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Learning in Infancy Is Active, Endogenously Motivated, and Depends on the Prefrontal Cortices

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Abstract

A common view of learning in infancy emphasizes the role of incidental sensory experiences from which increasingly abstract statistical regularities are extracted. In this view, infant brains initially support basic sensory and motor functions, followed by maturation of higher-level association cortex. Here, we critique this view and posit that, by contrast and more like adults, infants are active, endogenously motivated learners who structure their own learning through flexible selection of attentional targets and active interventions on their environment. We further argue that the infant brain, and particularly the prefrontal cortex (PFC), is well equipped to support these learning behaviors. We review recent progress in characterizing the function of the infant PFC, which suggests that, as in adults, the PFC is functionally specialized and highly connected. Together, we present an integrative account of infant minds and brains, in which the infant PFC represents multiple intrinsic motivations, which are leveraged for active learning.

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INTRODUCTION

A satisfactory description of the development of the human brain should, among other things, give insight into the development of the human mind. The structure and function of infant brains should illuminate what infants can (and cannot) perceive, understand, and accomplish. Maturational changes in the brain should help explain when new capacities emerge.

One such synthesis of cognitive and neural development has been proposed. In this view, the newborn infant's mind is described as a succession of fleeting sensations evoked by the environment. The newborn infant's brain is described as functioning with mainly primary sensory and motor regions and neural activity driven by mostly local connections. A brief sketch of early development would go like this: At first, infants' primary sensory cortices are activated and their minds experience simple disconnected sensations or percepts; with extensive experience, infants' secondary sensory cortices organize around statistical patterns of input and their minds extract higher-order representations; during childhood, association cortices, and particularly the prefrontal cortex (PFC), mature as children begin to manipulate abstract representations, to actively make choices, to pursue goals, and to inhibit distractions. The close correspondence between the proposed stages of brain development and the proposed stages of cognitive development is satisfying.

In this article, we critique this common account. The sketch above is a misleading account of the infant mind. The last 40 years of research in developmental psychology have established unambiguously that infants do not merely passively accumulate exposure to the environment. From birth and constantly thereafter, infants make choices as to how to experience their environment, they understand the world in terms of abstract representations, and they actively pursue endogenous motivations. The sketch above is also, as it turns out, wrong about the infant brain. Neuroimaging has revealed that infants have functional long-range connectivity extending across all regions of cortex, and even the PFC, famed for its slow development, is functionally active and involved in learning. Updating our understanding in light of this evidence will, we hope, produce a new and better integrative account of early development of the human mind and brain.

The focus of this review is to provide such an account. We argue that infants' learning is active, motivated, and supported by mechanisms in the PFC. Our proposal credits infants' minds and brains with substantial endogenous structure, including both (*a*) intrinsic motivations and (*b*) a functionally specialized and highly connected PFC to represent and communicate those motivations across cortices. Importantly, we do not deny the profound transformations that occur as infants learn from the environment. We propose that infants are born knowing not what to learn, but how.

Recent accounts of early development have touched on elements of our proposal. In terms of behavior, we echo the view outlined by Dweck (2017) that infants are born with built-in, basic needs, which drive goal-directed behaviors. These goal-directed behaviors support infants' development in many domains, such as emotional, cognitive, and motor skills. With regard to the infant PFC, we concur with the framework proposed by Werchan & Amso (2017) that the PFC is not immature, but rather adapted to the demands of infants' age-specific ecological niche. Similarly, Dehaene-Lambertz & Spelke (2015) highlight the PFC as a key player in infant cognition, particularly for language acquisition. Here, we expand on and integrate these frameworks for thinking about infants' minds and brains.

We begin by surveying the view of infants as predominantly incidental learners. We then contrast this view with evidence for infants as active learners in two domains: First, we describe how infants guide their attention toward informative events and how the lateral PFC supports this objective. Second, we argue that infants have distinct social motivations that guide their behavior and that the medial PFC supports these. We then discuss broader implications of our account for cognitive and neural development.

THE INFANT AS AN INCIDENTAL LEARNER

It is tempting to see infants as passive and at the mercy of their environment for stimulation. For instance, newborns have an exceptionally limited motor repertoire. It takes many months for infants to produce the simplest interactions with the environment, for example, reaching and grasping or pointing to elicit joint attention. In the absence of these behaviors, early infant learning may appear to rely primarily on gradual, external provisioning of inputs (Gottlieb 1991, Jayaraman et al. 2017).

Classic developmental psychology experiments reinforced this picture of infants as passive receptacles unable to manipulate information in their minds to guide their actions. The classic evidence for these limitations comes from Piaget's (1955) A-not-B task. An object is repeatedly hidden in one location (A) and then later, in full view of the infant, hidden in a new location (B). For much of the first year, infants typically reach to the old location (the A-not-B error). The longer the delay between observing the hiding at B and the searching, the older the infants must be to succeed.

In subsequent work, infants' poor performance was attributed to the immaturity of a critical brain region. Infants' failures on the A-not-B tasks resemble the failures of adults after destruction of the dorsolateral prefrontal cortex (DLPFC; Diamond 2002). In healthy adults, DLPFC activity is related to demands for working memory and inhibitory control (Barbey et al. 2013, Shackman et al. 2009). Thus, it seemed plausible that the cognitive limitations of infants might reflect the immaturity, and therefore functional unavailability, of the PFC.

Indeed, there is plenty of evidence that the PFC is structurally immature in newborns and develops disproportionately slowly relative to other cortical regions. Measures of synaptic development (Collin & van den Heuvel 2013, Huttenlocher & Dabholkar 1997), axon myelination (Deoni et al. 2012, Dubois et al. 2014), and gray matter density (Gogtay et al. 2004) all show the PFC lagging behind other cortical regions in infants.

The slow and late maturation of the PFC might thus correspond to the limitations on infants' cognitive abilities, especially with respect to tasks that require infants to coordinate their actions and goals (Keunen et al. 2017). A common conclusion from these results is that "the functional network architecture [of infant brains] is linked to support tasks that are of a perception–action nature" (Fransson et al. 2010, p. 145), rather than high-level tasks, such as the A-not-B task.

