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# The neural mechanisms of object working memory: what is where in the infant brain?

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## Abstract

The question of how representational capacities develop in humans has been engaging cognitive psychologists for decades. Looking time studies have explored when infants start to show signs of perceiving and remembering the properties of specific objects at specific locations. Here we integrate these findings into the neuroscientific framework of human visual working memory. We suggest that the development of a system involving the temporal cortex, thalamic and hippocampal structures and possibly the dorsolateral prefrontal cortex (later in development) can account for these behavioral results. Our explanation differs from most of the current approaches in developmental science as we put less emphasis on the contribution of lateral prefrontal areas. We discuss shortcomings of the theories that propose a functional subdivision of these areas and their difficulty in accounting for results from monkey lesion and infant studies. We believe that this shift in focus is desirable both in light of what recent results on medial temporal lobe processing reveal about object working memory, and given how well these results fit the behavioral developmental data.

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**Keywords:** Working memory; Development; Object; Temporal cortex; Human

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## 1. Introduction

Knowing and remembering where things are around us is one of the most important cognitive tasks in our everyday life. Indeed, forgetting where objects are is regarded as one of the first symptoms of Alzheimer's disease [19,55].

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The question of how this type of memory develops in human infants has become the focus of some recent behavioral studies. Parallel with these developments, neuroscientific research of working memory for objects and locations has accumulated evidence about the brain structures underlying and the mechanisms subserving these cognitive processes. In this paper, we attempt to connect these two surprisingly segregated areas of research: the behavioral literature on the development of object cognition and the current questions surrounding the neural basis of working memory for objects.

## 2. Recent behavioral results on object-location memory in infants

In Ref. [53], we have shown that 9-month-old infants are able to remember two objects and their respective locations, even when their attention is distracted by an intervening object during the retention phase. Infants were not able to simply associate particular objects with locations over time in this paradigm, because the location of the objects alternated from trial to trial. Since objects were hidden sequentially, a control study was conducted to test if infants remembered the more demanding, first-hidden object. Findings of a subsequent study [54] pointed out that younger, 6-month-old infants can only remember the last object in the same paradigm, and they fail if their attention is distracted during the retention phase by another object. Fig. 1 summarizes the experimental set-up and the main findings.

According to these results, 9-month-old infants spontaneously bind their object representations to moment-to-moment locations; otherwise, they would not have shown surprise by seeing the two objects in switched positions. Leslie, Xu, Tremoulet and Scholl [63] hypothesized that the process of setting up object representations was driven primarily by location and that the integration of featural information-integrating the ‘what’ with the ‘where’ in

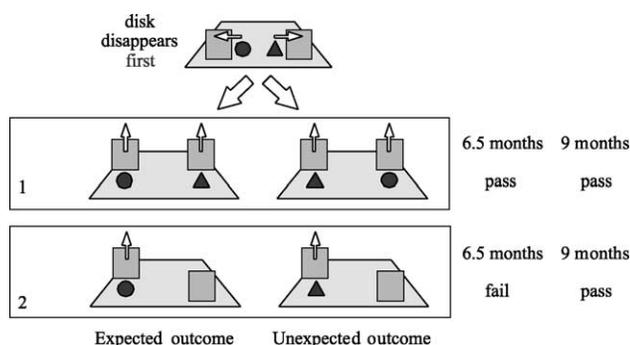


Fig. 1. Summary of main behavioral findings of [53]. Following the general logic of violation-of-expectation paradigms, *pass* signals that infants looked significantly longer at the unexpected outcome than at the expected outcome, *fail* signals that there was no significant difference between reactions to the two different outcomes. Before the test, infants were systematically familiarized with both of the objects appearing on alternating sides of the stage. Objects were hidden sequentially; in the presented sequence the first object hidden was the disk on the left.

working memory-would occur developmentally later. Based on their computational model, Mareschal, Plunkett and Harris [70] have predicted that performance on tasks that require the integration of cortically separable representations in the presence of occluded objects will be delayed compared with tasks that do not require such integration. Specifically they have predicted that integration of ‘what’ and ‘where’ information in brief occlusion situations should be expected around 7.5–9.5 months of age. The present results confirm the above prediction and suggest that this integration can take place as early as 9 months of age.

