REVIEW | *Working Memory: Neural Mechanisms*

Visual working memory in early development: a developmental cognitive neuroscience perspective

Aaron T. Buss, Shannon Ross-Sheehy, and ⬤ **Greg D. Reynolds**
Department of Psychology, University of Tennessee, Knoxville, Tennessee

Buss AT, Ross-Sheehy S, Reynolds GD. Visual working memory in early development: a developmental cognitive neuroscience perspective. *J Neurophysiol* 120: 1472–1483, 2018. First published June 13, 2018; doi:10.1152/jn.00087. 2018.—In this article, we review the literature on the development of visual working memory (VWM). We focus on two major periods of development, infancy and early childhood. First, we discuss the innovative methods that have been devised to understand how the development of selective attention and perception provide the foundation of VWM abilities. We detail the behavioral and neural data associated with the development of VWM during infancy. Next, we discuss various signatures of development in VWM during early childhood in the context of spatial and featural memory processes. We focus on the developmental transition to more adult-like VWM properties. Finally, we discuss computational frameworks that have explained the complex patterns of behavior observed in VWM tasks from infancy to adulthood and attempt to explain links between measures of infant VWM and childhood VWM.

cognitive neuroscience; early childhood; infancy; visual working memory

INTRODUCTION

Visual short-term memory (VSTM) is a capacity-limited memory system involved in the brief storage of visual information. Because VSTM is fundamentally involved in other processes, such as perception and learning, it has been recognized as a visual working memory (VWM) system (Luck 2008; Oakes et al. 2013). VWM allows us to actively represent our visual environment for the purpose of mental tasks such as planning, comparison, and response selection (Baddeley 1986) and is functionally and anatomically distinct from long-term memory (Baddeley and Hitch 1974). Although we know much about the development of long-term memory over the first few years of life (for reviews, see Bauer 2009; Cowan 1995; Nelson 1995; Pelphrey and Reznick 2003; Reynolds 2015; Rose et al. 2004; Rovee-Collier and Cuevas 2009), we are only just beginning to understand the development of VWM in infancy and beyond. In this article, we review research on VWM in infancy and early childhood. We begin by reviewing foundational research on early visual behavior and highlighting the role of lower level visual processes in VWM. We then briefly review tasks exploring VWM development in infants and children, discussing important task-based considerations. Finally, we discuss neurally grounded computational models of VWM and highlight their important contributions to our un- derstanding of mechanisms of developmental change. Throughout, we focus on research examining both behavioral and neural correlates of VWM.

ORIGINS OF RESEARCH ON INFANT VISUAL MEMORY

Although infant VSTM is a relatively young research area, it comes from a long tradition of research examining simple visual behaviors in preverbal infants. This pioneering work by Robert Fantz and others was foundational and established critical parameters for using simple visual preferences to infer perceptual and even cognitive development (Colombo and Fagen 1990; Fantz 1964). In a now famous series of studies, infants were presented with a pair of images, one on the left and one on the right, and duration of looking to each image was measured. On subsequent trials, one of the images remained the same, whereas the other was swapped with a new image (locations of the novel and familiar images varied randomly from trial to trial). As memory for the familiar image grew, looking to the novel stimulus increased. Thus the appearance of a "novelty preference" could be taken as evidence for memory of the familiar image. This was some of the earliest work to systematically explore the development of visual memory in infancy.

Fantz theorized that these kinds of early visual exploratory behaviors may be necessary for typical postnatal development. If this is the case, he reasoned that infant eye movements must be selective, peripheral and central visual structures must be

Address for reprint requests and other correspondence: G. D. Reynolds, Dept. of Psychology, Univ. of Tennessee, Knoxville, TN 37996 (e-mail: greynolds@utk.edu).

sufficiently developed to support discrimination, and infants must be able to remember what they have seen (Fantz 1964). Because the demonstration of even a moderate novelty preference requires attainment of all three competencies, memory is inextricably linked to selectivity and discrimination. Following is a brief review on the development of each of these visual competencies and how they influence the emergence of VSTM.

Visual Selectivity

For visual exploration to fuel early learning and development, eye movements must be selective; that is, they must reliably be directed to events and objects that are currently relevant, such as a parent's face or a bottle being moved into view. Some of this selectivity is apparent in the first weeks of life and can be accomplished through simple bottom-up processing of perceptual characteristics such as motion, luminance contrast, or salience (Johnson 1992; Johnson et al. 1991; Nagata and Dannemiller 1996). Although the exact mechanisms of attentional selectivity in infancy are not as well understood (Johnson et al. 1991; Reynolds et al. 2013; Reynolds and Roth 2018), these early biases are typically thought to be largely involuntary.

Development from 3 to 6 mo is characterized by significant gains in the voluntary control of eye movements (Johnson 1990), and this selectivity is often described as a property of endogenous, or goal-directed, visual attention (Bahrick and Lickliter 2014; Yantis and Jonides 1990). Although specific brain areas may support aspects of attention such as switching or vigilance (Frick et al. 1999; Posner and Petersen 1990), attentional selectivity in general is most likely a distributed property of the entire brain (Desimone and Duncan 1995; Reynolds 2015). The rapid improvement in eye movement control across this age range is likely tied to further development of a network of structures involved in orienting, including the pulvinar nucleus of the thalamus, posterior parietal areas, and the frontal eye-fields (Johnson et al. 1991; Posner and Rothbart 2013; Reynolds and Romano 2016). These improvements in visual orienting and selective attention foster more efficient perceptual processing and memory (e.g., Reynolds and Richards 2005, 2017; Richards 1997), which in turn further facilitates learning.

Attentional selectivity may also be critical for VSTM, particularly when infants are young. For example, previous research examining the development of memory in infants has revealed that although VSTM improves rapidly between the 6th and 10th month of life (Oakes et al. 2006; Ross-Sheehy et al. 2003), it is highly constrained before 7.5 mo of age (Oakes et al. 2006). However, when an attention cue is used to direct attention, even 5-mo-old infants demonstrate memory for stimulus arrays that are beyond their memory abilities when their attention is not cued (Ross-Sheehy et al. 2011). Infants also appear to be able to update the contents of VSTM, a process that necessarily requires selective attention (Moher and Feigenson 2013; Yamaguchi and Feigenson 2008). This clearly demonstrates a critical interaction between selective attention mechanisms and VSTM, and this dynamic interaction influences looking behavior as early as 5 mo of age.

