation shows significant
203 development across this age range, Figure 1 shows results from a look duration study by Courage
204 and colleagues (2006) in which infant look duration dropped significantly to a wide range of
205 stimuli from 3 to 6 months of age (i.e., 14 to 26 weeks of age).

206
207 **Insert Figure 1 here**

208

209 At around 6 months of age, the anterior attention system reaches functional onset and infants
210 begin the drawn out process of developing inhibitory control and higher order attentional control
211 (i.e., executive attention). Not only do infants have better voluntary control over their visual
212 fixations, they can now inhibit attention to distractors and maintain attention for more prolonged
213 periods when it is called for. As can be seen in Figure 1, Courage and colleagues (2006) found
214 that from 6 to 12 months of age (i.e., 20 to 52 weeks), infants continue to show brief looks to
215 basic, geometric patterns but begin to show longer looking toward more complex and engaging
216 stimuli such as Sesame Street or human faces. This indicates the emergence of some
217 rudimentary level of attentional control at around 6 months of age. Given that several models
218 emphasize some aspect of attentional control as a core component of working memory (e.g.,
219 Amso & Scerif, 2015; Astle & Scerif, 2011; Baddeley, 1996; Cowan & Morey, 2006; Kane &
220 Engle, 2002; Klingberg et al., 2000), it stands to reason that the emergence of attentional control
221 at around 6 months of age would contribute significantly to the development of working
222 memory.

223
224 The theoretical models for the attention systems discussed above are largely based on findings
225 from comparative research with monkeys, adult neuroimaging studies, or symptomology of
226 clinical patients with lesions to certain areas of the brain. Unfortunately, developmental
227 cognitive neuroscientists are highly limited in non-invasive neuroimaging tools available for use
228 in basic science with infant participants. However, we have conducted multiple studies utilizing
229 event-related potentials (ERPs) along with heart rate measures of attention and behavioral
230 measures of recognition memory (Reynolds et al., 2010; Reynolds & Richards, 2005). Findings
231 from these studies provide insight into potential areas of the brain involved in attention and
232 recognition memory in infancy.

233
234 The ERP component which is most clearly related to infant visual attention is the Negative
235 central (Nc) component. The Nc is a high amplitude, negatively-polarized component that
236 occurs from 400 – 800 ms post stimulus onset at frontal and midline leads (see Figure 2). Nc has
237 been found to be greater in amplitude to: oddball compared to standard stimuli (Courchesne,
238 Ganz, & Norcia, 1981), novel compared to familiar stimuli (Reynolds & Richards, 2005),
239 mother's face compared to a stranger's face (de Haan & Nelson, 1997), and a favorite toy
240 compared to a novel toy (de Haan & Nelson, 1999). These findings indicate that regardless of
241 novelty or familiarity, Nc is greater in amplitude to the stimulus that grabs the infant's attention
242 the most (Reynolds et al., 2010). Additionally, Nc is greater in amplitude when infants are
243 engaged in sustained attention (as measured by heart rate) than when infants have reached
244 attention termination (Guy, Zieber, & Richards, in press; Reynolds et al., 2010; Richards, 2003).
245 The Nc is also ubiquitous in ERP research utilizing visual stimuli with infant participants. Taken
246 together, these findings indicate that Nc reflects amount of attentional engagement.

247
248 Insert Figure 2 here

249
250 In order to determine the cortical sources of the Nc component. Reynolds and colleagues
251 (Reynolds, Courage, & Richards, 2010; Reynolds & Richards, 2005) conducted cortical source
252 analysis on scalp-recorded ERP. Cortical source analysis involves computing a forward solution
253 for a set of dipoles, and comparing the simulated topographical plots produced by the forward
254 solution to the topographical plots obtained from observed data. The forward solution is iterated

