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Neurodevelopment of Attention, Learning, and Memory Systems in Infancy

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Abstract

Understanding how we come to make sense of our environments requires understanding both how we take in new information and how we flexibly process and store that information in memory for subsequent retrieval. In other words, infant cognitive development research is best served by studies that probe infant attention as well as infant learning and memory development. In this article, we first review what is known about infant attention and what is known about a selection of learning systems available in infancy. Then, we review what is known about the interactions between attention and these systems, focusing on infancy when possible but highlighting relevant child and adult literatures when infant research is yet scarce. Finally, we close by proposing a path forward, which we believe will result in a clearer understanding of the interactions between attention and memory that govern infant learning.

Contents

INTRODUCTION

Learning to navigate the world around us is a daunting task, especially for infants with little information about what might be useful for success in present or future contexts. Understanding how we come to make sense of our environments requires understanding both how we take in new information and how we flexibly process and store that information in memory for subsequent retrieval. In other words, infant cognitive development research is best served by studies that probe infant attention as well as infant learning and memory development. Although researchers have made valuable progress on these two fronts, a third aspect of cognitive development is only recently being formally examined through the lens of rigorous science. Specifically, attention and memory interact in nuanced ways to predict later learning. In this review, we propose that understanding this interaction requires a characterization that accounts for the ecology of infants, who have different experiences, goals, and neural hardware available to them.

This article is divided as follows. First, we review what is known about infant attention and what is known about a selection of learning systems available in infancy. For the purposes of this article we highlight spatial learning, statistical learning, reward and reinforcement learning, threat-based learning, and early memory retrieval processes. We note at the outset that we use the terms learning and memory interchangeably, as befitting the reviewed tasks. Then, we review what is known about the interactions between these systems and attention, focusing on infancy when possible but highlighting relevant child and adult literatures when infant research is yet scarce. Finally, we close by proposing a path forward that we believe will result in a clearer understanding of the interactions between attention and memory that govern infant learning.

VISUAL ATTENTION DEVELOPMENT

In this first section, we review the development of alerting, orienting, executive, and selective attention processes. In 1990, Michael Posner and Steven Petersen published a seminal piece that described attention as a group of these distinct but related processes (Posner & Petersen 1990). In the years that followed, scientists were able to examine these processes using specific tasks and to link task-based behavior with brain activation using functional magnetic resonance imaging (MRI) as well as to neurotransmitter function. Their framework has been used to structure studies that aim to understand the development of attention in human infancy. Recently, a more nuanced developmental perspective on attention has emerged, where these same processes can be understood to emerge hierarchically in response to increases in sensory experience via a biased competition lens (Amso & Scerif 2015, Lynn & Amso 2021). We discuss each in turn. We acknowledge that although the focus of this work is on reviewing the development of visual attention processes, auditory attention is equally valuable but less studied in the context of attention and memory interactions.

Visual Attention Development Through the Lens of Networks

The attentional process of alerting refers to being in a state of preparedness to respond to an external cue (Posner & Petersen 1990) and recruits the locus coeruleus, parietal, and frontal regions in studies of both children and adults (Fan et al. 2002, Konrad et al. 2005). It is modulated by the neurotransmitter noradrenaline (Clark et al. 1989, Witte & Marrocco 1997). Behavioral data from human infants indicate that alerting responses emerge early in development, with full-term newborns spending about 20% of their time in an alert state (Colombo & Horowitz 1987). Between birth and 3 months, the amount of time spent in an alert state increases significantly (Wolff 1965). Early in development, it appears that alert states are initiated by exogenous cues (i.e., perceptually salient information) or by lower-level mechanisms of arousal, such as tactile stimulation via feeding or swaddling (for a review, see Colombo 2001), rather than being internally driven.

Later to emerge than alerting is visual attention orienting, which involves shifting attention toward or away from different information, either space or objects (Colombo 2001). Very early in life, orienting is involuntary—direct pathways from the retina to the superior colliculus lead newborns to fixate on motion and high-contrast edges (Johnson 2001, Johnson et al. 1991). Moreover, there is a pattern of oculomotor behavior called sticky fixation, where infants have trouble disengaging from one source of information to fixate on something else (e.g., Frick et al. 1999, Hood 1995). Later, voluntary shifts of attention orienting can be overt (involving movement of the head or eyes) or covert (without movement of the head or eyes). Visual attention orienting recruits brain regions distinct from alerting, including (as mentioned) the superior colliculus, frontal eye fields, the parietal cortex, and the pulvinar nucleus of the thalamus (Colombo 2001, Posner & Petersen 1990), which together have been referred to as the posterior attention system (Colombo 2001). Unlike alerting, orienting is modulated by the neurotransmitter acetylcholine.