In agreement with the above prediction and findings, earlier results of Baillargeon and her colleagues have demonstrated that 8-month-old infants could remember the location of an object out of two possible hiding locations with delays of 15, 30 and even as long as 70 s [8,9]. Ahmed and Ruffman [1] confirmed these results with infants 8–12 months of age and various looking-time paradigms. Wilcox and her colleagues have shown that infants can use featural information to individuate objects very early on [121], and are even able to identify objects in a simplified paradigm [122]. Moreover, Mareschal and Johnson [69] recently demonstrated that this integration is definitely not present at 4 months of age. However, their suggestion that the maintenance of the information presumably involves the frontal lobes should be reevaluated.

## 3. Selective overview of the primate object and location-coding literature

Based on anatomical, physiological and lesion studies the primate visual system is thought to consist of two relatively separate subsystems [11,42,45,60,118]. The ‘dorsal’ pathway originates from the occipital lobe, continues into the parietal lobe and supports object localization, motion perception and visual-guided action. It is often called the ‘where’ or ‘how’ pathway. The ‘ventral’ pathway also originates from the occipital lobe, but continues into the temporal lobe, and is thought to be important for object recognition. It is often called the ‘what’ pathway (Fig. 2). This idea of two visual pathways has been a most influential one in neuroscience, as it combines simplicity and experimental support. The role of the two pathways and the degree of their segregation is the focus of ongoing research, which has enriched the initial notion with interesting findings, such as considerable communication between the two pathways [37,119], shape selectivity [108] and responses to static images that imply motion [61] in the ‘dorsal’ stream, as well as motion selectivity in the ‘ventral’ stream [96,97,105]. For a comprehensive review of the arguments against the oversimplified idea of the two separate visual streams [72].

Recent studies have shown that 9-month-old infants were able to remember *what* went *where*, suggesting that information from both of the visual pathways are accessible

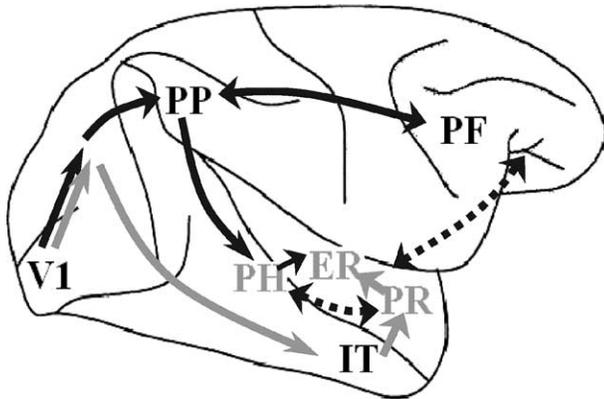


Fig. 2. A simplified diagram of the basic system of visual working memory in primates. Solid black lines represent mainly dorsal routes ('where'), gray lines represent mainly ventral routes ('what'), and dashed black lines represent mixed input. V1: primary visual cortex, IT: inferotemporal cortex, ER: entorhinal cortex, PR: perirhinal cortex, PP: posterior parietal cortex, PH: parahippocampal cortex, PF: prefrontal cortex. Gray letters indicate areas that are located on the inner, hidden surface of the temporal lobe. Based on Refs. [111,117] (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.).

and can be integrated at this age. Furthermore, we will suggest that even though some working memory tasks involve the prefrontal cortex, this type of task may not. We propose that a more posterior recognition system that comprises the medial temporal cortex in connections with some parietal centers may be sufficient to solve the task.