255 until the best fitting solution is found. The results of the cortical source analysis can then be
256 mapped onto structural MRIs. Figure 3 shows the results of our source analysis of the Nc
257 component measured during brief stimulus ERP presentations and also during performance of
258 the VPC task. As can be seen in Figure 3, the cortical sources of the Nc were localized to areas
259 of prefrontal cortex (PFC) for all age groups including 4.5-month-olds. Areas which were
260 common dipole sources included inferior and superior PFC, and the anterior cingulate. The
261 distribution of the dipoles also became more localized with increasing age. These findings
262 support the proposal that PFC is associated with infant attention, and indicate that there is
263 overlap in brain areas involved in both recognition memory and working memory tasks.
264 Neuroimaging research with older children and adults indicates that there is a neural circuit
265 including parietal areas and PFC involved in working memory (e.g., Crone et al., 2006; Fuster,
266 1997; Goldman-Rakic 1995, 1996; Kane & Engle, 202; Klingberg, Forssberg, & Westerberg,
267 2002).

268 .

269

Insert Figure 3 here

270

271 The late slow wave (LSW) ERP component is associated with recognition memory in infancy.
272 The LSW shows a reduction in amplitude with repeated presentations of a single stimulus (de
273 Haan & Nelson, 1997, 1999; Reynolds, Guy, & Zhang, 2011; Reynolds & Richards, 2005;
274 Snyder, 2007). As shown in the two lower ERP waveforms in Figure 2, the LSW occurs from
275 about 1 – 2 s post stimulus onset at frontal, temporal, and parietal electrodes. By examining the
276 LSW, Guy and colleagues (Guy, Reynolds, & Zhang, 2013) found that individual differences in
277 infant visual attention are associated with utilization of different processing strategies when
278 encoding a new stimulus. Infants who tend to demonstrate brief but broadly distributed fixations
279 (referred to as short lookers; e.g., Colombo & Mitchell, 1990) during exposure to a novel
280 stimulus subsequently showed evidence of discriminating hierarchical patterns based on changes
281 in the overall configuration of individual elements (or local features). In contrast, infants who
282 tend to demonstrate longer and more narrowly distributed visual fixations (referred to as long
283 lookers) showed evidence of discriminating patterns based on changes in local features but not
284 based on changes in the overall configuration of local features. Furthermore, research utilizing
285 heart rate measures of attention during performance on a recognition memory ERP task have
286 provided informative findings regarding relations between attention and memory. Infants are
287 more likely to demonstrate differential responding to familiar and novel stimuli in the LSW
288 when heart rate indicates they are engaged in sustained attention (Reynolds & Richards, 2005;
289 Richards, 2003).

290

291 No studies to date have utilized cortical source analysis to examine cortical sources of the LSW.
292 Late-latency and long duration ERP components can be more problematic for cortical source
293 analysis due to greater variability in the timing of the latency of the component across
294 participants and trials, and the likely contribution of multiple cortical sources to the ERP
295 component observed in the scalp-recorded EEG. However, research with non-human primates
296 and neuroimaging studies with older children and adults indicates the role of a medial temporal
297 lobe circuit in recognition memory processes. Cortical areas involved in this circuit include the
298 hippocampus and parahippocampal cortex; entorhinal and perirhinal cortices; and the visual area
299 TE (Bachevalier, Brickson, & Hagger, 1993; Begleiter, Porjesz, & Wang, 1993; Brown &
300 Aggleton, 2001; Desimone, 1996; Eichenbaum, Yonelinas, & Ranganath, 2007; Fahy et al.,

1993; Li, Miller, & Desimone, 1993; Reynolds, 2015; Wan, Aggleton, & Brown, 1999; Wiggs & Martin, 1998; Xiang & Brown, 1998; Zeamer, Heuer, & Bachevalier, 2010; Zhu, Brown, McCabe, & Aggleton, 1995). Regardless of the potential areas involved in recognition memory in infancy, attention is clearly an integral component of successful performance on recognition memory tasks. Performance on recognition memory tasks is influenced by the development of each of the attention systems described above and it stands to reason that these attention systems would influence performance on working memory tasks in a similar manner. Furthermore, working memory and recognition memory are closely related and some of the tasks used to measure maintenance of items in working memory (i.e., visual short term memory) in infancy are slightly modified recognition memory tasks. Thus, distinctions between working memory and recognition memory can be particularly difficult to make during the infancy period.