Without mature prefrontal mechanisms for goal-directed behavior, how might infants learn? One route is implicit learning. That is, they may extract regularities from their environment spontaneously, effortlessly, with no active intention to learn. In adulthood, a lot of learning is incidental, or implicit (Sherman et al. 2020), and the knowledge gained this way is powerful and diverse (Batterink et al. 2019, Sisk et al. 2019).

Critical for the developmental hypothesis, implicit learning and active learning depend on separable neural mechanisms that mature at different rates (Loonis et al. 2017, Reber 2013). Implicit learning is mainly supported by sensory and motor regions of the brain as well as subcortical structures, such as the basal ganglia and cerebellum (Batterink et al. 2019, Reber 2013). Active learning is often supported by high-level association cortices, such as the PFC (Reber et al. 2017). Damage to the PFC can leave implicit learning performance intact (Foerde & Shohamy 2011, Gabrieli et al. 1993).

There are strong reasons to believe that infants, like adults, learn implicitly. Indeed, young infants appear to retain information through incidental learning across modalities and input types (Sherman et al. 2020). Like adults, infants learn from the statistics of their environment, extracting both visual and auditory regularities (Fló et al. 2019). More complex behaviors, such as motor and language learning, can then be built on a foundation of implicitly learned knowledge (Monroy et al. 2019).

Since brain regions involved in explicit learning develop later than those required for implicit learning, it is intuitive to think that the primary mode of learning during infancy is implicit. Indeed, some have even speculated that slow and late prefrontal development, and its cognitive consequences, could be a feature of human development rather than a bug. In these views, the late onset of prefrontal maturation, and concomitant immaturity of goal-directed learning, can confer specific benefits on cognition, such as learning broader environmental generalizations (Gopnik et al. 2015, Thompson-Schill et al. 2009).

A related idea is that early unguided implicit learning could provide a more robust foundation for learning. An inspiration for this is the idea of pretraining in supervised learning with artificial neural networks. In a pretraining phase, the network is first exposed to a very large unlabeled data set and only subsequently trained to match inputs with labels. The unsupervised pretraining phase allows the network to discover statistical structure in the data before ever being exposed to the true labels and so can prevent overfitting and improve generalization (Hinton 2006). By analogy, an initial phase of passive sensory and implicit learning in infancy could effectively constitute pretraining. Like neural networks, infants could benefit from extracting statistics from the world before they begin active (supervised) learning (Cusack et al. 2018).

For these reasons, infants are often viewed as incidental learners who learn mainly by extracting statistical structure from their environment, using brain mechanisms that do not depend on the PFC. However, we argue that this view is misleading.

THE INFANT AS AN ACTIVE LEARNER

In this section, we challenge the notion that infants are primarily incidental learners. A central challenge for the incidental learning account comes from a decades-long research program in developmental psychology measuring patterns in infant looking behavior. The key observation underlying all of this research is that infants do not merely observe their surroundings but rather choose to look more at some things than at others. Starting the day they are born, infants actively control their attention. We argue that infants' looking can be understood only as motivated behavior, reflecting their intrinsic motivations. Thus, infants actively scaffold their learning about the world.

A second challenge comes from recent progress in developmental cognitive neuroscience. While the PFC appears to mature slowly anatomically, aspects of PFC function do not mirror this immaturity (Dehaene-Lambertz & Spelke 2015, Werchan & Amso 2017). Progress in infant functional neuroimaging is revealing functional specialization and connectivity of the infant PFC. Much like in adults, the infant PFC appears to be involved in guiding goal-directed behaviors, such as looking. The locus of the neural representations of those motivations broadly reflects the mature functional subdivisions within the PFC.

Together, we hope these observations can engender a new integrative account of the infant mind and brain. This account emphasizes the importance of intrinsic motivations for active learning and designates the PFC as a central neural substrate for these behaviors.

We consolidate evidence for this view from two main domains. We first discuss how infants actively orient toward informative inputs. We then survey infants' social motivations.

Information-Seeking Motivations: Behavioral Evidence

Though their behavioral repertoire is limited, infants have control over their gaze and visual attention from the first hours after birth. Infants control where they look in a visual scene and for how long. Though some preferences can be explained by simple features of the stimulus (e.g., high-contrast edges attract infants' gazes; Atkinson et al. 1977), many systematic patterns in infants' gazes can be explained only in terms of the infant's state and intrinsic motivations. Thus, patterns of infant looking offer a powerful window into infants' endogenous motivations.

One robust feature of infant looking patterns is habituation: After repeated exposure to the same stimulus, infants lose interest, looking for shorter and shorter periods of time. Habituation occurs faster for simpler than for complex stimuli and for older than for younger infants (Colombo & Mitchell 2009), suggesting that habituation reflects the speed and depth of encoding: The faster infants can learn a stimulus, the faster they lose interest in it.

The probability that an infant will look away from a sequence of visual or auditory events, for example, can be captured in terms of information-theoretic notions of surprise, the probability of each event given the sequence (Kidd et al. 2012, 2014). The success of these models provides evidence that infants' looking time reflects their statistical inference rather than merely external perceptual features of the stimulus (Sim & Xu 2018).

Infant habituation is also selective. As the infant is fully familiarized with one stimulus, preference for other, novel stimuli increases (Hunter & Ames 1988, Roder et al. 2000). Longer looking provides evidence that infants can discriminate between the familiar and novel stimuli and thus has been used by researchers to test infants' perceptual acuity and working memory (Reynolds & Romano 2016). The success of this experimental method critically depends on infants' ability to actively choose their own inputs.