Visual Discrimination

The widespread adoption of infant visual preference paradigms resulted in a veritable boon of research examining the perceptual abilities of infants. This body of work suggests that most key visual perceptual abilities develop very early in infancy. For example, by 4 wk of age, infants can reliably discriminate colors such as red and green, even when controlling for brightness (Hamer et al. 1982), and by 3 mo, infants are likely trichromatic (i.e., fully functioning short-, medium-, and long-wavelength cones) and can discriminate red, green, and yellow (Adams and Courage 1995). Infant acuity similarly undergoes rapid postnatal development. By 3 mo of age, techniques that rely on reflexive orienting behaviors (optokinetic nystagmus, or OKN, and visual evoked potentials, or VEP) suggest Snellen equivalencies that range from 20/150 to around 20/300 (Dobson and Teller 1978). Although 3-mo-old infants have surprisingly well-developed color vision and acuity (at least for relatively close distances), these impressive abilities are partially mediated by relatively low-contrast sensitivity; a typical 3-mo-old requires ~50 times more luminance contrast than an adult to detect fine details in an image (Banks and Salapatek 1981; Brown and Lindsey 2009). However, given most functionally significant objects can be identified on the bases of their high-contrast, low-spatial frequency information (e.g., the face of a conspecific), even early infant learning can be relatively robust.

Visual Memory

It is likely that the early visual behaviors described above are influenced by limitations in VSTM. When an infant looks at an object, she or he begins to form a memory representation (Roder et al. 2000). This rapidly formed memory likely resides in VSTM, where capacity limits may influence the fidelity of the representation. When the infant then subsequently looks to a new image, this fading memory trace may interact with the current focus of gaze. Comparison via a VSTM mechanism such as this may support the detection of novelty, further influencing looking behavior. Although this interplay between previously fixated and currently fixated items is clearly memory dependent, deficits in either attention or discrimination also may influence both the fidelity of the memory trace and the subsequent detection of familiarity or novelty. Thus the appearance of deficits in memory may be driven by limits in VSTM (e.g., capacity limits, decay, interference), by limits in attentional selectivity, or by limits in perceptual discrimination. We focus on the development of VSTM in infancy and beyond, in an attempt to identify key neural and behavioral developmental events.

MEMORY IN INFANCY

Short-Term Memory or Working Memory?

As stated previously, work with adults suggests VWM is a rapidly decaying short-term "working" memory store, marked by its highly limited capacity of around three to four integrated objects (Baddeley and Hitch 1994; Baddeley and Logie 1999). Although the term "working memory" is often used with tasks that include some sort of behavioral response (i.e., remember the location, sort the cards, press a button, etc.), the terms

"working memory" and "visual short-term memory" are often conflated in both the infant and adult literature. In the adult literature, this distinction is largely theoretical, because most adult tasks require adults to act on their memory (e.g., press a button if you noticed a color change). To the extent that working memory is a short-term memory used in service of a task (e.g., a decision followed by a button press), then nearly all adult tasks test both working memory and short-term memory. However, there is growing consensus that working memory may also operate below the level of awareness (Hassin et al. 2009; Joyce 2016). This is important for work exploring infant VSTM and may help bridge the gap between infant, toddler, and adult tasks.

The term working memory, as it is now commonly understood, was first used by Atkinson and Shiffrin (1968) to describe the function of their hypothesized "short-term store." This short-term store was distinct from both the long-term store and the sensory register, and had some unique properties, including rapid decay and limited capacity. This model was important in that it supported the distinction of long- and short-term memory stores, an idea that had fallen out of favor at the time. Drawing on the strengths of the Atkinson and Shiffrin model, Baddeley and Hitch (1974) reconceptualized working memory as a multimodal system consisting of two short-term memory stores (the "phonological loop" for auditory information and the "visuospatial sketchpad" for visual information) under the attentional control of a "central executive." This inclusion of an attentional control process subsequently broadened the role of working memory to include critical "on line" cognitive processes such as reasoning, problem solving, response selection, and decision making (this model was later elaborated to include a multimodal "episodic buffer"; see Baddeley 2007). Although the Baddeley and Hitch (1974) model remains prominent, there are now multiple alternative frameworks, each of which has generated much empirical support (e.g., Cowan 2005; Kane and Engle 2002; Klingberg et al. 2002).

Importantly, one common feature of all of these models is the inclusion of some aspect of attentional or "executive" control. In adult tasks, this executive control is typically measured by using some sort of behavioral response; however, it is not clear that the behavioral response or explicit awareness of the task is required, per se. Recent studies utilizing "one-shot" change detection tasks indicate that infants can utilize information stored in VSTM in the service of other cognitive processes (Mitsven et al. 2018; Oakes et al. 2013), which according to some views would qualify VSTM as a working memory system (e.g., Baddeley 1986; Luck and Vogel 2013). For example, Mitsven et al. (2018) designed a cued visual search task to test the possibility that 10-mo-old infants' VSTM representations influence their subsequent looking behavior. Infants were shown a single 500-ms presentation of a central stimulus followed by a 300-ms delay and then a test array of two items presented to either side of the central fixation point. One item in the test array matched the one-shot stimulus presumably stored in VSTM, and the other item did not. Across two experiments utilizing colored squares and complex objects as stimuli, 10-mo-olds were found to be more likely to look at the nonmatching item than the matching item. These findings indicate that the infants' VSTM guided their subsequent visual search during the test trials. Thus it is likely that VSTM tasks do tap into VWM processes in infancy (Mitsven et al. 2018; also see Kibbe 2015). These findings also indicate that VSTM can direct infant selective attention and support the idea that attention and memory are linked in a bidirectional manner by mid to late infancy.

