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The promise of awake behaving infant fMRI as a deep measure of cognition

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What are the contents of the infant mind? In the last decade, computational advances in fMRI have allowed researchers access to the internal representations of adults. Applied similarly in infants, fMRI stands to revolutionize our understanding of cognitive development. By measuring representations at their source, infant fMRI overcomes some of the limitations of behavioral measures. We discuss example domains where this approach could be fruitful, including episodic memory, semantic cognition, spatial representations, and theory of mind. In these and other areas, the richness of fMRI data could give new insight into how infants represent the world and potentially help resolve ongoing debates in developmental science.

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Introduction

Psychologists have developed tools to measure infant cognition through behavior, revolutionizing our understanding of the infant mind. Despite this progress, however, the infant mind remains difficult to decipher, in part because of limitations in infant behavior. In this review, we consider an approach to understanding the infant mind that has recently gained traction: functional magnetic resonance imaging (fMRI) in awake infants performing tasks. fMRI is uniquely positioned to extract rich, multifaceted information about infant cognition. We discuss our framework for deeply measuring infant cognition. We then consider how awake infant fMRI can reveal internal states that may not cleanly manifest in infant behavior, and may help resolve extant debates in the developmental literature. Altogether, we hope to highlight the value of using awake infant fMRI for understanding deeper aspects of the infant mind.

A deep measure of infant cognition

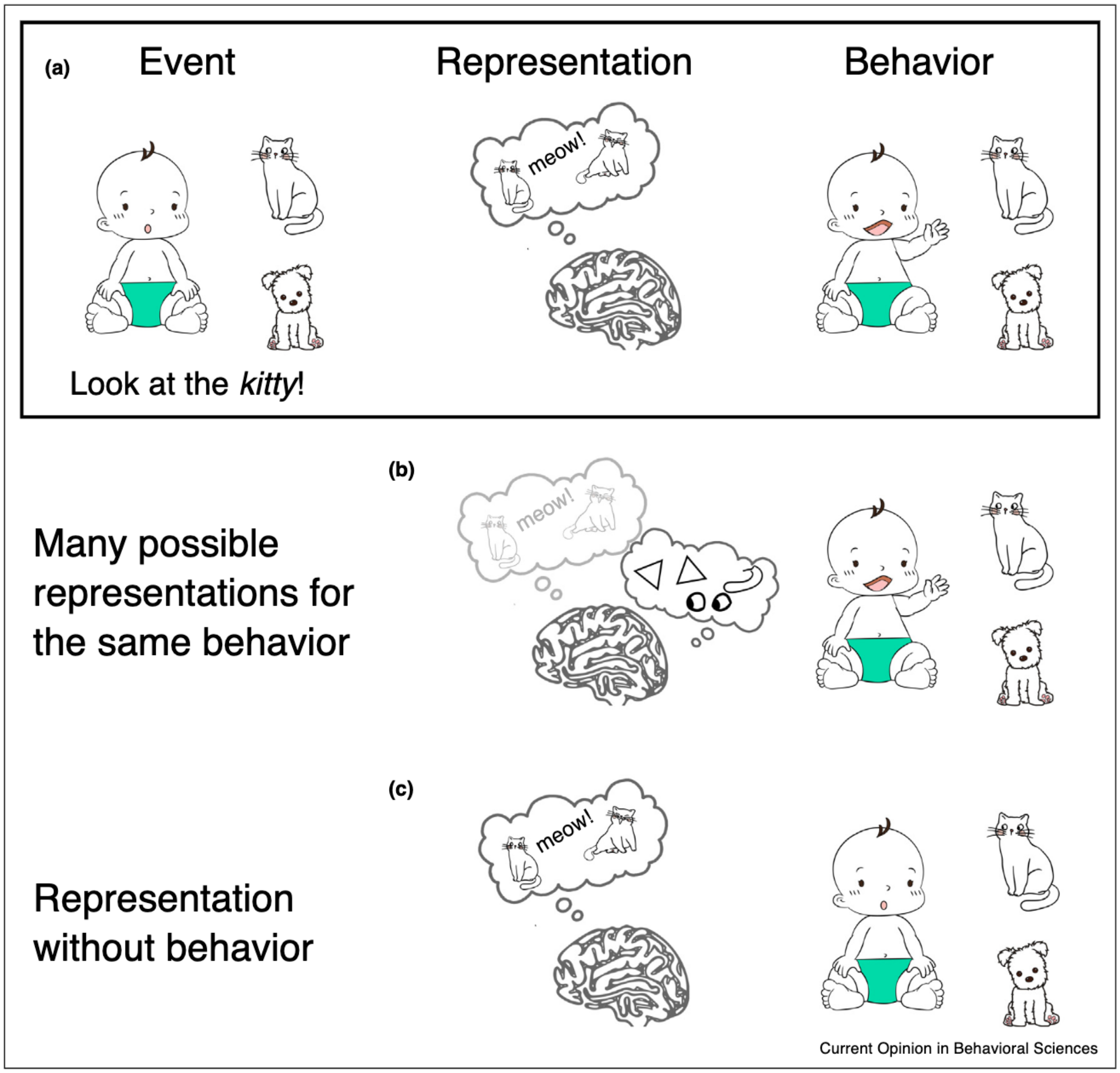
Given the constraints of the behavioral repertoire of infants — an inability to speak, understand complex instructions, execute complex actions, etc. — researchers have developed clever measures of cognition, such as looking-time duration [1], pupillometry [2], head-turn preferences [3], reaching [4], and locomoting [5]. However, it is increasingly evident that when the goal is to index infants' mental states, reliance on one simple behavioral measure can be problematic [6••]. Consider showing an infant two images and asking them: 'where is the kitty?' (Figure 1). From behavior alone, it can be difficult to ascertain whether infants represent the meaning of the word *kitty*. To help resolve this issue, neuroimaging techniques such as electroencephalography (EEG) and functional near-infrared spectroscopy (fNIRS) [7] have increasingly been utilized in infant research. These techniques provide a powerful window into the dynamics and representations of the infant mind.