Most importantly, not only do infants prefer novel (never experienced) to familiar (previously experienced) perceptual stimuli, but they also prefer to look at unexpected or potentially informative events, even when they are perceptually familiar, rather than perceptually novel but predictable events. In the classic introduction of this violation of expectation method, Baillargeon and colleagues (Baillargeon 1987, Baillargeon et al. 1985) familiarized infants to a rotating wall blocked from complete rotation by an obstacle. On the key test trials, the obstacle was removed, and infants were shown two events: the perceptually familiar partial rotation (now inexplicable) or a perceptually novel complete rotation. Infants looked longer at the familiar, inexplicable partial rotation, suggesting that infants showed greater interest in perceptually familiar but unexpected, potentially informative events than in perceptually novel but expected events. Hundreds of experiments have subsequently found that infants look longer at events that are surprising relative to

their predictions, even when those events are not novel relative to their perceptual experiences (reviewed in Csibra et al. 2016).

The inferences that support infants' predictions for future events can be remarkably sophisticated and abstract. For example, Werchan et al. (2015) exposed 8-month-old infants to two people, each giving different novel labels to novel objects. One person would call an object dax, while another would call the same object mip. Then, a third speaker used the same object-word mappings as the first speaker for the familiar objects and then introduced a new label for a new object. Infants subsequently looked longer when the second speaker used the third speaker's new mapping than when the first speaker did, suggesting infants were representing not local associations between speakers and words, but generalized hierarchical rule sets. These expectations subsequently bias infants' attention toward features of the environment that best disambiguate which rule set is currently active (Werchan & Amso 2020).

These findings establish that infants have looking preferences that go beyond their immediate perceptual experiences and raise the question of why. Why would infants spend more time engaging with unexpected stimuli? One answer is that picking out and attending to surprising events provide the infant with opportunities for learning. The formal, information-theoretic notion of surprise (surprisal) is in fact closely related to the potential for information gain (Shannon 1948). Events that are deemed improbable by an observer require more units of information to integrate into their existing knowledge when they occur. These units reflect the amount of information that can be gained by observing the event. Therefore, the potential for information gain is maximal for unexpected events. Attending to such events, rather than any random target, may confer specific benefits for learning.

Indeed, infants not only look longer at unexpected events, but also learn more from them, and when slightly older, selectively and actively explore them more in other ways. For example, Stahl & Feigenson (2015) first showed 11-month-old infants events that violated their expectations, such as a rolling object seemingly passing through a solid wall. Next, they gave infants a chance to learn a seemingly unrelated fact: the sound the object made. They then presented the infant with both the rolling object and a novel, distractor object, played the sound, and measured which object the infants chose to look at to test whether they learned the object-sound mapping. Infants learned the mapping for objects that violated their expectations but not for objects that did not (e.g., when the object stops before the wall). Also, infants actively explore the object to receive an explanation for violation. When an object seemingly floated in midair, infants often subsequently dropped it; when an object seemed to pass through a wall, infants subsequently banged it on the table. These behaviors are tuned to whether an event needs to be explained: If an explanation for the violation is provided (e.g., the solid wall had a hole through which the object could pass), infants no longer selectively explore that object (Perez & Feigenson 2020). These findings underscore how information gained from infants' looking at informative events calibrates subsequent exploration and learning (reviewed in Stahl & Feigenson 2018).

In summary, even though very young infants have limited motor repertoires, they already engage in intrinsically motivated behaviors to learn. Increased looking at unexpected events enhances learning and serves as a basis for subsequent, targeted exploration. These behaviors likely allow infants to learn much more efficiently than in a purely incidental learning regime, in which inputs are not selected. Active information-seeking behaviors are central to infant learning from birth and throughout the first year. Next, we turn to the neural basis of these information-seeking behaviors.

Information-seeking brain: evidence from adults. In adults, information-seeking behaviors critically depend on lateral portions of the PFC (**Figure 1**). Classical accounts of the lateral PFC

Lateral prefrontal cortex
Medial prefrontal cortex
Thalamus
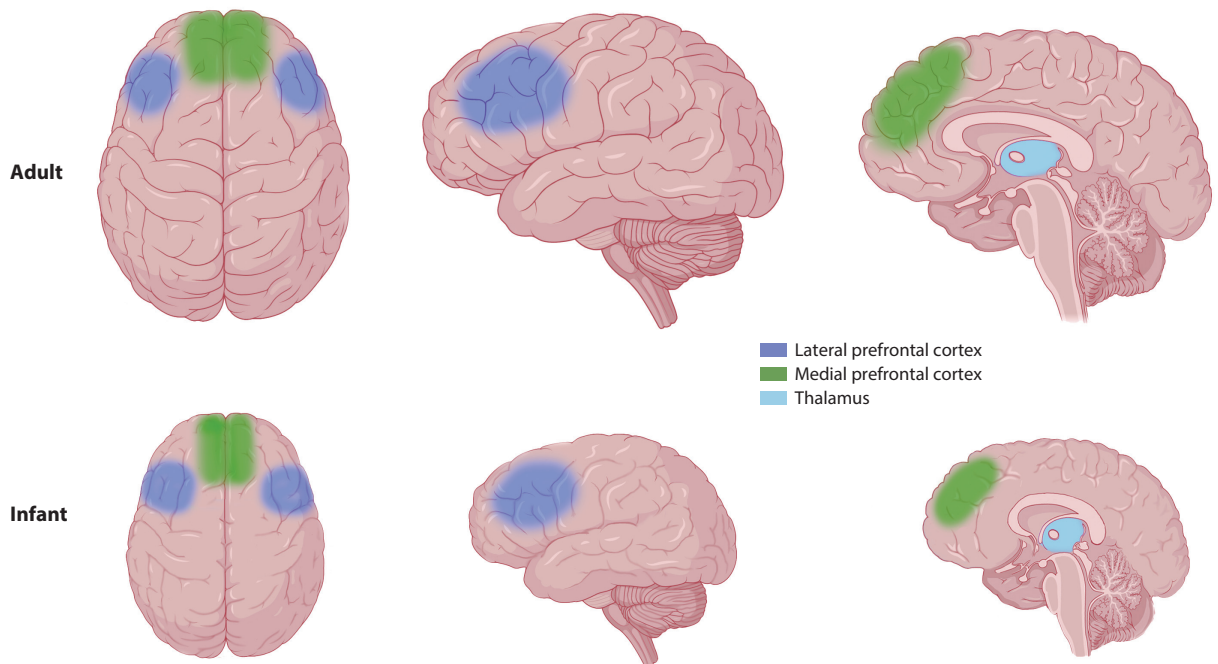
Adult

Infant

Figure 1

Brain regions discussed in this review: the adult and infant prefrontal cortices (PFC) and thalamus. Figure adapted from images created with BioRender.com.

emphasize its role in high-level regulatory processes, such as executive control and working memory (Barbey et al. 2013, Miller & Cohen 2001). Human patients with focal lesions in the lateral PFC show marked deficits in these domains (Kam et al. 2018). More recent approaches have parceled the lateral PFC into distinct subcomponents that manage hierarchical generation, planning, and execution of goals together with other PFC regions (Pezzulo et al. 2018).