Improvements in VWM Across Infancy: Capacity and Features

Capacity limits constrain the amount of information that one can keep active in memory, which has important consequences for cognitive processes that involve comparison across multiple exemplars (e.g., learning to recognize a parent's face, learning to discriminate a bottle from toys, etc.). Despite its obvious importance, there has been relatively little work addressing this topic in infancy, partly because it is difficult to isolate VSTM from other longer term memory mechanisms. One key issue stems from the use of a novelty preference as test criterion and the relatively long encoding durations typically required for this behavioral response.

In an attempt to address this constraint, researchers have begun to rely on rapid, serial presentations during which arrays of colored squares appear and disappear rapidly (e.g., 500 ms on, 250 ms off, 500 ms on, etc.). With the use of a modified paired-comparison procedure, infants are presented with two blinking arrays, one on the left and one on the right. In one array, the color of a single, randomly selected square changes at every onset. In the other array, the colors of the squares remain constant across each onset (see Fig. 1, *top*). If infants can rapidly encode all the squares in the array and remember that information across the 250-ms delay interval, then they should notice when one changes color and look preferentially to that side. In other words, they should show a "change preference." Results across a series of studies using this approach have revealed that VSTM develops rapidly the first year of life. As shown in Fig. 1, 6.5-mo-old infants are able to detect change only for arrays with a set size of one item (*set size 1*), whereas older infants can detect change for arrays of up to three or four items (Oakes et al. 2006, 2009; Ross-Sheehy et al. 2003). Additional studies have revealed that these capacity limits in young infants are not driven by perceptual limitations (Ross-Sheehy et al. 2003), and performance is not improved even when every square in the changing arrays changes at every onset (Oakes et al. 2006). These dramatic deficits appear to be at least partially driven by a failure to bind color and location (Oakes et al. 2009), which may be ameliorated by the addition of an attention cue (Ross-Sheehy et al. 2011). More recent work with eye tracking suggests that, like adults, infant memory is about the same for simple features as it is for integrated objects (Kwon et al. 2014), and encoding speed rivals that of adult participants (Oakes et al. 2013). Although some similarities exist between certain characteristics of VSTM for infants and adults, at the end of the infancy period VSTM is still relatively immature.

Improvements in VWM Across Infancy: Duration and Stability

Although change preference tasks typically are used to assess VSTM capacity for simple features such as color and are typically assessed using computerized tasks, other aspects of memory improve rapidly between 6 and 9 mo and can more
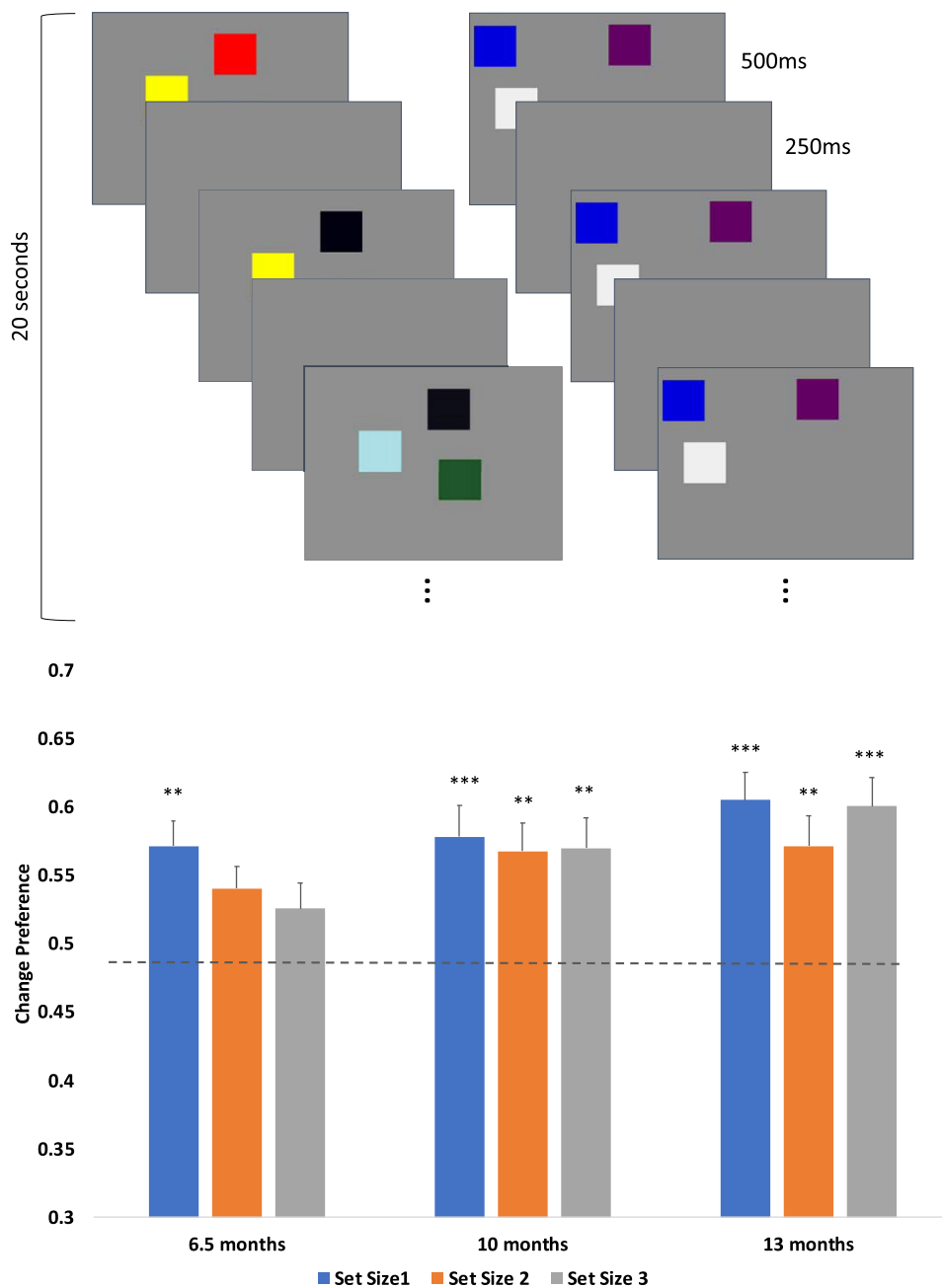
Fig. 1. Schematic of a *set size 3* trial (*top*) and preference for the changing stream by age and set size (*bottom*). Error bars are SE. **$P <$ 0.01; ***$P < 0.001$, significant difference from chance (0.5). [Adapted from Ross-Sheehy et al. (2003) by permission.]