312

313 **The Development of Working Memory in Infancy**

314

Similar to work on attention and recognition memory, research on the early development of working memory has focused on the use of behavioral measures (looking and reaching tasks) with infant participants. Neuroscience models of early working memory development have also largely relied on findings from comparative research, clinical cases, and neuroimaging with older children and adults. However, there is a rich and growing tradition of cognitive neuroscience models and research on working memory development. In the sections that follow, we focus specifically on developmental cognitive neuroscience research on working memory in infancy (for more exhaustive reviews on memory development, see: Bauer, 2009; Cowan, 1995; Courage & Howe, 2004; Nelson, 1995; Pelphrey & Reznick, 2003; Rose, Feldman, & Jankowski, 2004; Rovee-Collier & Cuevas, 2009).

325

Much of the research on working memory in infancy has focused on tasks similar to the Piagetian A-not-B task, and generally all tasks involve some delayed response (DR) with the correct response requiring some level of attentional control. The A-not-B and other DR tasks typically involve the presentation of two or more wells. While the participant watches, an attractive object is placed in one of the wells and the participant's view of the object is then occluded. Following a brief delay, the participant is allowed to retrieve the object from one of the wells. In the A-not-B task, after multiple successful retrieval trials, the location of the hidden object is reversed (again while the participant observes). The classic A-not-B error occurs when the participant continues to reach for the object in the original hiding location after observing the reversal of the hiding location.

336

Diamond (1985, 1990) has attributed perseverative reaching on the A-not-B task to a lack of inhibitory control in younger participants and attributes higher success rates in older infants (8 – 9 months) to further maturation of dorsolateral prefrontal cortex (DLPFC). It has been noted (Diamond, 1990; Hofstadter & Reznick, 1996; Stedron, Sahni, & Munakata, 2005) that participants occasionally look to the correct location after reversal but continue to reach to the incorrect (previously rewarded) location. Hostadter and Reznick (1996) found that when gaze and reach differ in direction, infants are more likely to direct their gaze to the correct location. Thus, poor performance in the A-not-B reaching task may be influenced by immature inhibitory control of reaching behavior as opposed to a working memory deficiency. Alternatively, Smith and colleagues (1999) conducted a systematic series of experiments using the A-not-B task and

346

347 found that several factors other than inhibition contribute to perseverative reaching; including
348 infant posture, direction of gaze, preceding activity, and long-term experiences in similar tasks.
349 However, using an oculomotor version of the DR task, Gilmore and Johnson (1995) found that
350 infants as young as 6 months of age were able to demonstrate successful performance. Similarly,
351 using a peek-a-boo looking version of the DR task, Reznick and colleagues (2004) found
352 evidence of a developmental transition at around 6 months of age associated with improved
353 working memory performance.

354
355 In several studies utilizing looking versions of the DR task, significant development has been
356 found to occur from 5 to 12 months of age. With increasing age, infants show higher rates of
357 correct responses, and infants can tolerate longer delays and still demonstrate successful
358 responses (Cuevas & Bell, 2010; Hofstadter & Reznick, 1996; Pelphrey et al., 2004). Bell and
359 colleagues (e.g., Bell, 2001, 2002, 2012; Bell & Adams, 1999; Bell & Wolfe, 2007; Cuevas &
360 Bell, 2011) have integrated EEG measures in looking versions of the A-not-B task in a
361 systematic line of work on the development of working memory. Bell and Fox (1992) found
362 developmental change in baseline frontal EEG power was associated with performance
363 improvement on the A-not-B task. Power changes from baseline to task in the 6 – 9 Hz EEG
364 frequency band also correlate with successful performance for 8-month-old infants (Bell, 2002).
365 Additionally, higher levels of frontal-parietal and frontal-occipital EEG coherence as well as
366 decreased heart rate from baseline to task are all associated with better performance on the
367 looking version of the A-not-B task (Bell, 2012).