Crucially for our account, the lateral PFC plays a key role in guiding attentional shifts. Early lesion studies in primates found that damage to the lateral PFC impairs their ability to shift their attention to task-relevant features of a stimulus (Rossi et al. 2007). These task-relevant attentional shifts are often information-seeking behaviors, such as the violation-of-expectation effect observed in infants. Indeed, functional magnetic resonance imaging (fMRI) in humans has shown that the lateral PFC activates when subjects are shown stimuli that violate learned regularities (Browning et al. 2010) and that this activity is related to the amount of learning occurring as a result of the violation (Fletcher et al. 2001).

The role of the lateral PFC in attentional guidance is supported by its functional connections to the rest of the brain. Functional connectivity analyses show that portions of the lateral PFC are a part of a larger set of brain regions that together form the frontoparietal control network (Dixon et al. 2018). This network, which includes the anterior cingulate cortex and intraparietal sulcus, is strongly engaged when humans endogenously initiate top-down behavioral control, implicating this network in many of the information-seeking behaviors surveyed above (or analogous adult behaviors).

Given the robust evidence that infants actively guide their gaze and visual attention to seek information and that adult information seeking depends on the lateral PFC (and its cortical network), we next survey whether infants' information seeking depends on the same neural system.

Information-seeking brain: evidence from infants. In infants, the lateral PFC is well connected, functionally active, and supports information-seeking behaviors. In light of the classic evidence that the lateral PFC is slow to mature relative to other regions, this is a surprising finding.

Over the past decade, there has been a surge of studies measuring functional networks in sleeping infants from the correlation patterns in spontaneous activity. By these measures, the infant lateral PFC is functionally correlated with a set of cortical regions resembling the adult attention network. A recent large-scale analysis of resting-state fMRI data from over 300 neonates (i.e., infants less than 1 month old) could reliably detect an adult-like frontoparietal network (Eyre et al. 2020), which resembles the dorsal attention network described in adults and similarly includes lateral PFC and eye field regions (Vossel et al. 2013).

There is also mounting direct evidence that the lateral PFC is active in infants. As described in the section titled Information-Seeking Motivations: Behavioral Evidence, behavioral evidence for infant information seeking comes from patterns of habituation: Infants' attention to repeating stimuli is reduced and is enhanced to novel or unexpected stimuli. The lateral PFC activity shows the same pattern. Using functional near-infrared spectroscopy (fNIRS), Nakano et al. (2009) found that lateral PFC activity in sleeping 3-month-olds attenuated with exposure to an increasingly familiar sound and then increased when given a novel sound. Similarly, the lateral PFC of awake 6-month-olds showed attenuated responses to a sequence of repeating stimuli compared to a sequence of variable stimuli (Emberson et al. 2017).

Behaviorally, infants direct their gaze not only to novel or variable events, but specifically to events that are unexpected relative to the infants' learning and inferences; again, lateral PFC activity shows the same pattern. After sleeping 3-month-olds were exposed to a predictive regularity (one sound that reliably predicted another), lateral PFC activity increased selectively when the learned regularity was violated (Nakano et al. 2008).

The lateral PFC is particularly involved when infants learn abstract, hierarchical representations, similar to observations in adults (Helfrich et al. 2017). As described above, Werchan et al. (2016) showed 8-month-old infants three speakers, apparently using two different rule sets to label objects; when a speaker appeared to switch rule sets, infants looked longer. The right lateral PFC showed increased activity during the unexpected event (i.e., a rule switch), especially in the infants who showed the largest behavioral effect on their looking (Wimmer et al. 2015).

In summary, the infant lateral PFC (and its cortical network) is plausibly the neural mechanism underlying infants' attention to, and enhanced learning from, informative events. In this respect, infant lateral PFC function resembles adult lateral PFC function. However, infants are not small adults, either behaviorally or neurally. The cognitive functions classically associated with the lateral PFC, such as working memory and executive function, are clearly not fully mature in infancy, and the lateral PFC is substantially anatomically immature. In the section titled Implications, we discuss how to reconcile these signatures of similarity and difference between infant and adult minds and brains.

Next, however, we turn to another example of infant endogenous motivation and PFC function: social motivation.

Social Motivations: Behavioral Evidence

Although maximizing information is a key motivation for infant looking, it is not the only one. Infants (like other humans) are also motivated to form and sustain social relationships. Infants thus look longer at events or stimuli that provide an opening to a positive social interaction, even when there is no additional immediate potential for information gain. The distinction between information-seeking and relationship-forming motivations mirrors a major division in the adult

PFC. While information seeking is related to lateral PFC function, social motivations are represented in the medial PFC. In this section, we review behavioral evidence for infant social motivations, neural evidence for medial PFC involvement in adult social motivations, and converging evidence that the medial PFC plays a similar role in infant social motivations.

Infants are born into a social world. Humans are obligately social, depending on cooperation with others for food provision, childcare, safety, and more. Human infants are hyperaltricial and thus even more radically dependent on other people to provide for their every need. In this context, infant behavior appears to be guided by a distinct motivation to form and sustain positive social relationships. Although looking at other people is often an effective way to gather information about the world, infants' looking to people reflects not only their information-seeking motivation, but also a distinctively social motivation.