readily be tested using explicit behavioral responses such as reaching. For example, in the A-not-B task, infants are presented with two or more hiding wells. While the infant is watching, an object is hidden inside one of these wells. After a brief delay, the infant is allowed to reach to retrieve the object. After a series of successful retrievals from a given well, the hiding place is switched to a different well. The A-not-B error refers to the strong tendency of young infants to continue to reach to the original well (A location) even after watching the experimenter switch hiding places to the second well (B location). Infants are less likely to show this perseverative error after 8–9 mo of age (Cuevas and Bell 2011; Hofstadter and Reznick 1996; Pelphrey et al. 2004).

Diamond (1985, 1990) has proposed the higher success rate for older infants on the A-not-B task is based on gains in inhibitory control tied to maturation of dorsolateral pre-frontal cortex (dlPFC). Support for the possibility that younger infants may lack sufficient inhibitory motor control and cognitive flexibility for successful A-not-B performance has come from studies demonstrating that when infants' gaze behavior and looking behavior do not match on a given trial, they are more likely to gaze at the correct hiding location than to reach for the correct hiding location (Hofstadter and Reznick 1996). Importantly, Smith et al. (1999) showed that beyond a lack of inhibitory control, several contextual factors contribute to the A-not-B error for younger infants, including the number of training trials, the number of reaches to the A location before the switch, and the participant's posture on a given trial. Thus, although the A-not-B task clearly involves VWM, successful task performance also likely involves inhibitory processes and a certain level of cognitive flexibility.

To examine neural correlates of VWM and inhibitory control in infancy, Bell and colleagues have utilized the electroencephalogram (EEG) while infants perform looking versions of the A-not-B task (e.g., Bell 2012; Bell and Adams 1999; Bell and Wolfe 2007; Cuevas and Bell 2011). From these studies, it has been shown that both baseline frontal EEG power and task-related changes in EEG power from 6 to 9 Hz are correlated with successful performance on the A-not-B task (Bell 2002; Bell and Fox 1994). Frontal parietal and frontal occipital EEG coherence values also correlate with successful A-not-B performance (Bell 2012). In a recent study, Bacher et al. (2017) utilized spontaneous blinking as an indirect measure of dopaminergic function and found that variability in spontaneous blink rate was positively associated with 10-mo-olds' VWM performance on the A-not-B task.

At a broad level, these findings support the possibility that a frontal parietal network and the dopaminergic neurotransmitter system are involved in VWM in infancy. This is consistent with findings from comparative research showing increased extracellular dopamine in prefrontal cortex for nonhuman primates during performance of a VWM task (Watanabe et al. 1997). Research utilizing oculomotor delayed response tasks has found evidence of spatial tuning of neurons in dPFC associated with visuospatial working memory in nonhuman primates (Goldman-Rakic 1995; Rao et al. 1999). Delay period activity within spatially selective cells in dPFC has been proposed to represent the neural basis of spatial visuospatial working memory (Funahashi et al. 1989). However, according to Sreenivasan et al. (2014), sensory cortices maintain specific representations of VWM content, whereas lPFC maintains representations of goal-related variables that may be involved in attentional control aspects of VWM.

Until recently, research examining functional neural activation in human participants during early development faced many practical challenges. However, recent applications using functional near-infrared spectroscopy (fNIRS) have allowed researchers to begin to observe functional neural activation in infants and children. fNIRS overcomes many of the challenges of using functional magnetic resonance imaging (fMRI) to measure cortical blood flow by using a lightweight cap with embedded near-infrared laser emitters and detectors. By monitoring light intensity changes as near-infrared light is absorbed by oxy- and deoxyhemoglobin, this technology can measure regional changes in blood oxygen concentration as infants and children perform a cognitive task. For example, Baird et al. (2002) measured activation from lateral frontal cortex of 10- to 12-mo-olds in the A-not-B task and reported that infants who correctly searched at the B location on B trials showed stronger activation in lateral frontal cortex compared with infants who perseverated on reaching to the A location. Unfortunately, both fNIRS and EEG/source analysis techniques for neuroimaging are primarily constrained to activity produced in cortical regions and cannot provide evidence regarding the potential contributions of subcortical regions to a given process. However, findings from VWM studies utilizing EEG (e.g., Bell 2012; Cuevas and Bell 2011) and fNIRS (Baird et al. 2002) with infant participants are consistent with findings from comparative research (Goldman-Rakic 1995; Watanabe et al. 1997) and neuroimaging research on older children and adults indicating areas of dlPFC, ventrolateral prefrontal cortex (vlPFC), intraparietal cortex, and posterior parietal cortex are recruited

during VWM tasks (Courtney et al. 1997; Crone et al. 2006; Fuster 1997; Klingberg et al. 2002; Scherf et al. 2006; Sweeney et al. 1996).

Improvements in VWM: Binding Features to Locations

Binding in infants has been explored using a modified change preference task (Oakes et al. 2006, 2009). As described by Ross-Sheehy et. al (2003), infants are shown two arrays, each consisting of three colored squares that blink on and off for 20 s (500 ms on, 300 ms off, 500 ms on, etc.). In one array, the colors of the three squares stay the same at every onset, and in the other array, the color-location bindings for all three squares are swapped at every onset. If infants bind color to location in VSTM, they should notice when the bindings change and look preferentially to the changing side. Note that this task should be trivially easy, because infants need only encode a single square to detect a change. Results demonstrate that 6.5-mo-old infants show no evidence of recognizing the binding swap, whereas infants just 1 mo older do (Oakes et al. 2006).