Experimental evidence for the mechanisms underlying visual attention-orienting behavior is frequently obtained using spatial cueing paradigms (Posner 1980), which measure how quickly someone attends to a target, in response to either a predictive cue or an unpredictive cue. In these paradigms, infants attend to a central fixation stimulus while a brief cue is presented to either the right or left. Infants as young as 3–4 months old (Johnson et al. 1991, Markant & Amso 2013) can show a facilitation of their orienting response if the interval between the cue and target is brief. In other words, a covert shift of attention to the cued location results in a facilitation of eye movement response to the target when it is presented at that same location, relative to eye movement reaction time if the cue had not previously directed attention to that location. However, if the target is presented after a delay (i.e., on the order of 600–2,000 ms after the cue), reaction times to previously cued locations actually increase, suggesting the previously cued location becomes suppressed relative to the noncued location (Markant & Amso 2013, Markant et al. 2015, Posner et al. 1985, Richards 2000). This is called inhibition of return (IOR), and it emerges around 6 months of age before stabilizing by 9 months (Amso & Johnson 2008, Hood 1993, Johnson & Tucker 1996, Markant & Amso 2013, Markant et al. 2015, Richards 2000).

This IOR mechanism has been argued to be important for effective visual search in complex displays (Klein 2000). Visual search tasks generally involve a target that participants aim to find among an array of distractors. Data from infant visual search studies are consistent with the developmental timing of visual attention orienting alongside concurrent suppression (i.e., IOR). For example, in one study, infants started attending to a moving target in a display of static targets between 2 and 4.5 months of age (Dannemiller 2005). In line with this, other studies have shown that 3-month-olds can attend to a moving target in a display of static targets and attend to an oriented bar from a display of vertical bars (Amso & Johnson 2006) but that performance on both of these tasks improves between 3 and 10 months of age (Frank et al. 2014).

While the majority of studies on visual attention orienting have been focused on the spatial dimension, visual attention orienting can also be studied by examining object-based attention. Object-based attention is attention to one or more objects or features over others, which results in a processing benefit for the attended object. In 2013, Bulf & Valenza (2013) demonstrated object attention in 8-month-olds by presenting babies with two identical bars on a screen. Then, a cue was presented at the end of one of the bars. After a short delay, infants were faster at detecting a target that appeared on the other end of the cued bar than they were at detecting a target that appeared just as far away but on the other bar. A more recent study compared how infants orient toward targets that matched a cue on either the shape of the cued object or one of its other distinctive features (color, orientation, or motion) (Werchan et al. 2019). For example, an infant would be presented with a yellow apple as a cue in the center of a screen. This apple would then disappear, and a red apple and a yellow banana would appear on either side of the screen. The experimenters interpreted orienting to the object match (i.e., looking at the red apple) as evidence of object-based attention and interpreted orienting to the feature match (i.e., looking at the yellow banana) as evidence of feature-based attention. They report a nuanced pattern of results—overall, object-based attention increased as the shape of the object match looked more like the cued object and the particular feature in question interacted with age to predict object-based attention. By 3–5 months of age, babies oriented to the object match over an orientation match, and by 9–12 months of age babies oriented to the object match over a motion match. Variability in features aside, these results also suggest babies can use object-based attention to orient within the first year of life (Werchan et al. 2019). Finally, studies that use faces as stimuli may be informative with respect to object-based attention development. For example, early in infancy, babies look at the most physically salient stimulus in a set of objects, even if that object has no meaning to them. By 6 months, they instead look at a face present in the object set, suggesting that using object familiarity to guide attention emerges before 6 months (Kwon et al. 2016).

The final attention network according to the Posner & Petersen (1990) approach is the executive attention network. Executive attention is a process that resolves conflict between competing inputs in order to select a goal-relevant action. In adults and children, this process recruits the anterior cingulate, anterior insula, frontal cortex, and striatum and is modulated by dopamine (see, for example, Colombo 2001, Posner & Petersen 1990). Tasks used to measure executive attention include cueing tasks (described above), flanker tasks (in which a central arrow pointing left or right is flanked by arrows on either side, and participants indicate which direction the central arrow points) or antisaccade tasks (in which participants are trained to look away from a stimulus rather than toward it) (for a review, see Amso & Scerif 2015). Rudimentary patterns of executive attention processes may start to emerge in the control of eye movements around 4 months of age yet continue to mature into adulthood. It is around 4 months of age that participants can be trained to look away from a stimulus in an antisaccade task (Johnson 1995). Thus, around 4 months, infants may start to exert volitional control over what they attend to. Still, performance on executive attention tasks (Luna et al. 2004, Scerif et al. 2005) shows protracted development into adolescence (see also Diamond 2013), suggesting executive attention continues to develop long past infancy. Neurally, the regions recruited for executive attention, especially the frontal cortex (Gogtay et al. 2004, Lenroot & Giedd 2006) and long-range connections between the frontal cortex and other brain regions (Calabro et al. 2020, Lebel et al. 2012, Tamnes et al. 2017), are particularly slow to develop. In line with this slow development, attentional control networks show continued change into adulthood—long-range neural connections increase while local connectivity decreases (Dosenbach et al. 2010; cf. Power et al. 2012), suggesting large scale reorganization in neural recruitment during executive attention tasks (Crone 2009, Hwang et al. 2010).