Infants are biased to look at human faces within hours after their birth. When pitted against other shapes that are equally novel and matched for visual contrast and complexity, infants nevertheless prefer to look at face-like configurations: an oval containing two eyes above and a mouth below (Johnson et al. 1991). Remarkably, neonates even prefer to look at a shape with dark pupils on white sclera versus a shape with white pupils on a dark sclera (Farroni et al. 2005, Johnson et al. 2015), though they show no preference for a shape with light versus dark background coloring or skin. By biasing early attention, a specific motivation to look at human faces could launch infants' social learning.

Over succeeding months, infants continue to look preferentially at faces but shift their attention to different parts of the face (or person) depending on the context (Frank et al. 2011, Libertus et al. 2017). Young infants preferentially orient toward eyes, while older infants look toward mouths during speech and hands during manual actions (Boyer et al. 2020, Frank et al. 2011). Videos from infant-mounted headcams reveal that these differences are manifest in ecologically relevant settings and have dramatic effects on infants' cumulative visual experience (Smith et al. 2018). In summary, there are large, self-generated biases in infants' perceptual input about other people.

When infants are biased to look at people, how can we test whether their motive is distinctively social? An alternative interpretation is that infants look at people to gather information, resolve uncertainty, and test predictions about the sensory world. In many cases, the motives underlying infant looking are ambiguous. For example, infants prefer to look at a person who is speaking to them in infant-directed speech, with its characteristic high pitch and variable prosody (ManyBabies Consort. 2020). Even later, in silence, infants sustain their looking preference for social partners who previously talked in infant-directed speech (Schachner & Hannon 2011). However, it is an open question whether this preference reflects a distinctively social motivation (detecting a person whose speech is directed at and thus relevant to the infant, with positive intent) or information seeking (detecting acoustic and lexical properties that directly facilitate language learning) (Falk & Kello 2017; but see Cristia et al. 2017).

In other cases, though, distinctively social motivations can be more clearly inferred. Infants prefer to look at people who appear reciprocally attentive and positively inclined toward them; these patterns of looking cannot be explained in terms of perceptual novelty or violation of infants' expectations. Infants prefer to look at faces that are gazing toward them versus gazing away (Farroni et al. 2002, Urakawa et al. 2014) or that are responding contingently to the infants' own behavior compared to the same faces when played as a nonresponse video (Mesman et al. 2009, Nagy 2008, Schachner & Hannon 2011). Another social cue, affective touch by a caretaker (but not nonsocial touch), enhances infants' learning of face identity (Della Longa et al. 2019), consistent with the notion that attention to faces is socially motivated. When observing other agents interact, infants prefer to look at and reach for prosocial actors, such as helpers over hinderers and imitators over nonimitators (Hamlin et al. 2011, Powell & Spelke 2018).

Infants' preference for self-relevant social stimuli may help them form relationships and may promote social convergence (Kalashnikova et al. 2017). Infants play an active role in establishing relationships with their caretakers (Tomasello 2020). Early attention to faces is correlated with infants' later social development, such as the propensity to help and empathize with others in early childhood (Peltola et al. 2018). The frequency of face-to-face interactions predicts later social skills in both humans (Murray et al. 2016) and rhesus monkeys (Dettmer et al. 2016).

Beyond merely attending to social cues, young infants actively intervene in their social environment through smiles and vocalizations. They reciprocate smiles and time their smiles optimally to make their caretaker smile (Murray et al. 2016, Ruvolo et al. 2015), thereby leveraging a strong, universal bonding measure (Martin et al. 2017). Through vocalizations, infants initiate complex communicative loops and reinitiate them when they have been disrupted (Bourvis et al. 2018).

Thus, we argue that the endogenous motivation for social connection is independent of, though in many cases complementary to, infants' motivation to gather information about their environment (Dweck 2017). Even when pitted against novelty or potential for information gain, infants use their gazes, smiles, and vocalizations to enhance their social relationships. Could these proximally social behaviors still reflect information-seeking motivations ultimately? That is, are infants preferentially interacting with people whom they expect to be most useful sources of information in the long run? This question is hard to directly address with behavioral evidence alone and may be best addressed with computational models (see the section titled How Do Endogenous Motivations Affect What Infants Learn?). One converging source of evidence for genuinely distinct social motivations, though, comes from neuroimaging. The dissociation between social and information-seeking motivation in infant behavior mirrors a major division in the functions of the adult PFC (**Figure 1**).

The social brain: evidence from adults. Human adults' ability to form, maintain, and manage social relationships is supported by dedicated neural mechanisms (Frith & Frith 2010, Schilbach et al. 2013). A number of brain regions are selectively active in social contexts, and lesions and disorders affecting these brain regions have profound consequences on social behavior (Henry et al. 2015, Kennedy & Adolphs 2012). A key brain region supporting these behaviors is the medial PFC.

In adults, the medial PFC is structurally and functionally dissociable from other parts of the PFC (**Figure 1**). The medial PFC itself is functionally divided along its ventral-dorsal axis (Lieberman et al. 2019). Dorsal portions of the medial PFC are most likely to respond to social information processing, such as viewing strangers in a social interaction and inferring other people's mental states (Skerry & Saxe 2015, Tamir et al. 2015). Self-relevant information is most likely to evoke responses in the middle portions of the medial PFC (Martinelli et al. 2012), while positively valenced stimuli evoke responses in both middle and ventral parts of the medial PFC (Bartra et al. 2013). We conflate these functional subdivisions here partly because neuroimaging of infants often lacks the spatial precision to distinguish them but mainly because infants' social motivations, as described above, likely reflect a mixture of social cues, self-relevance, and positive valence.

Patients with lesions in the medial PFC show impairments in affective processing and theory of mind and self-referential thought (Jenkins et al. 2014, Philippi et al. 2012). Temporary disruption via noninvasive brain stimulation can induce similar changes in affective and social cognition, for example, by altering emotional recognition in self-relevant social partners (Gamond & Cattaneo 2016).