### 3.1. The ventral pathway: the temporal lobe

Electrophysiological studies in monkeys have shown that cells in the temporal cortex have memory-related activity [15,40,80]. In monkeys, visual recognition memory is most commonly measured by the delayed matching to sample (DMS) task. Typically in these studies, a sample object is presented at the start of the trial, followed by a delay and then one or more test objects. The animal is rewarded for indicating which test object matches the sample. To solve the DMS task the monkey needs to solve three problems [28]. First, it must discriminate among the different objects. Then, it must retain the memory of the sample for the length of the trial. Finally, it must make a decision about whether the current test object matches the sample held in memory. Cells in the temporal cortex contribute to all three of these tasks [28].

#### 3.1.1. The inferotemporal cortex (IT: superior temporal sulcus, TE, TEO)

The inferotemporal cortex (IT) is considered the highest level processing center of visual information about objects [27,66,114]. Neurons in IT have large receptive fields that include the fovea, and they are highly selective to shapes, with a high degree of tolerance for their size and position on the retina [87] (but see Ref. [33] for a recent discussion of

receptive field size). The anterior part of IT has been shown to discriminate between complex two- and three-dimensional objects [58,65,109,120].

A recent study by Baker and his colleagues [12] demonstrated that neurons in the anterior banks of the superior temporal sulcus (STSa) respond to objects that gradually become occluded. (Regions around STS and the different parts of IT are heavily interconnected [104]). This response is maintained for up to 11 s following complete occlusion. This is the first study to use natural, progressive occlusion of 3D objects; in previous studies, objects disappeared suddenly on a computer screen (Fig. 3). This methodological aspect makes it very relevant for infant studies of object cognition, as infants respond differently to progressive occlusion than to impulsive disappearance: infants only expect object persistence in the case of progressive occlusion [14].

#### 3.1.2. The medial temporal lobe (MTL: hippocampus and perirhinal/area 35–36, entorhinal/area 28, parahippocampal cortices)

The next processing stage of visual information is the medial temporal lobe (MTL). We will discuss the functional

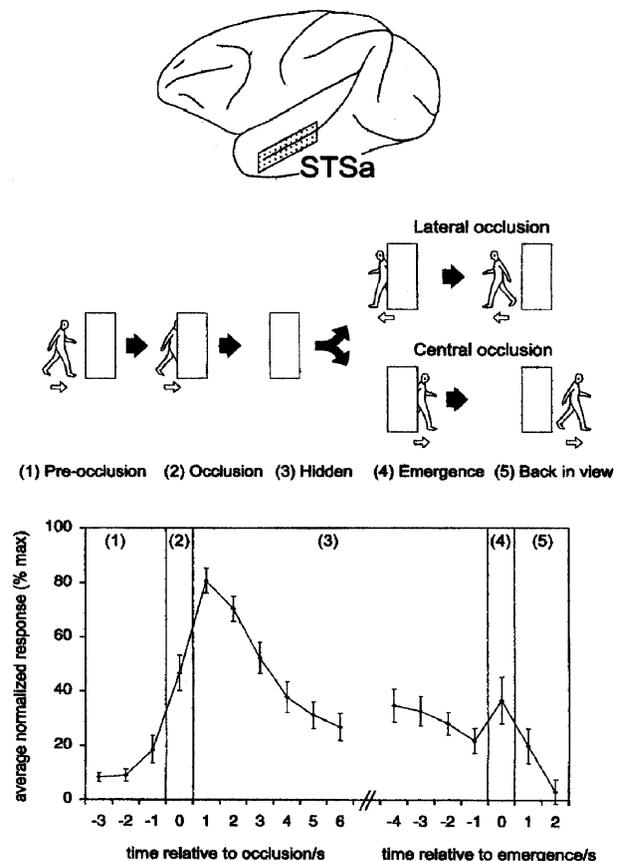


Fig. 3. Cells were recorded in the anterior STS while monkeys watched gradual occlusion events. Graph in lower panel shows mean normalized population response during these events. (Reproduced with permission from Ref. [12], p. 376).

role of three cortical areas in the MTL: the perirhinal cortex, the entorhinal cortex and the parahippocampal cortex.