Visual Attention Development: Selective and Sustained Attention Processes

The attention-as-networks approach offers an important framework that is best supplemented by additional mechanistic insight. For example, terms such as selective attention and sustained attention reflect processes that transcend any one network. Selective attention, which involves upweighting the processing of one information source while simultaneously downweighting the processing of other, competing information sources (Amso & Scerif 2015, Hendry et al. 2019), is a computation that can occur anywhere within and across cortical regions, for example.

Amso & Scerif (2015) conceptualized visual selective attention development, across both orienting and executive networks, as an emergent property of the interaction of visual development with the biased competition computations happening across levels of the cortical hierarchy (for recent reviews, see Amso & Scerif 2015, Lynn & Amso 2021). To elaborate, evidence for this idea stems from data showing that different cortical areas code for increasingly higher-order properties of the environment along the caudal-to-rostral axis (back-to-front) beginning in the early developing visual cortex (V1) and extending along the dorsal and ventral visual pathways. V1, for example, codes for highly specific aspects of a stimulus, such as the orientation of a line, thanks to densely packed neurons with highly specialized receptive fields (Charvet et al. 2015; Collins et al. 2010, 2016). Extrastriate region V4 (color) or V5 (motion) along the dorsal pathway and the fusiform face area (faces/objects) and inferior temporal cortex (object recognition/invariance) along the ventral visual pathway work in parallel to process increasingly complex visual scene features. In this way, visual development that engages V1, V4, V5, and other regions in processing a single visual scene may be the catalyst for engaging selective attention processes. As visual processing along multiple feature dimensions increases, so does the need to suppress target-irrelevant information in complex natural scenes. In other words, attentional selection is a process of neural competition within a local cortical region, as well as across cortical regions (Kastner & Ungerleider 2001, Kastner et al. 2001, Moran & Desimone 1985, Reynolds et al. 1999). At the same time, higher-order cortical areas, which code for more abstract aspects of our environment (Badre & D'Esposito 2009, Jung et al. 2018) via less densely packed neurons (Collins et al. 2010, 2016), send information about goals backward to early sensory areas, which bias the neuronal activity in the sensory cortex (Gilbert & Li 2013). This bias is reflected in neuronal activity being upweighted in the regions that code for the relevant stimulus relative to the irrelevant stimulus (Desimone 1998, Reynolds et al. 1999). The combination of these bottom-up sensory signals and top-down goal-directed signals results in neural activity, which may be reflected in both selective and sustained attention processes.

Data from infant natural scene viewing are consistent with this perspective. Saliency maps are a computational representation of the processes described above, where each visual feature (e.g., color, orientation, motion) in a natural scene is weighted relative to its surroundings (akin to biased competition within a cortical region) in a conspicuity map, and those maps are linearly combined to identify a winner-takes-all location with the most salient visual content relative to surrounding scene locations (see Itti et al. 1998). Using this framework, both Althaus & Mareschal (2012) and Amso et al. (2014) showed that infants' fixations in natural scenes became more consistent with adult saliency maps across the first two years of life. These data are in line with the prediction that increased efficiency in visual processing is key to visual attention engagement (Amso et al. 2014).

Another study expanded on this finding: Pomaranski et al. (2021) presented 4-to-12-month-olds with natural scene images and found that there was increasing overlap in different learners' fixation patterns with age, reflecting a developmental pattern of increasing use of saliency, but also of adult-like semantic meaning, in infant eye movements from 4–12 months of age. These data are also consistent with other studies that show that 3-, 6-, and 9-month-olds who spent more time looking at faces in cartoon videos (a conceptually relevant part of the scene) showed better performance on attention-orienting tasks, even controlling for age (Frank et al. 2014).

Infants also improve on their ability to sustain attention—in other words, alongside improvements in the ability to select objects or locations, development also brings with it an improved ability to sustain focus at a particular attended location (Hendry et al. 2019, Yuan et al. 2019). Sustained attention in infancy has been studied using heart-rate markers as a physiological index of attentional engagement (Richards & Casey 1991). Heart-rate deceleration shows increases from 3 to 6 months and scales with developing visual processing measures of attention and learning, such as the time it takes for infants to become familiar with stimulus characteristics (Frick & Richards 2001). Data also suggest that across the first postnatal year, an increasing amount of variability and complexity is required to maintain infants' sustained attention (e.g., Courage et al. 2006). Evidence from electroencephalography work suggests that in infant event-related potential (ERP) research, the negative central (Nc) component is most clearly related to visual attention: Richards (2003) found that periods of sustained attention were associated with greater Nc amplitude in 4.5-to-7.5-month-old infants. Relatedly, the Nc component has been found to increase in amplitude as the infant ages and may reflect increased attention-related activity in the prefrontal cortex, ostensibly reflecting top-down feedback processes, during infancy (Reynolds & Richards 2005). Together these results all converge to suggest that conceptualizing attention development as a process that reflects the involvement of both top-down and bottom-up competition will be fruitful for future work on the development of both sustained and selective attention.