368
369 Taken together, these findings provide support for the role of a frontal-parietal network in
370 working memory tasks in infancy which is consistent with findings from neuroimaging studies
371 with older children and adults showing recruitment of DLPFC, ventrolateral prefrontal cortex
372 (VLPFC), intraparietal cortex, and posterior parietal cortex (Crone et al., 2006; D' Esposito et
373 al., 1999; Courtney et al., 1998; Fuster, 1997; Klingberg et al., 2002; Scherf et al., 2006; and
374 Sweeney et al., 1996). For example, Crone and colleagues (2006) utilized fMRI during an object
375 working memory task with children and adults and found that VLPFC was involved in
376 maintenance processes for children and adults, and DLPFC was involved in manipulation of
377 items in working memory for adults and children older than 12. The youngest group of children
378 tested (8 – 12 years of age) did not recruit DLPFC during item manipulation, and did not perform
379 as well as adolescents and adults on the task.

380
381 The change-detection task is used to examine capacity limits for number of items an individual
382 can maintain in visual short term memory (VSTM), and the analogous change-preference task is
383 used to measure capacity limits with infant participants. Similar to the VPC task, the change-
384 preference task capitalizes on infants' tendency to prefer novel or familiar stimuli. Two sets of
385 stimuli are briefly and repeatedly presented to the left and right of midline with items in one set
386 of stimuli changing across each presentation and items in the other set remaining constant.
387 Infant looking to the left and right stimulus set is measured and greater looking to the changing
388 set side is utilized as an index of working memory. Set size is manipulated to determine capacity
389 limits for participants of different ages. Ross-Sheehy, Oakes, and Luck (2003) found a capacity
390 increase from 1 to 3 items across 6.5 to 12.5 months of age. The authors proposed that the
391 increase in capacity limits on this task across this age range is driven in part by development of
392 the ability to bind color to location. In a subsequent study, the authors (Ross-Sheehy, Oakes, &

393 Luck, 2011) found that providing infants with an attentional cue facilitated memory for items in
394 a stimulus set. 10-month-olds demonstrated enhanced performance when provided with a spatial
395 cue and 5-month-olds demonstrated enhanced performance when provided with a motion cue.
396 These findings demonstrate that spatial orienting and selective attention influences infant
397 performance on a VSTM task, and support the possibility that further development of the
398 posterior orienting system influences maintenance processes involved in working memory in
399 infancy.

400
401 Spencer and colleagues (e.g., Perone, Simmering, & Spencer, 2011; Simmering, 2012;
402 Simmering & Spencer, 2008; Simmering, Schutte, & Spencer, 2008; Spencer, Simmering,
403 Schutte, & Schoner, 2007) have utilized dynamic neural field (DNF) to explain developmental
404 changes in the change-preference task. Using the DNF model, Perone et al. (2011) did simulation
405 tests of the spatial precision hypothesis (SPH), predicting that the increased working memory
406 capacity limits found to develop during infancy are based on the strengthening of excitatory and
407 inhibitory projections between a working memory field, perceptual field, and an inhibitory layer.
408 According to the DNF model, the perceptual field consists of a population of neurons with
409 receptive fields for certain feature dimensions (e.g., color, shape), and activation in the working
410 memory layer leads to inhibition of similarly tuned neurons in the perceptual field. The results
411 of their simulation experiments were very similar to past behavioral findings and provided
412 support for the SPH in explaining the increases in capacity limits that have been found to occur
413 with increasing age in infancy.