Since the seminal study of Scoville and Milner on patient H.M. these medial temporal structures have been at the center of memory research [107]. Numerous attempts to replicate H.M.'s severe and global amnesia in monkeys with medial temporal cortical ablations have not been successful [41]. In the meantime, several findings from nonhuman primate ablation studies have provided evidence that MTL (including the hippocampus, the rhinal and parahippocampal cortices) does not operate as a single functional memory system; instead, they show clearly that different parts of the MTL subserve different functions [82]. The perirhinal and entorhinal cortices have complex roles in object perception and memory [84,111]. Recent evidence for the roles of these structures in perception and memory comes from various sources: electrophysiological [36,48], lesion [16,73,83], and metabolism (local glucose utilization [26]) studies on monkeys, in addition to human neuropsychological [47] and imaging work [99,106].

Electrophysiological studies of awake, behaving monkeys have shown that neurons in TE, in the perirhinal and in the entorhinal cortices exhibit three types of responses in a DMS task. A large portion of the neurons exhibits *repetition suppression*: the neural responses are suppressed upon a repeated exposure to an object, relative to its initial exposure. This suppression occurs even if several non-matching objects are presented between the two exposures. However, suppression is not unique to to-be-remembered objects, and seems to be just a consequence of simple repetition [74] (see Ref. [51] for an fMRI study on humans)—a fact that suggests that suppression is a 'passive' memory phenomenon, like priming or habituation.

Moreover, several neurons in the entorhinal, perirhinal and prefrontal cortices show enhanced responses to the test stimulus that matches the sample held in memory, a so-called *response (or match) enhancement* [74,112,113]. Miller and Desimone [74] have shown that responses in the perirhinal cortex are enhanced with repetition of the to-be-remembered (sample) stimulus, while there is no enhancement when non-matching objects are repeated.

Finally, a subset of neurons in the entorhinal, perirhinal and prefrontal cortices exhibit object- and/or place-specific *delay activity* [113]. While this activity may be broken by intervening non-matching stimuli in the perirhinal cortex [76], it persists both in the entorhinal and the prefrontal cortices regardless of intervening stimuli [75,113]. This delay activity can act as a bridge between the sample and the matching stimulus, even with several intervening stimuli. Prior to this report by Suzuki and her colleagues, only prefrontal neurons were believed to respond in such way.

Importantly, the visual response and the delay activity of the entorhinal neurons can carry both object-selective and place-selective information [113]. Our hypothesis is that repetition enhancement and stimulus selective delay activity in the perirhinal and entorhinal cortices are the neural

signals that carry the information about object and location identities in the infant behavioral tests described earlier.

A recent ERP study with human infants also supports the temporal cortex hypothesis. Kaufman, Csibra and Johnson [56] measured high-density ERP responses in 6-month-old infants while they were watching a possible and an impossible outcome scenario in a simple object permanence task. Their results showed that brain activity was different in the temporal cortex in these two conditions.

Sections 3.2 and 3.3 examine areas involved in processing spatial information and how their connections with temporal lobe structures can enrich the place-specific information available to the ventral stream.

### 3.1.3. *The parahippocampal cortex*

Information from posterior parietal neurons (Section 3.2.1) is transmitted to the parahippocampal cortex, which is part of the medial temporal lobe, and it has strong connections to the entorhinal cortex [62].

Starting from the seminal study by Smith and Milner [110], neuropsychological studies increasingly support the notion that the human parahippocampal area is crucial in object-location memory. For a summary, see [77] have summarized these findings. Patients with such lesions are impaired at recalling the location of familiar objects even after a few minutes of delay, yet they perform normally without any delay. This finding suggests that the role of this area is not in initial encoding, but in maintenance and retrieval.