LEARNING AND MEMORY SYSTEMS DEVELOPMENT

We turn next to reviewing some of the learning and memory processes available early in life. We specifically highlight those that might be relevant to guiding, and being guided by, developing visual attention. Some of the most exciting findings of the past decades have involved the discovery of a panoply of learning and memory systems in infancy. Here, we review studies that provide evidence for statistical learning, spatial learning, reward and reinforcement learning, threat-based learning, and early memory retrieval processes. We review what is known about the neural substrates and developmental time courses of these processes before turning to their interaction with attention in the next section of our review.

Statistical learning refers to the ability to extract reliable patterns from environmental input. It is beyond the scope of this article to thoroughly review the large infant statistical learning literature, so instead we focus on key relevant findings. Statistical learning is credited as a domain-general learning mechanism that helps learners of all ages understand the structure of the world (Aslin 2017). Canonical statistical learning studies involve presenting a repeating stream of images or sounds containing a hidden structure that is learnable via many repetitions of that structure. For example, a seminal study on statistical language learning presented 8-month-old infants with a stream of uninterrupted nonsense speech, which contained three-syllable groups that formed "words." Words were defined as deterministic (100%) transitions among three syllables in an otherwise monotonic speech stream with no other cues to word boundaries. The babies were then tested on their knowledge of these words by measuring how long they listened to either correct words or reorganized groups of those same syllables. The babies showed a novelty preference for the reorganized syllables, which was taken as evidence that infants can track the statistics of which sounds appear together most reliably in the language (Saffran et al. 1996). Since then, the ability to discriminate between experienced statistics and reorganized versions of the same input has been demonstrated in infants for other types of auditory structures (e.g., Gomez 2002) and for visual input (e.g., Kirkham et al. 2002; for recent reviews on infant statistical learning, see Saffran 2020, Saffran & Kirkham 2018).

Investigations into the neurobiology of statistical learning in development suggest that from immediately after birth, the brain is sensitive to the regularities of its input (Fló et al. 2022, Teinonen et al. 2009). For example, in sleeping neonates (Fló et al. 2022), like in sleeping and awake adults (Batterink & Paller 2017, Batterink & Zhang 2022), exposure to structured information results in electrical oscillations in the brain entraining to, or aligning with, the frequency of the structured signal. This entrainment measure has also been used to measure learning rate: 6-month-olds and adults show a similar rate of entrainment to word-level frequencies (Choi et al. 2020), suggesting that the rate at which the brain tunes to structured information might be similar across development. Importantly, this entrainment does not necessarily result in good memory for statistical structure unless the learners are awake (Batterink & Zhang 2022, Fló et al. 2022), in line with proposals that sensitivity to structure and committing structures to memory represent different subcomponents of statistical learning (Arciuli 2017, Batterink & Paller 2019, Conway 2020, Siegelman et al. 2018).

Anatomically, the regions implicated in adult structure learning include parts of the prefrontal cortex (inferior frontal and medial prefrontal cortices) (Karuza et al. 2013, McNealy et al. 2010, Schapiro et al. 2013), the basal ganglia (Karuza et al. 2013, McNealy et al. 2010), the hippocampus (Covington et al. 2018; Schapiro et al. 2012, 2014, 2016), and relevant sensory cortices (e.g., Turk-Browne et al. 2009). In line with adult findings, the limited number of structural MRI studies in children have linked the size of the hippocampus (Finn et al. 2019, Schlichting et al. 2017) and inferior frontal gyrus (Finn et al. 2019) to successful statistical learning in older children and adolescents. Also in line with adult research, the hippocampus and regions of the ventromedial prefrontal cortex are active when infants (Ellis et al. 2021) view structured information. However, a growing body of empirical (Raviv & Arnon 2018, Slone & Johnson 2018) and theoretical (Gomez 2016, Krogh et al. 2013) work suggests potential developmental variance in the content of statistical learning, although the exact developmental profile remains to be mapped out (Forest et al. 2023). Important for understanding developmental change in statistical learning could be the type of input that is being learned (Forest et al. 2023, Raviv & Arnon 2018). In other words, the extent to which statistical learning is its own mechanism rather than computations that are pervasive across many input types (e.g., distinct reward- or threat-based learning regions engage in statistical learning for their input) remains unclear. It is in that spirit that we now turn to reviewing (arguably) more domain-specific learning mechanisms.