In adults, spontaneous activity in the medial PFC is highly correlated with activity in other cortical regions. This overall pattern of functional correlations is often called the default-mode network (DMN) because it was first described in terms of its increased activity at rest (Raichle et al.

2001). More recent research has identified multiple distinct networks falling within the overall territory of the DMN (Buckner & DiNicola 2019), including separable networks involved in social versus episodic processing (DiNicola et al. 2020).

One network that overlaps significantly with the DMN is the theory of mind network, which includes the temporoparietal junction, the precuneus, and the medial PFC. This network of brain regions is active when someone thinks about other people's mental states (Kanske et al. 2015, Saxe & Kanwisher 2003) and can be found in children as young as 3 years old (Richardson et al. 2018). Functional correlations in this network, specifically between the medial PFC and the right temporoparietal junction, increase after learning new social information, and the size of the increase correlates with retention of the social information (Meyer et al. 2018).

In adults, the cortical networks underlying information-seeking and social motivations are clearly dissociable. Both spontaneously at rest and in response to external tasks, there is a clear dissociation between activity of the default-mode or social networks including the medial PFC and the frontoparietal executive network including the lateral PFC (Esposito et al. 2017). This dissociation suggests that in adults, these networks guide behaviors in the service of separate motivations. While the lateral PFC plays an important role in guiding attention toward informative, task-relevant information, the medial PFC plays a separable role in guiding attention toward self-relevant, social, and affective events.

The social brain: evidence from infants. Evocative of its function in adulthood, the medial PFC of infants supports socially motivated behaviors already in early infancy (**Figure 1**).

The functional network of the medial PFC appears to take somewhat longer to emerge than the frontoparietal network, yet it is clearly present within the first year. Some studies have identified a full pattern of DMN functional correlations in young infants and even in fetuses (Turk et al. 2019). Yet, a recent study of 300 neonates that robustly identified the frontoparietal network including the lateral PFC observed only a fragmentary version of the DMN in the same infants (Eyre et al. 2020). Other studies found functional correlations between the medial PFC and other default-mode regions in 6-month-olds (Gao et al. 2014). One outstanding question is whether some of the differences observed between infant and adult functional correlations are confounded by the fact that infants are typically scanned asleep, while adults are typically scanned awake. Functional connectivity at rest differs when people are awake versus asleep (Stevner et al. 2019), and the functional correlations of sleeping infants are more similar to those of sleeping adults than awake adults (Mitra et al. 2017). In all, it is still debated how much of the medial PFC's adult functional network is available at birth, but by the middle of the first year, functional correlations with temporoparietal and medial precuneus regions are clearly present and could support the infant's increasingly sophisticated social behaviors.

There is also mounting direct evidence that the medial PFC of infants responds to social, self-relevant, and valued stimuli. In a rare fMRI study of awake infants, 4–6-month-olds showed medial prefrontal activity in response to dynamic videos of children's faces compared to dynamic videos of natural scenes (Deen et al. 2017). This finding fits with substantial evidence from fNIRS studies, implicating the medial PFC in infant social cognition (reviewed in McDonald & Perdue 2018). Already in newborns, the medial PFC responds more to infant-directed speech than to adult-directed speech (Saito et al. 2007a,b). In 7-month-old infants, the medial PFC scales with self-relevance: When playing peek-a-boo, medial PFC activation was strongest for mutual gaze with an infant-directed sound, weaker for an averted gaze with an infant-directed sound, and weakest for an averted gaze without the sound (Urakawa et al. 2014).

These medial PFC responses are related to infant social behaviors. Infants' attentional bias to their mothers compared to a stranger correlates with medial PFC activation (Imafuku et al. 2014),

suggesting a link between socially motivated behavior and medial PFC function. One fNIRS study took simultaneous neural measurements of interacting dyads in naturalistic social settings (Quaresima & Ferrari 2019), such as parents and their children (Nguyen et al. 2020). Infants interacting with an adult show temporally synchronized medial PFC responses (Piazza et al. 2019), which implicates this brain region as a developmental driver of the neural coupling that typically happens during natural communication (Hasson & Frith 2016).

Together, these findings suggest that even in infants, the medial PFC already plays a role in infants' pursuit of social motivations. Importantly, in infants as in adults, information-seeking and social motivations appear to depend on separable brain mechanisms (**Figure 1**). This suggests that young infants pursue multiple, distinct intrinsic motivations, relying on more than one PFC-dependent mechanism to actively direct their attention.

IMPLICATIONS

Having surveyed two domains of active learning, we now turn to broader implications of our account. We first address the apparent discrepancy between relatively immature anatomy but relatively mature PFC function in infancy. We then discuss the implications of our hypothesis about how infants learn for what they might learn by situating our view within related empirical and computational literature.

Reconciling PFC Anatomy and Function: A Role for the Thalamus?

Thus far, we have argued that the infant PFC is functionally more mature than its anatomy would suggest. Both the lateral and medial PFCs are functionally active in similar contexts to their adult roles and are correlated with the same brain regions as adult functional networks. However, this argument raises a question: Why doesn't anatomical immaturity have more dramatic effects on infants' PFC function and associated cognition and behavior?

One answer is that perhaps there is not much of a puzzle after all. Recent large-scale histological analyses suggest that several anatomical markers do not show as clear of a protracted development in the PFC as was previously suggested. The PFC may not reach its final gray matter volume or synaptic density much later than other brain regions (Huttenlocher & Dabholkar 1997, Jernigan & Gamst 2005). More importantly, it was never clear what any particular anatomical marker, such as synaptic density or myelination, implied about the functions the PFC can or cannot perform.

A second answer is that while infant PFC function resembles the adult PFC qualitatively in terms of major division and functional roles, PFC function is dramatically different from its adult state quantitatively (Crone & Steinbeis 2017). For example, the lack of myelination makes neural transmission almost certainly slower. A characteristic signature in adult event-related potentials occurs approximately 300 ms after stimulus presentation (called the P300; Polich 2007), but at 5 months old the onset of the putative homolog of the P300 is about 900 ms and decreases to about 750 ms by 12 months old (Kouider et al. 2013). A distinction between the kinds of computations that the PFC performs, versus the speed and efficiency with which it performs them, could bridge the gap between our argument and a more classic view.