Here, we focus instead on fMRI, a technique that is emerging as a way to study infant cognition but has a long and successful history in helping understand child, adolescent, and adult cognition [9]. Although MRI and fMRI are commonly used for understanding the structure and resting connectivity of sleeping infants [7], fMRI in awake infants performing tasks is the most direct way to study infant cognition. As a complex and rich data source, fMRI can tap into internal representations that may otherwise be overlooked in behavior and that may not be apparent in scalp-based measurements from EEG and fNIRS. In the last decade, computational advances [10] have also made 'mind-reading' a reality with fMRI. Researchers can construct models to decode what an individual is seeing [11], predicting [12], and recalling [13]. Additionally, the high spatial resolution of fMRI allows for indexing multiple representations during the same task, such as what someone is *simultaneously* seeing and predicting [14]. This is particularly promising for extracting multiple cognitively relevant functions during complex stimuli such as movies [15]. For developmental research, these naturalistic stimuli [16,17] may be especially important for simultaneously tapping into multiple cognitive functions without requiring multiple experiments.

Initial discoveries

So far, only three studies that used fMRI in awake infants during cognitive tasks have been published [18–20]. The

Figure 1



Ambiguity of behavioral measures given internal mental states. An infant is tested on their word knowledge. A parent or experimenter prompts the infant to look at the 'kitty' while showing a picture of a cat and a dog. **(a)** The infant correctly looks at the cat picture. It is assumed, especially based on performance aggregated across trials, that this behavior is possible because the infant has a mental representation of the word or concept *kitty* that was matched to the picture of the cat. If true, behavior is an accurate measure of cognition. However, this same behavior can occur with an entirely different mental substrate. **(b)** For instance, the behavior could be driven by the cat being more attractive, familiar, unusual, having pointy ears, whiskers, or a long tail, etc. Or, the shape of the cat may intrinsically be a better match to the phonological features of the word 'kitty' without any real comprehension [8]. In these cases, the behavior is attributed to the wrong cognitive process — semantic/conceptual rather than perceptual or linguistic. **(c)** Conversely, the infant may possess the appropriate mental representation but lack the motivation or ability to exert an interpretable behavioral response. Hence, by accessing an infant's mental representation more directly, it may be possible to circumvent the ambiguity of infant behavior.

first study was fortuitous: while investigating speech processing in sleeping 3-month-olds, six infants remained awake and attentive. Speech processing was evident in auditory regions of all infants, with sensical and non-sensical speech distinguished in the angular gyrus. However, only in awake infants was the dorsolateral prefrontal cortex also involved in processing sensical speech [18]. This suggested that the prefrontal cortex, thought to be minimally functional in infancy, may play a larger role in early development than previously assumed [21]. The second and third studies examined visual processing. In 7-week-olds, functional responses to motion were adult-like in anatomical localization, but differences in early visual cortex suggested some later refinement of motion processing [19]. In 6-month-olds, the functional responses evoked by faces and scenes were localized to similar regions as adults. However, these regions were less selective to their preferred category than in adults [20]. Together, these pioneering studies demonstrate the feasibility of awake infant fMRI for revealing previously unknown properties of the infant mind.