While statistical learning reflects learning about regularities broadly, spatial learning involves learning about, and memory for, the spatial locations or relationships of objects in an environment (Casasola 2018, Newcombe & Huttenlocher 2003) and is likely supported by dorsal cortical regions that extend from the back of the brain to the front and are also involved in attentional selection of objects and locations (Mishkin et al. 1983; cf. Freud et al. 2016). From quite early in life, infants have some understanding of spatial locations, or where an object is in space. For instance, 2-month-olds know which of two screens occludes an object (Wilcox et al. 1994), and 5-month-olds can remember a location in space for a short time (Newcombe et al. 1999). Spatial learning also includes understanding spatial relationships, or how objects are positioned relative to each other. After becoming familiar with objects in a particular spatial configuration, neonates and very young infants look longer at a novel arrangement of the same objects, evidence they are sensitive to spatial relations such as above/below (Quinn et al. 2003), left/right (Gava et al. 2009), and between (Quinn et al. 1999). The ability to learn abstract spatial relations (i.e., to learn spatial relationships independent of the objects used) emerges later, potentially around 5 or 6 months (Casasola & Ahn 2018; Hespos & Piccin 2009; Hespos & Spelke 2004; Quinn et al. 1996, 2003). Together, these results suggest that early spatial judgements could be made on a perceptual basis (Casasola 2018) and then become more abstract with age. In line with the idea that spatial knowledge changes in quality with age, much research also indicates that the maturation of spatial learning relates to motor development (e.g., Casasola et al. 2017) and continued linguistic development of spatial language long past infancy (Marcinowski & Campbell 2017, Newcombe & Huttenlocher 2003).

Reinforcement and reward learning are heavily studied in both human and nonhuman animals. In recent years, studies have provided some evidence for learning from reward and reinforcement in infancy. Learning to transfer value from a rewarding stimulus to a reward-predictive cue involves subcortical dopamine release in response to prediction errors, which signal how close the reward was to what was expected (Dabney et al. 2020; Glimcher 2011; Schultz 2010; Schultz et al. 1997, 2017; Watabe-Uchida et al. 2017; Wise 2005). Importantly, striatal dopamine neurons fire in response to primary rewarding stimuli (such as ice cream) as well as for stimuli that have been paired with inherently rewarding stimuli (such as the sound of an ice cream truck, referred to as conditioned stimuli).

Existing studies make use of a variety of indirect measurements to study reward mechanisms in early life, such as smiling (Messinger et al. 2008), eye-blink rate, or pupil size. Eye-blink rate, for example, is mechanistically linked to striatal dopamine responses (Jongkees & Colzato 2016) and decreases in infants during feeding and following the introduction of new stimuli (Bacher & Smotherman 2004). Pupil-size measurements, in turn, reflect arousal and increase in response to high-reward stimuli (Zhang & Emberson 2020). Much of the current research on reward learning in infancy capitalizes on the idea that social stimuli, in particular caregivers, are inherently rewarding. In 7-month-olds, for example, eye-blink rate was lowest and pupil size was higher in response to the baby's mother than to other female figures or to nonsocial stimuli, indicating that infants are sensitive to differences in reward across stimuli (Tummeltshammer et al. 2019). Moreover, infants also anticipate upcoming rewarding social stimuli, as evidenced by decreased blink rate (Tummeltshammer et al. 2019) and faster eye movements toward (Thiele et al. 2021) and ERP responses to (Ishikawa & Itakura 2022) expected social stimuli. By 8 months of age (but not by 4 months), social attentional cues also lead to better learning than nonsocial cues (Wu & Kirkham 2010). While there is much work to be done still on reward learning in infancy, these studies suggest that at least by 7 months of age, babies use relevant rewards to guide their learning about reward-predictive cues.

Not only can infants learn about reward, but there is also evidence that this learning is sensitive to the context a learner is in—in other words, infants can, via reinforcement, learn hierarchical rules, which specify that certain actions are appropriate in certain contexts while other actions are appropriate in other situations (e.g., speaking in Spanish with one parent and English with another). The ability to generalize such rules also allows for efficient learning in new contexts. This process is attributed to recursive connections between the prefrontal cortex and striatum (Collins & Frank 2013, Collins et al. 2014). Together, these regions select the context-appropriate rule and then constrain actions accordingly in infants (Werchan et al. 2016) and adults (Collins et al. 2014) alike. Existing evidence for hierarchical rule learning in infancy suggests this ability emerges around 8 months of age. For instance, 8-month-olds (but not 4–6-month-olds) successfully learn hierarchical patterns in the order of animated chicks emerging from eggs, which they can then generalize to novel eggs (Lewkowicz et al. 2018). Eight-month-olds also use generalizable hierarchical rules to learn the mapping between a shape and the location of a target image, as well as between a speaker and a target image location (Werchan et al. 2015). Evidence from the A-not-B task suggests that by 9 months infants can use social information in the form of a particular experimenter to guide context-relevant actions (Werchan & Amso 2020). While more research is needed, these studies suggest that hierarchical rule learning is present partway through the first year of life.