A speculative but intriguing third possible answer to this question is that the infant PFC leverages connections to another brain region to perform its functions: the thalamus. The thalamus is a collection of nuclei at the center of the brain (**Figure 1**). Historically, the thalamus was described as a simple sensory relay, connecting sensory inputs to primary cortical regions. More recent discoveries reveal that thalamic nuclei connect directly to higher-level association regions, such as the PFC, and in turn, the PFC has many feedback connections to the thalamus. These thalamocortical loops play key roles in adults in selective attention and cognitive flexibility (Hwang

et al. 2017, Parnaudeau et al. 2018). For example, the medio-dorsal region of the thalamus, which forms thalamocortical loops with the PFC, is necessary for mice to perform a (mouse-appropriate) inhibitory control task (Rikhye et al. 2018, Wimmer et al. 2015).

Thalamocortical connections emerge early during fetal development (Kostović & Judaš 2010), and unlike the PFC itself, myelination of thalamocortical connections (including those to the PFC) begins in utero and terminates around 1 year after birth (Hasegawa et al. 1992, Sampaio & Truwit 2001). Functional correlations between the thalamus and the medial PFC, for example, have been observed in 1-month-old infants (Ferradal et al. 2018). In neonates, sensory regions tend to be connected to a specific parcel of the thalamus, while high-level association areas tend to connect to multiple parcels of the thalamus (Toulmin et al. 2015), offering a potential integrative role for thalamic nuclei in which multiple high-level signals converge.

These thalamocortical loops may provide a way to reconcile the anatomical immaturity of the infant PFC with its role in many aspects of infant cognition. While adults rely on both thalamocortical and corticocortical connections for PFC functions, infants may compensate for the anatomical immaturity of corticocortical connections by relying more heavily on thalamocortical loops. By distributing information across cortex via the thalamus, the prefrontal computations discussed in this review may be less reliant on mature, myelinated corticocortical pathways. Tentative support for this hypothesis comes from correlational studies showing that structural and functional thalamocortical connectivity in infants predicts subsequent cognitive outcomes. Structural connectivity measured by diffusion MRI in preterm newborns predicts performance on a battery of cognitive tests at 2 years of age (Ball et al. 2015), and thalamic connectivity specifically to the PFC in neonates predicts cognitive, but not motor, function in 2-year-olds (Jakab et al. 2020). Furthermore, longitudinal analyses of resting-state correlations in the first 2 years of life show that correlations between the thalamus and a set of PFC regions predicted the progression of visuospatial working memory and general learning scores, composed of motor, perceptual, and language performance (Alcauter et al. 2014).

In summary, the role of thalamocortical loops in infants' PFC function, and endogenous control of behavior, is an exciting area for future research. It is important to identify how myelination of corticocortical tracts and protracted synaptic pruning in the PFC affect infants' developing cognition.

How Do Endogenous Motivations Affect What Infants Learn?

Infants appear to actively choose and control their environmental experience. How does endogenous motivation affect the content of what infants choose to learn and the representations that they form?

The classic but misleading view describes infant learning as primarily a process of extracting statistical structures from patterns of incidentally received bottom-up input. An influential contemporary version of this view proposes that infants initially represent the world in terms of simple features inherited from the structure of sensory input (Arcaro et al. 2019, Livingstone et al. 2019). For visual input, for example, these simple features include retinotopy, orientation, spatial frequency, and contrast. Then, through self-organization and activity-driven plasticity, neural populations extract the higher-order regularities in the incidental input (Arcaro et al. 2019, Livingstone et al. 2019).

We agree that infants must learn their representations of the world from the input they experience; however, we have suggested that infants actively select these inputs. That is, infants actively construct a curriculum for their own learning (Smith et al. 2018). These self-generated shifts in sensory experience likely allow learning to proceed more efficiently than with an arbitrary,

incidental input space. In machine learning settings, targeted sampling of relevant information reduces the amount of training data needed for learning by reducing the computational complexity of the learning problem. This active control over inputs confers benefits in terms of generalization and data efficiency (Bengio et al. 2009, Hacohen & Weinshall 2019). By analogy, the infant's self-generated curriculum may similarly serve as a scaffold for learning.

Contemporary computational models support the idea that endogenous motivations can promote learning. For example, artificial agents are endowed with an intrinsic motivation (often called curiosity) to explore their environment when predictions about the environment are violated (Ecoffet et al. 2019, Pathak et al. 2017). Even in the absence of external rewards, curiosity-driven agents quickly adopt exploratory behaviors that enhance their learning about their environment (Haber et al. 2018, Watters et al. 2019).

One important difference between infants and most curiosity-driven artificial agents, we argue, is that infants seem to simultaneously pursue more than one endogenous motivation. For most artificial agents, curiosity is implemented as a single objective: for example, to minimize discrepancies between predicted and actual inputs while simultaneously expanding the range of environmental situations that can be predicted (Haber et al. 2018). These intuitively plausible notions of curiosity correspond well to some basic aspects of infants' information-seeking behavior. By contrast, these agents have no analog to infants' motivations to form social relationships. We suggest that for human infants these objectives distinctly influence their sampling of the environment and therefore potentially the representations that they learn. Having multiple objectives may create unique dynamics of learning: For example, pursuing an objective in the social domain could lead to learning representations that later serve a nonsocial purpose. An interesting question for future computational models is, how is the content of what an agent learns about the environment different when learning occurs over input selected for all these distinct reasons?

Another intriguing possibility is that the PFC influences infant learning not only indirectly (by directing infants' attention and exploratory behaviors), but also directly via top-down feedback to the sensory regions where the contents of learning are stored. The top-down influence of the PFC on sensory areas is well studied in adults (de Lange et al. 2018). In adults, the PFC generates predictions of forthcoming sensory stimuli, which allows for highly compressed representations of bottom-up perceptual information and fast perceptual decision making (Alexander & Brown 2018, Rahnev 2017). There is emerging evidence that the PFC can likewise directly influence activity in sensory regions in infants (Emberson et al. 2015, Werchan & Amso 2020).