414
415 Findings from studies utilizing the change-preference task provide insight into capacity limits in
416 VSTM during infancy. However, this task simply requires identification of novel items or
417 objects based on maintenance of a memory representation over very brief delays (i.e., less than
418 500 ms). Given that delays between familiarization and testing on infant recognition memory
419 tasks are typically very brief and the length of the delay is often not specified, it is particularly
420 difficult to determine whether or not recognition memory performance is based on short-term
421 memory or long-term memory. Recall that 4-month-olds only demonstrate recognition with up
422 to 10 s delays (Diamond, 1990). Thus, it is also difficult to determine whether or not
423 performance on the change-preference task taps into maintenance of items in working memory
424 or simply measures recognition memory. Alternatively, one could argue that performance on
425 recognition memory tasks with brief delays may be driven by working memory. Interestingly,
426 Perone and Spencer (2013a, 2013b) again utilized the DNF model to simulate infant performance
427 on recognition memory tasks. The results of the simulations indicated that increasing the
428 efficiency of excitatory and inhibitory interactions between the perceptual field and a working
429 memory field in their model led to novelty preferences on VPC trials with less exposure to the
430 familiar stimulus. These simulated results are similar to the developmental trends found to occur
431 with increasing age across infancy in empirical studies utilizing the VPC task (e.g., Freese et al.,
432 1993; Hunter & Ames, 1988; Rose et al., 1982). The authors concluded that development of
433 working memory is a significant factor in the increased likelihood that older infants will
434 demonstrate novelty preferences on recognition memory tasks when compared to younger
435 infants.

436
437 In order to investigate working memory in infancy, Kaldy and Leslie (2003, 2005) conducted a
438 series of experiments with infants that involved both identification and individuation for

439 successful performance. Individuation involves item or object identification combined with
440 entering the identified information into existing memory representations. Infants were
441 familiarized with two objects of different shapes presented repeatedly in the middle of a stage.
442 The side position of the objects was alternated across presentations in order to require infants to
443 integrate object shape with location on a trial by trial basis. During the test phase, the objects
444 were presented in the center of the stage as in familiarization and then placed behind occluders
445 on the same side of the stage. After a delay, the occluders were removed. On change trials,
446 removal of the occluders revealed that the different shaped objects were reversed in location. On
447 no-change control trials, the objects remained in the same location upon removal of the
448 occluders. Longer looking on change trials indicated individuation of the object based on
449 identifying the change in object shape from the location it was in prior to occlusion. Results
450 indicated that while 9-month-olds could identify changes in object location for both objects
451 (Kaldy & Leslie, 2003), 6-month-olds were only able to bind object to location for the last object
452 that was moved behind the occluder in the test phase (Kaldy & Leslie, 2005). The authors
453 concluded that the younger infants' memory maintenance was more susceptible to distraction of
454 attention. Kaldy and Leslie (2005) also proposed that the significant improvements on this task
455 between 6 to 9 months of age are related to further development of medial temporal lobe
456 structures (i.e., entorhinal cortex, parahippocampal cortex) which allows older infants to
457 continue to hold objects in working memory in the presence of distractors.

458
459 Thus, Kaldy and colleagues (Kaldy & Leslie, 2003, 2005; Kaldy & Sigala, 2004) have proposed
460 an alternative model of working memory development which emphasizes the importance of
461 medial temporal lobe structures more so than PFC. They argue that the majority of working
462 memory models emphasizing the importance of DLPFC for working memory are confounding
463 the response inhibition required in typical working memory tasks (e.g., the A-not-B task) with
464 true working memory processes. To further address this limitation, Kaldy, Guillory, and Blaser
465 (2015) designed a delayed match retrieval task which involves location-object binding but
466 requires less response inhibition than the classic version of the A-not-B task. Infants are shown
467 two cards, each with pictures of different objects or patterns on them. The cards are turned over
468 and then a third card is placed face up which matches one of the face down cards. Infants are
469 rewarded with an attractive stimulus for looks toward the location of the matching face down
470 card. The authors (2015) tested 8- and 10-month-olds on this task and found the 10-month-olds
471 performed significantly above chance levels. 8-month-olds performed at chance levels but
472 showed improvement across trials. Thus, similar to previous work, significant gains in working
473 memory performance are found to occur in the second half of the first postnatal year on the
474 delayed match retrieval task.