Separate from learning to repeat previously rewarded behaviors, another important learning task for infants is to discern which parts of an environment present a threat and should thus be avoided. This threat learning can be either direct (i.e., via classical conditioning), in which a negative outcome is directly experienced (Pavlov 1927), or vicarious, in which watching someone else deal with a threat, or listening to someone else explain a threat, results in that stimulus being avoided (Bandura & Walters 1977; see also Skversky-Blocq et al. 2021). Evidence of fear (an emotional response to threat) exists from partway through the first year of life. For instance, babies have a lower heart rate (Thrasher & LoBue 2016) and increased pupil dilation (Hoehl et al. 2017) in response to snakes and spiders relative to other animals from 6 months of age. Eight-to-ten-month-olds are faster to detect a snake or spider than a flower and faster to detect an angry face than a happy one (LoBue & DeLoache 2010). In visual cliff paradigms, in which infants are encouraged to walk across an apparent visual drop-off by their parent, babies (like members of other species; Gibson & Walk 1960) tend to freeze or retreat away from the cliff from 8 months (Bertenthal et al. 1984, Gibson & Walk 1960), suggesting a fear of heights. It is important to note that many responses often cited as demonstrating fear in infancy have been recently reinterpreted as reflecting an increase in arousal or biased attention to certain stimuli rather than fear (LoBue & Adolph 2019). Still, responses such as increased attention to snakes highlight that from early in infancy humans are likely well equipped to learn about potentially risky things (Hoehl & Pauen 2017, Öhman & Mineka 2001).

Finally, and in order to review any potential interactions between the learning systems discussed above and attention in infancy, it is also important to (briefly) highlight some of what is known about memory retrieval and forgetting early in life. While infants can recognize stimuli they have previously encountered [the novelty preference procedures described throughout this review and that underlie much of developmental psychology (Fantz 1964) rely on this], memory is clearly not adult-like from birth (for reviews, see Barr & Brito 2014, Brainerd & Reyna 2004, Cuevas & Davinson 2022). For example, crucial early work on infant memory demonstrated that 9-month-olds show deferred imitation (i.e., produce an action they saw performed earlier) up to a day later (Meltzoff 1988). In seminal work from Rovee-Collier and colleagues (1980), 3-month-old infants were placed in a crib with a string tied around their ankle. The other end of this string was tied to a mobile on the ceiling, such that when the baby kicked their legs, the mobile moved. Rovee-Collier and her colleagues measured the number of kicks that the babies made during the initial learning sessions and then compared that to the number of times the babies kicked at a later session. By varying the amount of time that passed between the initial learning phase and the later test session, the scientists could estimate how much the babies would remember about the initial link between their kicking and the mobile moving. Impressively, even 3-month-olds kicked their feet to move the mobile up to 4 weeks later, provided they recently received a reminder about the mobile (Rovee-Collier et al. 1980). This same paradigm has also been used to understand other aspects of infant memory. For instance, as infants age they require less time to encode a stimulus (Davis & Rovee-Collier 1983) and can retain increasingly complex memories for longer amounts of time (i.e., their forgetting rate is slower, as evidenced by kicking in response to the mobile at longer intervals since learning; for a recent review, see Cuevas & Davinson 2022).

ATTENTION AND MEMORY AS INTERACTIVE: A REVIEW OF WHAT WE KNOW SO FAR

Having reviewed, albeit briefly, the existing literature on attention and some of the learning and memory processes available during infancy, we turn now to reviewing the evidence for interactions between these processes. Much of the literature on the interaction between attention and memory falls into one of two camps. Either it demonstrates that attention shapes the memories a learner forms or it demonstrates that the reverse is also true: Existing knowledge, or memories, bias our attention. In other words, attention impacts memory and memory impacts attention. Given the unique timelines that govern the development of the different processes we review, it is easy to envision just how complicated studying their interactions could be, particularly if the field took a pair-wise approach to understanding how each system relates. Our approach is instead to review this bidirectional relationship in the context of the systems outlined above and then to offer some paths forward for further study of these key interactive processes.

Visual Attention Development Impacts Memory

Data have shown that changes in attention orienting (both target selection and distractor suppression) impact what is learned and how well we remember it. The first evidence that how an infant attends to information during item learning shapes their subsequent memory comes from studies demonstrating that differences in how 3-month-old infants distribute fixation patterns during learning relate to differences in subsequent memory for objects across babies. For example, in one early study, 3-month-olds were presented with a display containing an occluded rod moving behind a box. Differences in fixation distribution to rod-relevant display regions (i.e., the top and bottom of the moving rod) related to the likelihood that 3-month-olds subsequently indicated that they perceived the occluded rod as one object versus two separate objects at test (Johnson et al. 2004). In a follow-up study, the likelihood that a baby perceived the rod as intact was related to visual search task performance by the same infants in a separate task, thereby directly linking the ongoing development of visual attention to object knowledge acquisition (Amso & Johnson 2006). In statistical learning tasks, too, patterns of eye movements differed between 14-month-olds who later demonstrated successful statistical learning relative to those who showed less robust learning (Yu & Smith 2011). Together these studies are likely among many that suggest that infants' distribution of visual attention orienting to information in their environment shapes what they later remember.