If so, then the patterns of activity in sensory regions that drive self-organization and activity-driven plasticity would actually reflect not only the structure of the external environment, but also endogenous biases. An influence of endogenous, top-down input on sensory learning could help explain the surprising resilience of some cortical response profiles to a major divergence in external input, such as the response to faces in the fusiform face area of congenitally blind adults (Ratan Murty et al. 2020, van den Hurk et al. 2017). That is, if visual cortical representations were wholly learned from, and thus dependent on, the structure of external input, they should not develop similar features when that external input is removed.

Conversely, a strong role for endogenous input could also explain the dramatic alteration of other cortical response profiles in the same blind people. When normal bottom-up input is removed from early visual areas, these regions do not atrophy (as some scientists once speculated they might) but instead take on new functional roles in language and math processing (Kanjlia et al. 2018, Pant et al. 2020). These new roles are plausibly derived from top-down input from prefrontal regions (Bedny 2017, Kanjlia & Bedny 2018). Since the most dramatic instances of plasticity occur in congenitally but not late-blind individuals, the causal influence of the PFC on sensory regions may be greatest early in life.

In sum, we argue that endogenous motivations, subserved by multiple components of the PFC, may directly bias the representations formed in infants' sensory cortices. This view thus suggests a strong influence of predisposition on the content of what infants learn and so is a flavor of nativism. However, by contrast to extreme nativist views, we focus heavily on the importance of learning, using endogenous motivation to select the appropriate inputs for learning, and possibly the priorities during learning, rather than to remove the need for learning altogether. Also, while some views highlight the contents of innate knowledge (e.g., the core knowledge hypothesis; Spelke & Kinzler 2007), here we focus on the structure of innate motivations. However, our view is consistent with the core knowledge hypothesis. For example, innate representations that parse the world into objects and agents generate expectations about how those objects and agents should behave. Violations of those expectations provide learning opportunities for the infant (Stahl & Feigenson 2018), which they pursue due to the intrinsic motivation to attend to informative events.

FINAL REMARKS

The traditional story of infant learning is one of the incidental accumulation of sensory experiences. Similarly, the traditional story of brain development is one of sequential primary-to-higher-order maturation, with the PFC maturing last. This account of the infant mind and brain has been a dominant force in our understanding of development.

Here, we have argued that this account is misleading. The last four decades of developmental psychology have shown that infants do much more than passively extract statistics from the inputs they happen to receive. Instead, infants have intrinsic motivations that drive active learning behaviors. By motivating careful selection of the appropriate inputs, intrinsic motivations provide the scaffold on which learning occurs.

Several qualifying points should be noted. First, the research we surveyed shows average trends, not universal rules that necessarily hold for every individual infant. How individual differences in goal-directed behaviors affect learning and exploration is an important perspective, which we largely neglected here.

Second, it can be useful to distinguish motivations and developmental outcomes (Adolph et al. 2018). Long-term effects do not have to be in the same domain as the real-time motivations that cause them. For example, immediate social motivations, such as attention to faces, likely have a plethora of nonsocial long-term outcomes, such as language learning. Relatedly, to make the point that infants use distinct motivations to guide their behavior, we have largely surveyed evidence in which a particular motivation, such as bonding with a caretaker, is distinguishable from other motivations, such as information seeking. In real-life settings, most situations pertain to many motivations simultaneously. How infants manage conflicting motivations, or jointly optimize for multiple motivations, is an open question.

Third, the two main motivations we outline here are certainly not exhaustive, and there are likely further drivers of infants' learning. Infants show similar active learning behaviors for motor learning (e.g., learning to walk; Adolph et al. 2018), threat detection (Fu & Pérez-Edgar 2019), and language acquisition (Dehaene-Lambertz 2017). A more complete account of infant learning should also try to address how these different drivers of infants' earliest behaviors interact. As an example, one could suggest that learning to walk enhances the reach of information-seeking motivations, since now infants can expand their set of potential inputs from only what is in their immediate field of view to what is on the other side of the room. It may be fruitful to study such dynamics of motivated behaviors experimentally and computationally.

In very young infants, distinctions between intrinsic motivations are hard to see and study. Infants' behavioral repertoire is limited, so distinct motivations converge on a single behavior.

Behavioral paradigms should attempt to disentangle different motivations for looking. Neural evidence may help to draw such distinctions, as evidenced by the functional subdivision between the lateral and medial PFCs, which subserve information-seeking and social motivations, respectively.

We have known for a long time that infants are intrinsically motivated, active learners. Yet, also for a long time, the neural substrates that support these behaviors in adulthood, such as the PFC, have been described as immature. Here, we have consolidated recent evidence from developmental cognitive neuroscience in an attempt to resolve this apparent contradiction. The function of the infant PFC is revealing itself to be strikingly adult-like. While many questions remain open (see Future Issues), we hope that these insights provide new avenues for studying how infants learn and, more broadly, for aligning our understanding of infants' brains and minds.

FUTURE ISSUES

1. Distinct motivations: Do infants' prefrontal cortices support further motivations, such as motor learning, threat monitoring, and language acquisition? What criteria should be used to distinguish motivations from one another? Can all behaviors ultimately be described as the result of a single, general-purpose objective?

2. Behavior and learning with multiple motivations: How do infants manage conflicting motivations? How do they jointly optimize for several motivations? Do artificial agents show more human-like behaviors and learning dynamics when they have multiple, distinct motivations?

3. The role of the thalamus: Do thalamocortical loops play a distinct role in infancy, supporting prefrontal influence over other cortical areas while corticocortical connections are still maturing?

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Contents

Errata

An online log of corrections to *Annual Review of Developmental Psychology* articles may
be found at http://www.annualreviews.org/errata/devpsych