475
476 Regarding Kaldy and Sigala's (2004) view that too much emphasis has been placed on the
477 importance of PFC for infant working memory, results from the DNF simulations done by
478 Perone and colleagues (2011) also support the possibility that areas involved in visual processing
479 and object recognition could account for successful working memory performance on the
480 change-preference task without requiring significant PFC contributions to attentional-control.
481 However, in recent exploratory studies utilizing functional near infrared spectroscopy (fNIRS) to
482 measure the BOLD response of infant participants during an object-permanence task. Baird and
483 colleagues (2002) observed activation of frontal areas during the task. However, receptors were
484 only applied to frontal sites, thus limiting the conclusion that the increased frontal activity during

485 this task was unique or of particular functional significance in comparison to other brain regions.
486 However, Buss, Fox, Boas, and Spencer (2014) utilized fNIRS to image cortical activity
487 associated with visual working memory capacity in 3- and 4-year-old children. In this study,
488 receptors were applied over frontal and parietal locations. Frontal and parietal channels in the
489 left hemisphere showed increased activation when working memory load was increased from 1
490 to 3 items. Results supported the possibility that young children utilize a frontal-parietal
491 working memory circuit similar to adults. Both of these findings from fNIRS studies provide
492 preliminary support for the role of PFC in working memory during early development.

493
494 Luciana and Nelson (1998) emphasize the critical role the PFC plays in integrating sensorimotor
495 traces in working memory to guide future behavior. According to Luciana and Nelson, the A-
496 not-B task may actually overestimate the functional maturity of the PFC in infant participants
497 because it does not require the accurate integration of sensorimotor traces in working memory.
498 They propose the integration of sensorimotor traces should be considered a core process in
499 working memory definitions. The majority of working memory definitions include executive
500 control components, and persistent activity in DLPFC has been linked with control functions
501 involved in the manipulation of information for the purpose of goal-directed action (e.g., Crone
502 et al., 2006; Curtis & D'Esposito, 2003). Thus, the exact contribution of PFC to working
503 memory functions in early development remains unclear. What is clear from the extant literature
504 is that infants beyond 5 to 6 months of age are capable of demonstrating basic yet immature
505 aspects of working memory, and significant improvement in these basic functions occurs from 5
506 to 6 months on (e.g., Cuevas & Bell, 2010; Diamond, 1990; Gilmore & Johnson, 1995;
507 Hofstadter & Reznick, 1996; Kaldy et al., 2003, 2005, 2015; Pelphrey et al., 2004; Reznick et al.,
508 2004).

509 510 **The Development of Attention Systems and Working Memory**

511
512 Similar to recognition memory, the improvements in working memory performance which occur
513 after 5 to 6 months of age are likely influenced by further development of the attention systems
514 previously discussed. The majority of the working memory studies discussed above examined
515 visuospatial working memory. Performance on all of these working memory tasks involves
516 voluntary eye movements and controlled scanning of the stimuli involved in the task. Thus,
517 functional maturity of the posterior orienting system would be key for successful performance on
518 these tasks. This system shows significant development from 3 to 6 months of age (Johnson et
519 al., 1991; Colombo, 2001; Courage et al., 2006; Reynolds et al., 2013). This timing coincides
520 with the time frame at which infants begin to demonstrate above chance performance on working
521 memory tasks. For example, Gilmore and Johnson (1995) reported successful performance on
522 an oculomotor DR task for 6-month-old infants, and Reznick et al. (2004) describe 6 months of
523 age as a time of transition for performance on a peek-a-boo version of the DR task.

524
525 Successful performance on working memory tasks involves more than just voluntary control of
526 eye movements. Working memory tasks also involve attentional control and inhibition. These
527 cognitive functions are both associated with the anterior attention system (Posner & Petersen,
528 1990), which shows significant and protracted development from 6 months on. Several studies
529 have shown significant improvement on DR and change-preference tasks from 5 to 12 months of
530 age (Cuevas & Bell, 2010; Hofstadter & Reznick, 1996; Pelphrey et al., 2004; Ross-Sheehy et

531 al., 2003), an age range that overlaps with the functional onset of the anterior attention system.
532 Given that some models emphasize the role of PFC and attentional control as being critical for
533 working memory (e.g., Baddeley, 1996; Kane & Engle, 2002; Klingberg et al., 2000), further
534 development of the anterior attention system would be critical for working memory development
535 (for further discussion of attention and memory relations in childhood and adulthood, see: Astle
536 & Scerif, 2011; Amsö & Scerif, 2015; Awh & Jonides, 2001; Awh, Vogel, and Oh, 2006).