The ability of infants to bind objects to locations has also been examined in a series of studies by Káldy and colleagues (Kaldy et al. 2016; Káldy and Leslie 2003, 2005; Káldy and Sigala 2004). For example, Káldy and Leslie (2003, 2005) designed an occlusion task aimed at testing infants' ability to perform both identification and individuation processes involved in VWM. Infants are familiarized with two objects, and then the objects are each placed behind an occluder. The occluders are then removed after a delay period. On change trials, removal of the occluders reveals the objects in reversed locations from their original hiding spots. On no-change trials, the objects remain in their original hiding locations. Infant looking behavior is measured in response to change trials vs. no-change trials. Longer looking on change trials indicates successful individuation of the object, which involves binding of object and location in VWM. Across studies, findings indicate that 6-mo-olds are only able to bind object to location for the last object placed behind an occluder, whereas 9-mo-olds are able to bind object to location for both objects (Káldy and Leslie 2003, 2005). Káldy and Leslie (2005) proposed that gains in VWM performance on occlusion tasks that occur from 6 to 9 mo of age are related to further development of medial temporal lobe structures, such as entorhinal cortex and parahippocampal cortex.

Research utilizing fNIRS to examine neural correlates of object processing in infancy has provided support for the possibility that regions of temporal cortex are involved in infant VWM for occluded objects (e.g., Wilcox and Biondi 2015; Wilcox et al. 2010, 2012). For example, Wilcox et al. (2012) tested 3- to 5- and 11- to 12-mo-old infants in an occlusion task in which objects moved behind a screen and then reappeared on the other side of the screen. Infants were tested in three conditions: shape difference, color difference, or control. In the shape-difference condition, the object changed shape but not color on reappearance. In the color-difference condition, the object changed color but not shape. The object remained unchanged in the control condition.

Analysis of the fNIRS data revealed that both age groups demonstrated activation of anterior temporal areas in difference conditions but not in the control condition. However, 3- to

5-mo-olds only demonstrated differential activation of anterior temporal cortex on the basis of changes in shape, whereas 11- to 12-mo-olds demonstrated differential activation on the basis of both shape and color. Based on the anterior temporal findings, the authors concluded that between 5 and 11 mo of age, infants develop the ability to individuate objects on the basis of VWM for both shape and color features. Younger infants also demonstrated activation of parietal areas on shape difference trials, an effect that was not found in 11- to 12-mo-olds in any of the three conditions. According to Wilcox et al. (2012), this activation of parietal areas was exclusive to the younger age group, because at 3 to 5 mo of age, infants are dependent on motion-carried information to extract information regarding shape. By 11 to 12 mo of age, infants are able to extract, and retain in VWM, both shape and color features of objects without relying on motion-based information.

In summary, infancy is characterized by major gains in VWM. Figure 2 tracks developmental trends in performance on the behavioral and neural measures of VWM discussed above. Findings across multiple infant tasks clearly indicate significant improvement in VWM from ~4 to 12 mo of age, with the most notable improvements coming after 6 mo of age (Cuevas and Bell 2010; Diamond 1990; Hofstadter and Reznick 1996; Kaldy et al. 2016; Káldy and Leslie 2003, 2005; Oakes et al., 2009, 2006; O'Gilmore and Johnson 1995; Pelphrey et al. 2004; Reznick et al. 2004; Ross-Sheehy et al. 2003). The improvements in VWM that occur primarily across the second half of the first postnatal year include the following: an increase in VSTM capacity measured using change preference tasks from one item to three to four items (Oakes et al. 2006, 2009; Ross-Sheehy et al. 2003), increased ability to bind features (such as shape and color) and location of objects in occlusion and change preference tasks (Káldy and Leslie 2003, 2005; Oakes et al., 2006, 2009), and improved performance on the A-not-B task (Cuevas and Bell 2010; Hofstadter and Reznick 1996; Pelphrey et al. 2004).

There has been some inconsistency in findings from studies measuring neural correlates of VWM in infancy. There is evidence from studies utilizing the A-not-B task that a frontal parietal network and the dopaminergic neurotransmitter system are critically involved in successful performance (Bacher et al. 2017; Baird et al. 2002; Bell 2012). In contrast, results from occlusion studies examining object individuation and VWM for features and locations highlight the importance of anterior temporal areas for successful performance (Wilcox et al. 2010, 2012). The inconsistencies in findings across studies may be due to the possibility that these tasks tap into different aspects of VWM, and in contrast to change preference and object identification tasks, the A-not-B task likely involves an inhibitory or attentional control component that goes beyond basic VWM processes (Káldy and Leslie 2003). However, there is currently no clear consensus in the field on exactly what, if anything, separates VSTM from VWM in infancy.

Mitsven et al. (2018) have claimed that VSTM qualifies as a VWM system because it has been found to influence subsequent visual search behavior (also see O'Gilmore and Johnson 1995). However, according to some, the ability to maintain task-relevant information in the face of task-irrelevant information is a key aspect of VWM that may not be met by basic visual search behavior (e.g., Vogel et al. 2005). Additionally, the length of familiarization on object identification tasks (e.g., Káldy and Leslie 2003, 2005) may push the limits of VSTM and instead tap into aspects of long-term memory. Further work focused on disentangling the neural mechanisms involved in VSTM, VWM, and long-term memory tasks in infancy is needed to help resolve issues related to whether these tasks tap into similar or distinct neural and cognitive processes. There has been a great deal of research on VWM in early childhood that provides insight into mechanisms involved in the development of VWM, which we now turn our focus to (for related research from middle childhood on, see Amso and Scerif 2015; Astle and Scerif 2011; Awh et al. 2006; Shimi et al. 2014).