Why might this be? A second line of research provides both another good example of how attention shapes object knowledge and a more mechanistic explanation for why differences in the development of visual selective attention orienting might lead to differences in memory. Markant, Amso, and colleagues (Markant & Amso 2013, Markant et al. 2015) conducted a series of spatial cueing studies where they placed target items in either the cued or uncued locations (i.e., with concurrent suppression or not, since, as reviewed above, the cued location will be suppressed after a short delay) and then measured how well these items were learned using a novelty preference procedure in infants (Markant & Amso 2013). Notably, items in cued and uncued locations appeared equally frequently during encoding, so if the researchers observed differences in looking times, this likely reflects differences in memory for items in the cued and uncued locations. In line with the prediction that suppression of the previously cued location (i.e., IOR) leads to better learning, infants showed novelty preferences for items encoded in the uncued location (Markant & Amso 2013). In adults and nonhuman primates, presenting objects alongside distracting information results in less target activation in relevant visual cortical regions than when those objects are processed alone (Kastner et al. 1998, 2001). However, when those same objects are selectively attended, that is, in the presence of a suppressed distractor location, they are processed with the same amount of activity in the visual cortex as if they were presented alone (Kastner & Ungerleider 2000, Moran & Desimone 1985). Taken together, these results collectively point to the value of developing selective attention-orienting processes for learning and memory in infancy—selectively attending to information in the presence of distractors allows for that information to be better remembered, likely with important implications for how well younger versus older infants learn from their experiences.

Learning and Memory Impact Attention

The data presented above suggest that developmental change in infants' visual attention systems impacts the memories they can form. We turn now to the other side of the reciprocal relationship between memory and attention to highlight evidence that, from an early age, prior experiences, or memories, also shape how infants distribute attention for subsequent learning.

First, and as highlighted in the above section on recognition memory in infancy, a great deal of developmental psychology relies on the idea that infants preferentially attend to information that is familiar or novel to them (Fantz 1964)—any study that measures differences in looking time to familiar or novel stimuli is indexing how much an infant attends to stimuli that match their prior experiences. That said, the particular function for predicting whether infants will show familiarity or novelty preferences depends on the age of the infant and the complexity of the information in question (Hunter & Ames 1988).

In line with this variability, learners seem to have a propensity for attending to information that is neither too simple nor too complex (Cubit et al. 2021, Kidd et al. 2012) and therefore is useful for their learning at any point in time based on what they already know (Forest et al. 2022, Itti & Baldi 2009, Poli et al. 2020; see also Kidd & Hayden 2015, Loewenstein 1994, Twomey & Westermann 2018). For example, Poli and colleagues (2020) recently presented 8-month-olds with a series of cue-target trials in which a central cue predicted the location of a peripheral target. Across trials, the predictability of the target location varied such that some cues determined the target location while other cues made one location more likely to contain the target. This variability allowed the experimenters to model how much an infant could learn about the target location on a particular trial. The researchers found this metric to be the best predictor for how likely an infant was to look away from the experiment on any particular trial, suggesting that within the first year of life subtleties in what a learner already knows shape their attention to, or interest in, a task.

Longer-term experience also shapes attention in infants and adults alike (e.g., Carrigan et al. 2019, Wu & Zhao 2017, Wu et al. 2018). For example, 4-month-olds raised in a home with a pet attend to more informative parts of animal images (e.g., their head) than do infants raised in a home without a pet (Hurley & Oakes 2015). This effect does not extend to infants' scanning behavior of other object categories (e.g., human faces), suggesting that the broader knowledge structures formed over long periods of time have a targeted impact on how learners distribute their attention in novel situations. The structure of the linguistic environment an infant grows up in also shapes their attention: Infants growing up in monolingual versus bilingual environments show a different profile of neural activity in attention-orienting tasks (Arredondo et al. 2022). Specifically, at 10 months, monolingual infants demonstrated greater activity in the frontal cortex on valid compared with invalid trials. Bilingual infants, however, showed greater activity for the invalid trials, and the strength of this effect related to how much language mixing they experienced in their daily lives. Importantly this difference was demonstrated only at 10 months and not at 6 months (when both groups' frontal cortices were more active for valid trials), suggesting that long-term differences in a learner's environment shape attention, likely because of ongoing impacts to the development of underlying neural systems.

Beyond having memory for a particular event or knowledge domain, particular learning systems discussed above, such as spatial learning, have their own demonstrated effects on basic attention mechanisms. For example, in classic contextual-cueing paradigms (Chun & Jiang 1998), participants are shown a display with many similar objects, one of which serves as a target (for example, a small "T" among a display of "L" stimuli). When participants are presented with the same display on a later trial, they are faster to find the target, suggesting that their attention orienting was biased toward that location on the basis of their prior experience in a particular context. Such contextual-cueing paradigms have also been adapted for infants (Tummeltshammer & Amso 2018, 2023). In these studies, the authors presented 6- and 10-month-old infants with a display of four shapes, which rotated to reveal that one of the shapes hid a face. This face thus served as the target stimulus for infants. Like adults, infants were faster to orient to the target on trials that repeated a spatial layout than they were for novel layouts, demonstrating that 6-month-olds already use their past knowledge of spatial layouts to orient their attention efficiently.