537
538 The general arousal/attention system shows significant developmental change across infancy and
539 early childhood characterized by gains in both the magnitude and duration of periods of
540 sustained attention (Reynolds & Richards, 2008; Richards & Cronise, 2000; Richards & Turner,
541 2001). Infants are more likely to demonstrate evidence of recognition memory if initial exposure
542 to the test stimulus occurs during sustained attention or if the infant is engaged in sustained
543 attention during the recognition test (e.g., Frick & Richards, 2001; Reynolds, Courage, &
544 Richards, 2010; Reynolds & Richards, 2005; Richards, 1997). It stands to reason that these
545 developmental gains in sustained attention would also facilitate improved performance on
546 working memory tasks. This reasoning is supported by Bell's (2012) finding that infants who
547 show decreased heart rate from baseline to task also show enhanced performance on the A-not-B
548 task. Studies utilizing the heart rate phases (Richards & Casey, 1992) during infant working
549 memory tasks would provide greater insight into the effects of sustained attention on working
550 memory performance.

551
552 Relations between arousal and attention are complex and change throughout development. The
553 significant and sustained decrease in heart rate associated with attention is most likely limited to
554 infancy and early childhood; however, individual differences in heart rate variability are related
555 to attention and cognitive performance throughout development (Porges, 1992; Reynolds &
556 Richards, 2008; Suess, Porges, & Plude, 1994). Relatively little work has examined the
557 influence of arousal aspects of attention on working memory in later development. An exception
558 would be the work by Thayer and colleagues (Hansen, Johnsen, & Thayer, 2003; Thayer,
559 Hansen, Saus-Rose, and Johnsen, 2009) examining relations between HRV and working memory
560 in adults. Their findings indicate that individual differences in baseline HRV are associated with
561 performance on working memory tasks. Individuals with high baseline HRV perform better on
562 working memory tasks than individuals with low baseline HRV, and the advantage is specific to
563 tasks requiring executive function (Thayer et al., 2009). Thus, attention and arousal appear to
564 influence working memory throughout development; however, the dynamics of these relations
565 are complex and would be expected to change significantly with age.

566
567 The development of attention and the development of working memory are closely related.
568 Significant gains on working memory tasks overlap in developmental timing with key periods
569 for development of sustained attention, the posterior orienting system, and the anterior attention
570 system. There is also significant overlap in neural systems involved in attention and working
571 memory. The cortical sources of the Nc ERP component associated with infant visual attention
572 have been localized to areas of PFC (Reynolds et al., 2005, 2010). Similarly, research with
573 fNIRS indicates that frontal and parietal areas are involved in working memory performance for
574 infants (Baird et al., 2002) and preschoolers (Buss et al., 2014). Given the substantial overlap in
575 developmental timing and neural systems involved in both attention and working memory, future
576 research should aim to examine relations between attention and working memory in infancy and

577 early childhood using both psychophysiological and neural measures. A multi-level analysis
578 approach would be ideal for addressing the controversy regarding the relative contribution of
579 PFC, parietal cortex, and medial temporal lobe structures to working memory performance.
580 Attention plays a key role in successful working memory performance, and the development of
581 attention systems most likely influences the development of working memory. Bidirectional
582 effects are common throughout development, and thus of equal interest is the potential influence
583 of working memory on further development of attention systems in infancy and early childhood.
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Provisional

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954

955 **Figure 1.** Mean peak look durations for faces, geometric patterns, and Sesame Street as a
956 function of age (figure adapted from Courage, Reynolds, & Richards, 2006).

957

958 **Figure 2.** ERP waveforms and electrode locations for the Nc and LSW ERP components. The
959 ERP waveforms are shown to the left. Change in amplitude of the ERP from baseline values is
960 represented on the Y-axis, and time following stimulus onset is represented on the X-axis. The
961 electrode locations for each of the waveforms are shown to the right in boxes on the layout of the
962 EGI 128-channel sensor net (figure adapted from Reynolds, Guy, & Zhang, 2011).