A human imaging study by Owen and his colleagues followed up on this idea and used PET to identify areas that are involved in object-location processing in healthy adults [88]. Selective activity for object retrieval was found in the right parahippocampal cortex, in agreement with the neuropsychological results. A later study confirmed and expanded those findings for retrieval tasks that stressed the object positions relative to external frames of reference, and for retrieval tasks that stressed the object locations relative to each other [52]. An environmental learning imaging study also showed selective activation of parahippocampal areas during exploration of environments that included salient objects (and not of empty environments), emphasizing the importance of these areas in the encoding of object location [67]. Finally, a recent elegant animal lesion study showed that one-trial memory for object-place associations, and one-trial memory for two different places, depend on the posterior parahippocampal region (and not on the hippocampal formation [68]).

## 3.2. *The dorsal pathway*

### 3.2.1. *The parietal cortex*

It is well established in the neuroscientific literature that the parietal cortex processes on-line visuo-spatial information in primates [3,21,125]. There is also neuropsychological evidence that patients with parieto-temporal lesions perform significantly worse in a task involving remembering

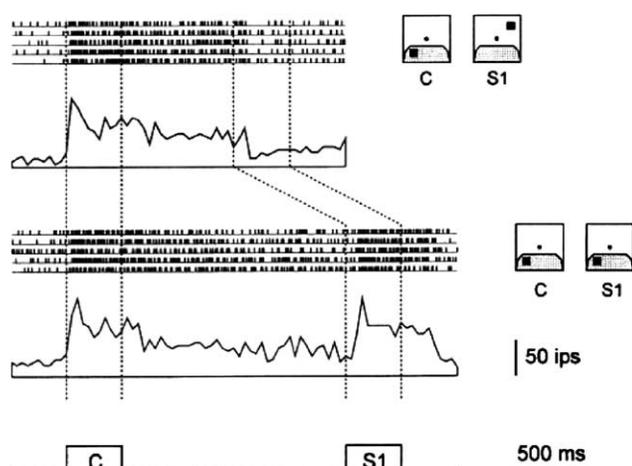


Fig. 4. Responses of posterior parietal neurons in a spatial working memory task. Black squares show locations of cue (C), non-match and match stimuli (S1). Sustained activity in the delay period is terminated by the presentation of the object in a non-match location (upper panel of the figure). Shaded area represents the neuron's receptive field. (Reproduced with permission from Ref. [22], p. 1353) (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

the locations of objects, while retaining memories of object identities [57].

The question of whether parietal cells are also engaged in memory for spatial locations has been addressed by Constantinidis and Steinmetz [22]. These researchers have found cells in the posterior parietal cortex of macaques (area 7a) with properties reminiscent of those found in perirhinal and entorhinal cells. Activity during the delay period in a spatial DMS task was elevated in 28% of the neurons tested. The upper panel of Fig. 4 shows the response of one of these neurons when the test stimulus's location did not match the sample's location. The sustained delay activity suddenly drops when the non-match object appears. The lower panel shows responses when the second stimulus matches the sample location. Besides maintaining elevated activity during the delay, these cells respond with a sudden burst when the match appears. Similar memory-related responses were found recently in another area of the parietal cortex, area LIP (lateral intraparietal area), by Pesaran, Pezaris, Sahani, Mitra and Andersen [91].

Constantinidis and Steinmetz have recently demonstrated that neurons in the same area of the posterior parietal cortex can also distinguish between salient items and other distracting items [23]. The location-specific responses of these neurons did not change when multiple objects were presented. These results suggest that these neurons can provide the spatial information required for directing attention to a salient stimulus in a complex scene.