Ensuring that infants are awake, still, and attentive long enough to collect adequate data are some of the many challenges of this work. Over the last several years, our lab has developed a new protocol for awake infant fMRI [22••]. To minimize movement, infants are positioned on a vacuum pillow within reach of a parent or experimenter. The comfort and state of the infant are monitored continuously via a camera in the scanner bore. The infant's face can be seen because only the bottom half of the head coil is used; it provides whole-brain coverage and reasonable signal-to-noise, given the smaller head size. Removing the top half of the head coil also allows good visibility by the infant of stimuli projected onto the bore ceiling above their face. The code that runs the experimental tasks is robust and flexible, allowing for breaks and switching between tasks. Together, these methods have enabled us to collect fMRI data from almost 200 sessions to date with an average success rate of one usable experiment per session (some infants have none, others complete 3–4 tasks). Several studies of infant perception, attention, learning, and memory are ongoing. For example, we have shown that key regions of adult attention networks, including in the frontal lobe, are recruited to orient infant attention, as measured behaviorally with eye movements [23]. Additionally, we have found that the infant hippocampus can quickly learn regularities from the environment, despite this memory system often being considered immature in infancy [24]. These initial steps highlight how fMRI has the potential to fundamentally change our understanding of early development. Below we explore the distinct advantages of fMRI as a deeper method to understand the infant mind.

Unpacking behavior

Given the potential ambiguity of infant behavior, developmental researchers carefully design studies to control for alternative explanations. Nonetheless, debates remain over whether certain behavioral outcomes can be explained by alternative accounts that were not considered. Furthermore, partial or failed replications suggest that additional measures could help resolve the cognitive capacities of infants [25]. While fMRI is valuable for a number of cognitive domains, it holds particular promise in understanding the characteristics of infant episodic memory, semantic knowledge, how they represent space, and how they reason about other minds.

Episodic memory

Early development is a period of immense learning, yet specific memories of experience obtained during infancy do not persist over time. This phenomena, called infantile amnesia, continues to be a developmental puzzle [26•]. Despite illuminating behavioral research on the memory capacities of infants [27], it remains unclear which phases of the episodic memory process — encoding, consolidation, and/or retrieval — contribute to memory failures [28]. In adults, certain regions of the brain, such as the hippocampus, are associated with subsequent recall [29]. Evidence that memory retrieval in the hippocampus relates to later explicit memory was also shown recently with fMRI in sleeping toddlers [30,31•].

fMRI with awake infants provides an additional opportunity to measure behavior and brain states simultaneously to understand how memory processes are supported in the infant brain. Combining fMRI and eye-tracking can answer a fundamental question in developmental science: namely, how does memory recall relate to looking behavior? When an infant is shown a stimulus that they have seen before along with a new stimulus, they sometimes look longer at the familiar stimulus and other times look longer at the novel stimulus [32]. Such novelty preferences have been hypothesized to reflect more complete encoding of prior viewings, whereas familiarity preferences may result from impoverished representations [33,34]. The ability of fMRI to access internal states provides a direct way to measure memory integrity by comparing the similarity of a representation when it is first encoded and when it is retrieved [35], which can in turn be related to looking-time measures. Moreover, it may reveal that novelty and familiarity preferences do not reflect two sides of the same learning process, but rather the control of attention by multiple memory traces [36].

fMRI additionally makes it possible to track how representations change over delay and development, which may be important to understanding the nature of infantile amnesia. This could be accomplished without an explicit or verbal retrieval task, for example, by measuring the reinstatement of patterns of neural activity from encoding during subsequent experience, rest, or sleep [37]. Thus, early episodic memory could be assessed by showing infants videos of complex, dynamic scenes during fMRI and testing if they later recall these memories neurally when cued. By targeting different aspects of the memory, this approach makes it possible to distinguish specific computations underlying episodic memory that have been measured with fMRI in adults, such as pattern separation, pattern completion, and relational binding [12]. These computations are difficult to assess behaviorally [38], and in adults rely on deep-brain structures like the hippocampus that are inaccessible to other techniques such as EEG and fNIRS. Thus, fMRI is a promising way to investigate the neural mechanisms of infant episodic memory.

Language and semantic networks

Although almost a year passes before infants produce their first words, they are processing speech even while in the womb [39]. They can understand some concrete words by 6 months [40] and can segment words from continuous speech streams by 8 months [41]. However, infants' understanding of semantic relationships between words is hard to measure, and the story of conceptual development often begins in young childhood [42]. In adults, co-occurrences in large text corpora can be used to accurately predict fMRI activity to concrete words [43] and abstract concepts [44]. Models could similarly be constructed using early language corpora [45,46] and compared to neural representations of words in the infant brain. Alternatively, infant semantic space could be determined in a more data-driven way through representational similarity analysis, using the similarity of neural patterns evoked by words to infer their semantic relatedness. Representational similarity in some regions of the brain may be governed by shared perceptual features of the words themselves (e.g. book and boot) or of their referents (e.g. milk and juice), whereas other regions may represent semantic features divorced from perceptual features (e.g. book and table; milk and refrigerator), as has been found in adults [47•]. The high spatial resolution of fMRI, unique for non-invasive neuroimaging, may be especially important for distinguishing these representational spaces.