963

964 **Figure 3.** Common equivalent current dipoles activated across recognition memory tasks. Age
965 groups are divided into separate columns. The best fitting areas in common between the ERP and
966 VPC tasks are indicated using the color scale. The majority of best fitting areas were located in
967 inferior prefrontal regions (figure adapted from Reynolds, Courage, & Richards, 2010).

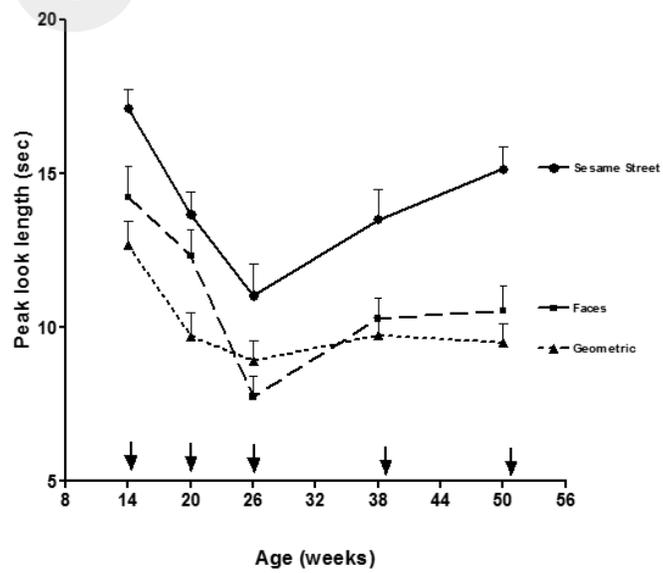
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Figure 1.TIF

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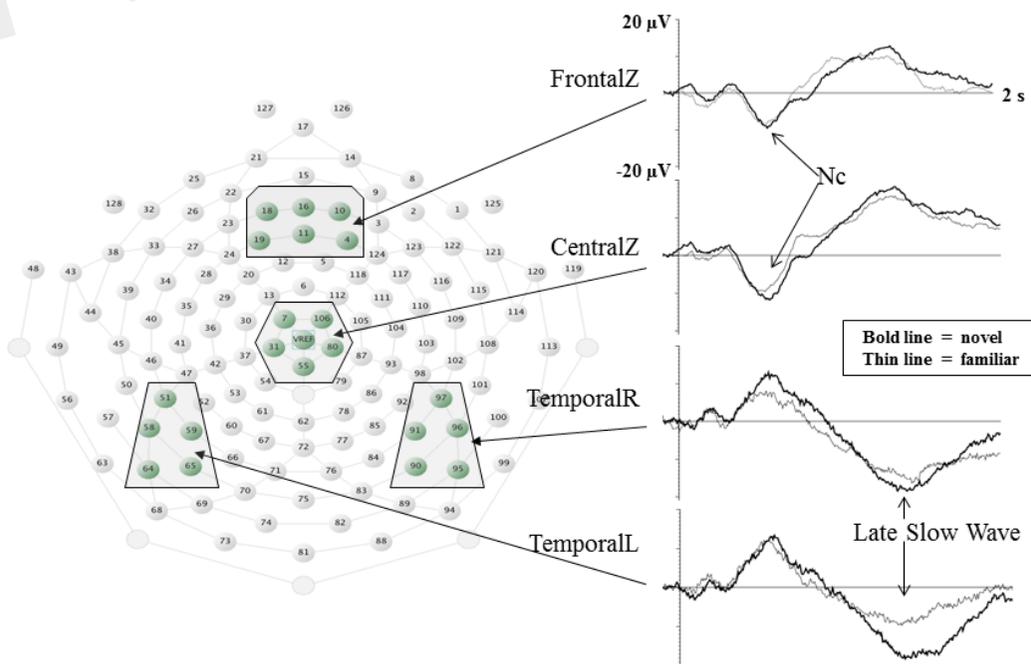


Note: Arrows indicate exact test age

Figure 2.TIF

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The Nc and LSW ERP Components



Cortical Sources of Nc ERP Component During Recognition Memory Tasks