It is also clear that information learned in the context of reward, reinforcement, and threat shapes later attention. Attention bias to threat is often shown to be learned in the sense that it is moderated by experiential variables such as maternal anxiety in infants' daily experience (Morales et al. 2017). Reward can similarly bias attention: One study on reward learning in infancy compared pupil dilation when infants were viewing their mother's face (a socially and emotionally rewarding stimulus) compared with nonrewarding stimuli and demonstrated greater pupil dilation when their mother's face was present. During the learning phase, shape cues predicted the screen location (quadrant) of the appearance of either the mother's face or strangers' faces and cartoons. Seven-month-old infants learned to predict the cue location of the mother's face only with trial exposure. Moreover, greater pupil dilation was subsequently observed for the shape cues that were paired with the mother's face, indicating a shift in value-based attention (Tummeltshammer et al. 2019) to a previously neutral cue. Similarly, data have shown that infants are biased toward using social stimuli as the context that governs hierarchical rules (Werchan & Amso 2021). However, any stimulus or feature dimension can be used in such a paradigm to engage learning of a higher-order context that governs action (Werchan et al. 2015, 2016). For example, if a shape or color cue is used in such a reinforcement learning task, data from 8-month-old infants show that this particular feature becomes more likely to be attended subsequently on the basis of its acquired value (Werchan & Amso 2020).

A PROPOSAL TO STRENGTHEN THE PATH FORWARD

Some progress has been made on understanding the development of learning and memory systems separately in infancy, and some progress has been made on their interaction. But, of course, open questions remain. Here we name a few areas of open research that seem particularly likely to address current gaps in our knowledge. Importantly, rather than enumerate every possible interaction between each type of attention and learning described in the earlier parts of this review, we point out themes in missing research.

In the visual attention development section, we review both the distinct networks framework (Posner & Petersen 1990) and a more recent approach that conceptualizes attention as a computation across the cortical hierarchy (see, for example, Lynn & Amso 2021). The data reviewed above highlight that there is overlap in the neural regions that are involved in object or spatial attention and the regions that are involved in learning about the content of what is being attended to. As a more specific example, one prediction that emerges from our review is that the same ventral visual pathway cortical systems that are engaged in learning about object shape, for example, are also involved in selectively attending to shape information. Better understanding this level of cortical overlap may inform experimental approaches designed to understand the tight coupling between cortical attention and learning mechanisms.

Second, and relatedly, this review leads us to question how best to understand statistical learning and its interactions with developing attention. One possibility is that, like the argument made by Amso & Scerif (2015) about visual selective attention being an emergent property, statistical learning is a computation deeply embedded in how neurons interact with one another across cortical and subcortical areas. If so, studies to understand how learning impacts attentional allocation might need to begin with operationally defining the content in question. That is, learning about neutral shape stimuli, to extend the example, may require more regular exposure to guide subsequent attention than learning from rewarding or threatening inputs, precisely because the latter also has high arousal value. This prediction leads to the idea that statistical learning may be a mechanism that operates differently within neocortical learning systems, particularly relative to basal forebrain and medial temporal lobe regions. In either case longitudinal data are likely to play a crucial role in understanding how the interaction between memory and attention unfolds across infancy and even childhood.

Finally, another branch of future research could aim to understand whether there are potential benefits with respect to the timing of the development of learning and memory processes for the development of attention processes or vice-versa. As one potential example, attended information is represented more consistently (Gilbert & Li 2013), which suggests less developed attention might result in less consistent representations in younger learners. What are the impacts of these less consistent representations for the concurrent building of knowledge structures? Other literatures have suggested, for example, that early reliance on learning systems that emphasize the commonalities across events (Gómez & Edgin 2016, McClelland et al. 1995) might result in infants learning generalities about the structure of their environments (Gomez 2016) rather than remembering the specifics of unique occurrences. Less developed attention might serve this same role—increased noise in neural activity would result in only the most consistent parts of an environment being stored in memory across experiences. This is a potential benefit to a young learner of slowly developing attention. As their representations become more precise, so too might the predictions they form (which might in turn or cyclically shape their attention). This example suggests one potential benefit of immature attention or learning systems, but there are likely many others.

All of the example research proposals presented here involve a move toward studying how information is transformed as a result of ongoing experience and its value for the learner. These proposals are in line with numerous proposals in the adult cognitive neuroscience literature to move away from conceptualizing different processes as being based on distinct neural systems and to move toward a process-based account that highlights the type of computations being performed to complete a certain task (Henke 2010, Shohamy & Turk-Browne 2013). We believe that, in adopting such an approach, previously disparate literatures studying different processes in infancy will be able to benefit from one another's work and work toward a more comprehensive understanding of how someone's past experience interacts with ongoing neural development to shape the way they interact with their environments across development.

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