Importantly, a task with behavioral responses is also not required to study the semantic representations of infants with fMRI. Indeed, from task-free movie-watching alone, researchers can construct a semantic space [48] and provide a text caption of the current scene [49]. This makes it possible to investigate infant conceptual knowledge longitudinally using a consistent paradigm. In this way, fMRI could demonstrate how the semantic network grows as infants acquire new word knowledge [50].

Navigating space

Infants appear to have a rich understanding of the social and physical world. Geometric and spatial relations are one of the building blocks of this understanding. By 5 months, infants are surprised when objects disappear and reappear in different spatial locations [51], and by 9 months, infants correctly look at goal locations when starting from different positions [52]. In the brain, rodent studies have shown that the infant hippocampus and entorhinal cortex code for places and directions during navigation through an environment [53]. At the same time, human infants can show relational errors, such as an inability to find objects when turned around [54]. Indeed, many aspects of spatial processing, such as coding metric distance and spatial perspective-taking, develop slowly [55•]. Hence, it remains unclear how precisely infants can represent space, which is especially hard to investigate before infants develop locomotor capacities. fMRI with awake infants could be used to test early spatial representations by examining relevant brain systems identified in adults [56]. The spatial layout of a scene (e.g. the presence and arrangement of walls) is represented in the occipital place area in a way that is invariant to texture and other visual properties [57]. Meanwhile, the category of a place (e.g. a coffee shop) is represented in the parahippocampal place area regardless of real-world location or proximity [58]. Broader maps of an environment are represented in entorhinal cortex and the hippocampus, with neural pattern similarity higher when viewing photographs of landmarks that are closer together in the real world [59]. Notably, several of these brain regions are medial, ventral, and/or subcortical, and thus cannot be directly measured with scalp-based techniques. Whether human infants navigate space with place and grid representations in the hippocampus and entorhinal cortex, respectively, is unknown but also potentially addressable with fMRI and virtual reality [60]. Although adults control their own navigation in most of these studies, viewing movement through space may be sufficient.

Theory of mind and false beliefs

The ability to represent that another person has a different belief than you or that their belief conflicts with reality was initially thought to develop around 4 years [61]. Recent studies have shown that infants can in fact possess such theory of mind, including predicting and representing the goals of others [62]. At the same time, there have been several failures to replicate infant false belief studies [63]. These discrepancies led to two accounts of infant theory of mind: The *continuous* account posits that infants represent the beliefs of others in a similar way to older children [64]. Early failures on certain tests of theory of mind, such as language-heavy tasks, are thought to reflect limitations in executive function [65•]. The alternative *two-system* account proposes that there is both an early developing, implicit system and a later developing, explicit system [66]. This account distinguishes between explicit tasks, in which participants need to demonstrate an understanding that what somebody else believes to be true can differ from their own knowledge, and implicit tasks, in which participants look longer when someone performs an action that is inconsistent with their knowledge or show anticipatory looking consistent with the other's belief. Success on implicit theory of mind tasks may not always result from representing another person as agentic, as much as using perceptual cues, which has been used to explain the performance of other species [67].

These two accounts make different predictions for the internal representations of infants. According to the continuous account, the same brain regions and patterns of activity should be recruited during theory of mind tasks in infancy as later in development [68]. For example, naturalistic viewing of a movie that evokes theory of mind induces similar activity in the temporoparietal junction between adults and children, and between young children who do and do not pass a battery of theory of mind tests [69•]. Importantly, fMRI has the resolution to distinguish the temporoparietal junction and the nearby superior temporal sulcus, which is involved in social perception but also many other functions [70], whereas other techniques lack this precision. According to the two-system account, there should be a dissociation between early and later development in terms of the nature or localization of representations related to theory of mind. In preschoolers, success on implicit and explicit theory of mind tasks is neurally dissociated in terms of brain structure [71], fitting with previous work showing a behavioral dissociation [72]. Investigations in infants could provide further insight into whether theory of mind is quantitatively or qualitatively different across development.

Conclusion

Awake infant fMRI allows for a deeper characterization of cognition and development by revealing representations that may not be behaviorally expressed or that are inaccessible to other neuroimaging techniques, and by distinguishing between mechanisms that could jointly drive behavior under different circumstances. The combination of fMRI as a sensitive tool with advanced data analysis methods has dramatically accelerated progress in cognitive neuroscience over recent years. Our hope is that importing these approaches from adult cognitive neuroscience into the study of infant cognition could likewise advance the field and unlock mysteries of how the infant mind functions and develops.

Conflict of interest statement

Nothing declared.

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