WORKING MEMORY IN EARLY CHILDHOOD

Improvements in VWM: Capacity and Features

Early childhood is a period during which children's performance on spatial working memory and VWM tasks improves to equivalent levels as adults. Measures of VWM during this period are predictive of intelligence and academic performance (Raghubar et al. 2010; Rose et al. 2008), suggesting that these changes influence important aspects of general cognitive functioning. Although working memory develops into a distinct aspect of cognitive functioning in adulthood (Miyake et al.
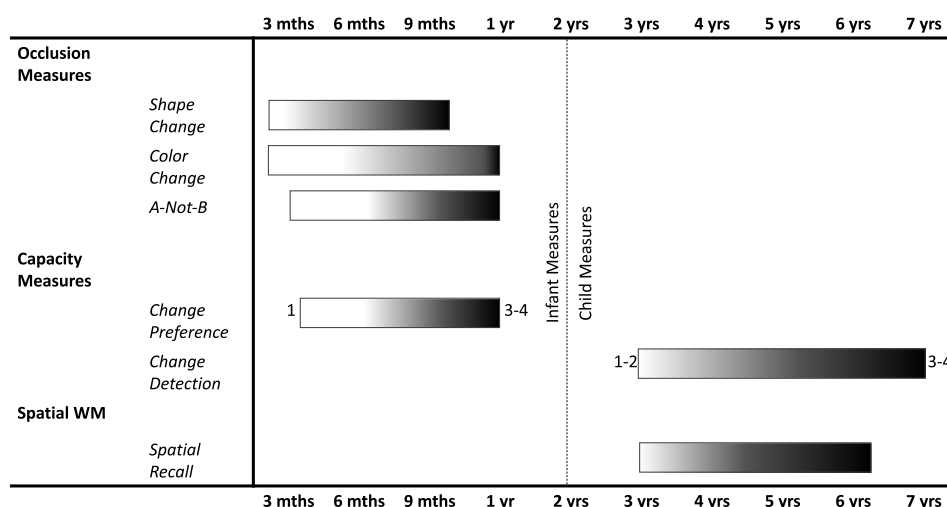
Fig. 2. General summary of developmental gains in visual working memory (VWM) performance by task and age as discussed in the literature review. Bars represent the age range each task has been typically used with, and dashed vertical line indicates the transition from the use of infant measures to child measures between 1 and 3 yr of age. Shading of bar at each age point (*x*-axis) is relative to peak performance on the task that bar represents. The darkest point in each bar represents the approximate age participants reach peak performance on that task. Numbers to *left* and *right* of bars representing capacity measures indicate the average set size for which participants demonstrate evidence of detecting changes at the earliest and oldest ages tested. mths, Months.

2000), during early childhood, measures of working memory are highly correlated with measures of inhibitory control (Tsujimoto et al. 2007; Wiebe et al. 2011). Change detection tasks can be used to test capacity limits in toddlers. Unlike infants, however, toddlers can indicate whether a given trial is a "same" trial or a "different" trial. In the context of the change-detection task, children's VWM capacity grows from around 1.5 objects at age 3 yr to a more adult-like three to four objects at age 7 yr (Riggs et al. 2006; Simmering 2012, 2016; Simmering et al. 2015). Interestingly, performance across same and different trials improves in a systematic fashion during this period. Very young children tend to respond with "change" at a higher rate than older children and adults. This leads to some children showing more frequent false-alarm errors relative to miss errors. As a consequence, 3-yr-olds perform more poorly on no-change trials but better on change trials (Buss et al. 2014; Simmering 2016; Simmering et al. 2015). Moreover, performance on tasks involving color is better than performance on tasks involving shapes, and performance with familiar colors is better than performance with less familiar colors (Simmering et al. 2015). Lastly, children's estimation of remembered color features becomes more precise (Simmering and Miller 2016).

Improvements in Spatial Working Memory: Duration and Stability

Unique signatures of development during early childhood have also been identified in the domain of spatial working memory. Between the ages of 3 and 6 yr, children's responses on spatial recall show systematic patterns of errors. In spatial recall tasks, a location is briefly cued by presentation of a stimulus, and then, after a delay, participants are instructed to indicate where the cue was presented. This task has been implemented with a reference line to divide a homogenous space. Early in development, children's responses are biased toward the reference lines. By the age of 6 yr, however, children's biases shift away from the midline similar to adults' spatial recall (Schutte and Spencer 2009). Similar to feature memory recall, spatial recall also shows increases in precision during early childhood (Schutte et al. 2003). Lastly, children's spatial recall is influenced by habits established in the context of a task similar to the A-not-B error. That is, Spencer and Schutte (2004) administered a task in which a toy was hidden within a homogeneous and continuous space to 2- to 4-yr-olds. After they observed a toy being hidden at an A location over a series of trials, the toy was then hidden at a B location and the children were allowed to search for the object. On these B trials, children's searches were biased toward the A location where they observed the toy being hidden.

Improvements in VWM: Neuroimaging Results

Neuroimaging studies with older children and adults have revealed a network of regions that are involved with different aspects of VWM, including encoding, maintenance, and comparison. These regions include intraparietal sulcus, temporoparietal junction, and lPFC, among other regions (e.g., Crone et al. 2006; D'Esposito et al. 1999; Courtney et al. 1997; Fuster 1997; Klingberg et al. 2002; Scherf et al. 2006; Sweeney et al. 1996; Wijeakumar et al. 2017). Buss et al. (2014) recorded fNIRS data from bilateral frontal and parietal cortices while 3-

and 4-yr-old children performed a change detection task with shape stimuli. Children showed task-related activation in frontal and parietal regions. Typically, a relationship between performance and hemodynamic activity is observed with adult participants such that activation in parietal cortex increases as a function of set size and asymptotes once the number of items exceeds capacity. However, activation in parietal cortex increased up to *set size 3* despite capacity estimates below two items (see Fig. 3). Developmentally, there was an increase in activation as a function of set size in parietal cortex such that 4-yr-olds showed larger increases in activation over set size relative to 3-yr-olds. Right frontal cortex showed an increase in activation between *set sizes 1* and *2*. However, at *set size 3*, activation dropped back to *set-size 1* levels. This suggests that activation within frontal cortex increases across set sizes that are within a child's ability but drops off as the number of items exceeds capacity.