### 3.3. The lateral prefrontal cortex

The dorsolateral prefrontal cortex (dlPFC) includes the cortex within and around the banks of the principal sulcus and comprises cytoarchitectonic areas 9 and 46. The ventral

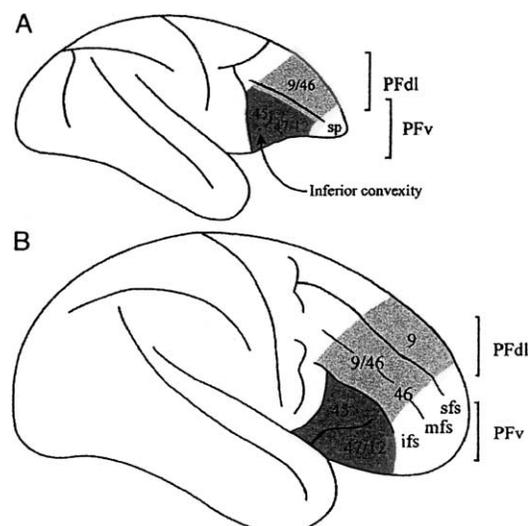


Fig. 5. Prefrontal cortex in macaque and human brains. Schematic drawing of the lateral surface of the macaque monkey brain (A) and the human brain (B) to indicate the location of the dorsolateral prefrontal cortex (dlPFC: areas 9, 46 and 9/46) and the ventrolateral prefrontal cortex (vPFC: areas 45, 47 and 12). ifs, inferior frontal sulcus; mfs, middle frontal sulcus; sfs, superior frontal sulcus; sp, sulcus principalis (reproduced from Ref. [103] with permission).

prefrontal cortex (vPFC) lies below dlPFC, on the inferior convexity and comprises cytoarchitectonic areas 12 (or 47/12) and 45 [92,103] (Fig. 5).

One model of functional organization of the prefrontal cortex posits that these two regions represent the last stage of the dual-route processing apparent in the visual system. According to this view, vPFC and dlPFC serve object and spatial working memory, respectively. Data from single-cell recordings [123], human imaging [24,71] and transcranial magnetic stimulation (TMS) [81,86] have supported this functional theory. However, a large number of studies have offered support for no such functional segregation between the dorsal and ventral lateral PFC. Several studies have reported involvement of both subdivisions of lateral PFC related to spatial and non-spatial information, using electrophysiological [98,100,101], imaging [29,89] and ablation techniques [78,93,102].

A still more relevant question is whether the prefrontal cortex shows any clear functional subdivisions. In spite of many ablation experiments in the macaque monkey that have tried to find double dissociations between the effects of different lesions, there has been only one possible success [17], discussed in Ref. [41]. On the other hand, while the evidence for subdivided function is unconvincing, there is solid evidence for parallel function within the prefrontal cortex. Results from Parker and Gaffan demonstrated that, although complete ablation of the prefrontal cortex in the monkey impairs the learning even of the simplest association, ablation of the vPFC (where objects and rewards are thought to be processed) does not prevent them from learning multiple concurrent object-reward associations [90]. A systematic meta-analysis of imaging studies also

reveals a frontal lobe network that is consistently recruited for solution of diverse cognitive problems, including aspects of perception, response selection, executive control, problem solving and memory, without evidence for regional distinctions [35]. With respect to the involvement of prefrontal cortex in working memory, Rushworth and colleagues showed convincingly that complete ablations of area 47/12 in the monkey have no effect on new learning and performance of a color-matching task involving delays of up to 8 s. In a second experiment, larger lesions of both areas 47/12 and 45A again did not cause a delay-dependent deficit for delays up to 8 s [102]. Following Petrides [94], they argued that *both* dlPFC and vPFC are involved in higher-order executive functions of spatial *and* object information, beyond those situations that stimuli must be held in memory.

A strong argument in support of the view that PFC is important in maintaining stimulus information, when this information is not available from the environment, is the activity of PFC cells during delay periods, recorded with electrophysiological and imaging techniques [25,39]. However, this delay activity is not unique in this part of the brain. Delay activity has also been reported in many other areas, such as the primary visual cortex [38], inferior temporal cortex [15], entorhinal [113] and perirhinal cortex [76], parietal cortex [59], lateral intraparietal cortex [64], caudal intraparietal sulcus [116], premotor cortex [124] and frontal eye fields [13]. This activity seems to play different roles in the different areas, instead of simply bridging delays. For example, in the temporal cortex, it seems to mediate associative long-term memory [79], in the frontal eye fields it is suggested to be part of a mechanism that allows for the superposition of multiple saccade plans [13], while in the premotor cortex it appears to be part of the available information that mediates the generation of a motor program [85].