Tsujimoto et al. (2004) used fNIRS to compare frontal activation during a spatial working memory task between a group of 5- and 6-yr-olds and a group of adults. Activation was observed in similar regions between age groups, suggesting that children engage similar neural mechanisms during spatial working memory. However, EEG data suggest that young children rely more on processing in posterior brain regions, whereas adults rely more on anterior brain regions (Barriga-Paulino et al. 2015). Perlman et al. (2016) used fNIRS to examine activation while 3- to 7-yr-old children performed a spatial working memory task. Increases in activation were observed in bilateral prefrontal cortex that corresponded to developmental improvements in spatial working memory. Furthermore, activation in these regions increased as the delay during which the memory was maintained increased. Taken together, these findings indicate that areas of frontal, parietal, and temporal cortex are involved in VWM throughout early childhood; however, children show increased activity in frontal areas during VWM tasks with increases in age, task demands, and task performance.

Modeling VWM Development

The development of VWM is marked by improvements in both the amount of information that can be maintained and the precision of the representations being stored. Theories of VWM typically frame performance around the idea of a fixed number of slots measured as the capacity of VWM (Luck and Vogel 1997; Pashler 1988; Rouder et al. 2011; Zhang and Luck 2008) or the allocation of resources to each representation indexed by the precision of representations in VWM (Bays et al. 2009; Bays and Husain 2008; Wilken and Ma 2004). More recent iterations of these theories have formulated Bayesian modeling methods to quantify and test predictions of capacity and precision models (e.g., Brady and Tenenbaum 2013; Donkin et al. 2013; Kary et al. 2016; Rouder et al. 2008; Sims et al. 2012). Developmental improvements in VWM are thought to reflect increases in the capacity of VWM (Cowan 2013; Riggs et al. 2006) or the precision of VWM representations (Burnett Heyes et al. 2012).

An alternative modeling approach focuses on the dynamics that give rise to the formation and maintenance of VWM representations. Improvements in performance described above have been formally explained using a neural process
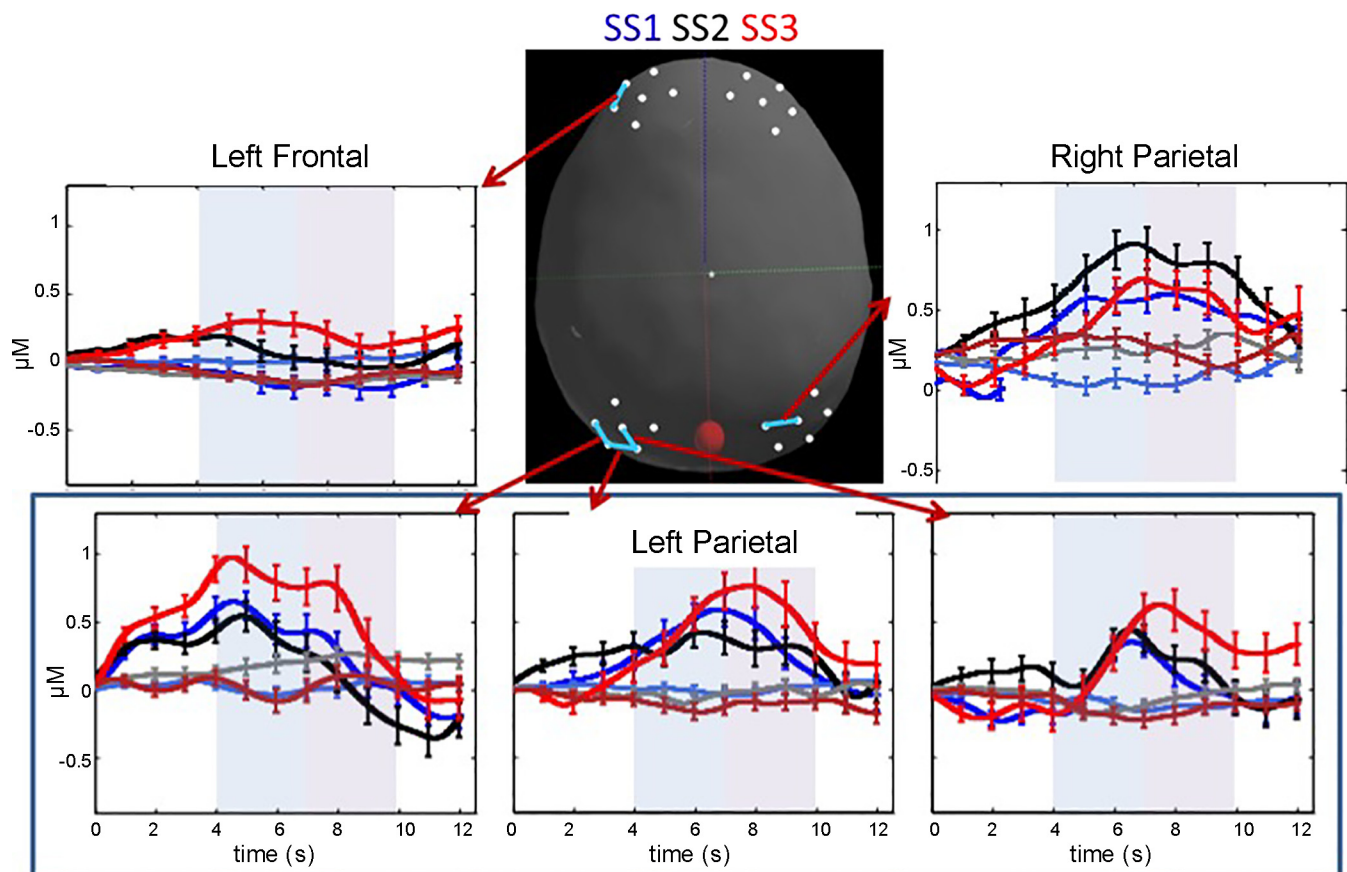
Fig. 3. Concentrations of oxyhemoglobin (dark lines) and deoxyhemoglobin (light colors) for channels showing an effect of set size (SS). *Inset* image shows the locations of the activated channels on frontal (*top left* plot), left parietal (*bottom* plots), and right parietal (*top right* plot) regions. The shaded regions are the expected peak response to the memory array (blue shading) and test array (pink shading). [Adapted from Buss et al. (2014) by permission.]

model. Dynamic neural field (DNF) architectures implement neural population dynamics that simulate the real-time dynamics of excitatory and inhibitory interactions that underlie the formation and maintenance of visual representations. The neural fields are composed of neural units that are tuned to dimensions of visual information such as space, color, or shape. In these applications, developmental improvements in VWM performance are explained through increasing the strength of excitatory and inhibitory interactions. Starting with the A-not-B task, Thelen et al. (2001) demonstrated how successful reaching on B trials can be supported through the ability to form an active representation of the B location that persists between the cueing and reaching events. In the context of the A-not-B task, stronger excitatory and inhibitory neural interactions allow the model to maintain an active representation of the B location after the cueing event and suppress the habit associated with reaching to the A location. This model has been extended to spatial recall tasks used in later development that require participants to maintain a spatial representation within a continuous space. By using increases in excitatory and inhibitory neural interactions as a proxy for development, this work explains increases in the precision of spatial VWM, drifts in VWM over increased delay times between encoding and reporting, changes in the shift toward midline to away from midline over development, and the influence of previous spatial memories on the dynamics of spatial VWM (Schutte and Spencer 2009; Schutte et al. 2003; Simmering et al. 2008).

Simmering (2016) describes a DNF architecture that explains development on change-detection tasks from early childhood through adulthood. In the model, active VWM representations are supported by local-excitatory/lateral-inhibitory neural interactions with populations of neural units that are tuned to metric perceptual dimensions such as color. The activation of VWM representations establishes an inhibitory perceptual filter on a population of neural units that are responsible for encoding stimuli. Through these processes, the model can build active VWM representations that can be compared with subsequently presented stimuli. Specifically, stimuli that match items maintained in VWM will encounter strong inhibitory suppression, but stimuli that do not match items maintained in VWM will not encounter such inhibition. Based on the comparison of activation in VWM and visual stimuli presented during the comparison phase of the trial, the model generates active decisions corresponding to same and different responses. This model architecture simulated accuracy on same and different trials (i.e., hits, misses, false alarms, and correct rejections) that matched the performance of children and adults. As neural interactions in the model were strengthened, model performance improved to match that of older age groups. Moreover, this model was able to address one of the primary factors that has limited our understanding of VWM development from infancy through early childhood and into adulthood. Specifically, the tasks used to probe VWM during these different age ranges rely on different types of responses.

The use of preferential looking tasks during infancy and change-detection tasks during childhood have led to inconsistencies in the estimated capacity between infancy, early childhood, and adulthood (see Fig. 2). Simmering (2016) was able explain associations in performance between these tasks. Specifically, the same VWM system was coupled to a system that implemented looking dynamics, and the model was allowed to freely look between inputs that matched the properties of the displays in the preferential looking task. Based on increases in the strength of neural interactions, the model matched performance in both tasks with a group of 3-, 4-, and 5-yr-olds and adults.

In summary, research in early childhood has uncovered various types of changes in VWM performance with spatial, color, and shape information. VWM processes in early childhood become more stable and precise. This is revealed by tasks that require recall of specific visual features and tasks that require comparison of remembered information with currently available stimuli. Neural process models suggest that the complex patterns of performance can emerge from changes in the strength of neural connectivity and demands imposed by different tasks.

CONCLUSION

VWM shows significant development across infancy and early childhood. Much of the developmental changes that occur across infancy in VSTM and VWM coincide with major gains in visual attention and perceptual processing. As the infant develops greater eye movement control in the first 6 mo of postnatal development (Courage et al. 2006; Johnson et al. 1991; Posner and Rothbart 2013), its capacity for directing selective attention in an efficient and functional manner for supporting VWM processes increases dramatically. Similarly, as perceptual sensitivity increases significantly across this same age range, the input available to the infant for memory processing expands dramatically. However, VWM also influences visual search in infancy (Mitsven et al. 2018), and thus there are likely bidirectional effects between visual attention and VWM in infancy and beyond (Amso and Scerif 2015; Astle and Scerif 2011; Awh et al. 2006; Reynolds and Romano 2016; Shimi et al. 2014). As can be seen in Fig. 2, from 6 to 13 mo of age, infants demonstrate a steady increase in VWM capacity (Ross-Sheehy et al. 2003, 2011). Within this age range, infants also show increased ability to bind objects and locations (Káldy and Leslie 2003, 2005). Gains in VWM capacity continue through the early childhood years, paired with increased accuracy in VWM for spatial and featural information (Riggs et al. 2006; Simmering 2012, 2016; Simmering et al., 2015).

Although there is some disagreement in the underlying neural underpinnings of these developmental changes, the extant literature indicates areas of frontal, parietal, and temporal cortex as well as the dopaminergic neurotransmitter system are involved in VWM in infancy (Bacher et al. 2017; Baird et al. 2002; Bell 2012; Wilcox and Biondi 2015; Wilcox et al. 2010, 2012) and childhood (Buss et al. 2014; Crone et al. 2006; Klingberg et al. 2002; Scherf et al. 2006; Sweeney et al. 1996). Increases in frontal activity are found to occur with increases in age, task demands, and task performance (Buss et al. 2016; Perlman et al. 2016; Tsujimoto et al. 2004). Modeling work

supports the likelihood that the strengthening of local-excitatory and lateral-inhibitory connections within this network is fundamentally involved in developmental gains in VWM (Schutte and Spencer 2009; Shutte et al. 2003; Simmering 2016; Simmering et al. 2008; Thelen et al. 2001). Pressing issues for future research will be to specify how changes in performance across different measures of VWM during early childhood arise from the types of neural processes that have been uncovered, to specify the mechanisms that create changes in the neurocognitive system over development and how these mechanisms are influenced by experiences, and to understand how performance in these relatively simple VWM tasks are related to processing and performance in more complex aspects of cognition.

DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

AUTHOR CONTRIBUTIONS

A.T.B., S.R.-S., and G.D.R. prepared figures; A.T.B., S.R.-S., and G.D.R. drafted manuscript; A.T.B., S.R.-S., and G.D.R. edited and revised manuscript; A.T.B., S.R.-S., and G.D.R. approved final version of manuscript.

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