In summary, the available experimental evidence does not designate one area of the brain as a specialized center for working memory. The proposition that the neural activity of the different posterior cortical areas supports perception, short- and long-term information storage [92] remains the most parsimonious and sensible one. Or, put explicitly “basic working memory, i.e. the temporary storage and further processing of incoming and recalled information, is an integral part of neuronal processing in modality specific and multimodal posterior association cortical areas” [92]. Also, the prefrontal cortex is poorly described as an area needed to combine ‘what’ and ‘where’ information, as the fundamental principle of the receptive field [44] is encountered in all brain areas without exception, and ensures that ‘what’ and ‘where’ is never fully separated. Perhaps the best way to describe prefrontal cortex, given the information available to date, is as an area highly adaptable to current task requirements [34], with a key role in learning and memory, but with no specialization of function [41,43].

Studies of the maturation of the prefrontal cortex—though the anatomical evidence is quite scarce—using measures such

as mean synaptic density and the peak of synaptogenesis show that this area matures relatively late compared to other areas, such as the primary visual cortex [49,50]. A unique PET study on infants has shown that levels of local glucose utilization rise in the temporal and parietal cortices around 3 months, while a similar rise in the frontal cortex does not happen until 6–8 months of age [20].

It is well known from the infant developmental literature that 7–12 month-olds fail the A-not-B test with delays [30]. In this classic test of object-location coding [95], the infant is shown two containers. First, an object is placed in one of the containers (A), and the infant is allowed to search and retrieve the object from it. Then the object is placed in the other container (B), and the infant is again allowed to search, but only after a certain period of delay. Nine-month-old infants consistently reach for location A after a 3 s delay (an A-not-B error), and search randomly after a 6 s delay. Adult monkeys with dlPF lesions behave identically [31].

Diamond has also shown that success on the A-not-B task depends on memory *and* the ability to inhibit a strong response tendency [32]. The studies mentioned earlier by Baillargeon and her colleagues and Ahmed and Ruffman have directly demonstrated that the reason why infants fail is not a memory limitation. If infants are tested in a looking time task instead of a reaching task, they can succeed, even with much longer delays [8,9]. The time delay in the most demanding object identification task Káldy and Leslie conducted, where 9-month-olds ‘passed’, was 7 s, slightly longer than the 6 s threshold found by Diamond. All these results taken together lead to the suggestion that subjects in these object-location experiments did not rely on frontal structures, but rather on the earlier maturing, more posterior object recognition system, namely, the temporal cortex. Alternatively, studies by Thelen and her colleagues have argued that instead of working memory and inhibition, the A-not-B task reflects motor habit formation and showed that the typical error occurs even in the absence of the object [115].

#### **4. Recent developmental neuroscience approaches emphasize the role of the prefrontal cortex in working memory**

Here we have argued for the role of medial temporal cortex in working memory, though this is a role rarely mentioned in the developmental neuroscience literature. The only exception is the work of Bachevalier and her colleagues [2,4,5] and their findings still need to find the way to a wider audience of developmental psychologists.

On the other hand, there are relatively more studies implicating prefrontal cortex in working memory, but these studies were inspired by a questionable link between the A-not-B task and memory. As was discussed above, the A-not-B task involves response inhibition and for this reason should not be considered a true working memory task (but this fact has not seemed to limit its influence on

the approaches of developmental neuroscientists). For instance, a recent review by Herschkowitz [46] discusses this task exclusively as a test of working memory abilities in infancy. Casey et al. [18] in their summary of human functional brain development, focus entirely on the prefrontal cortex. This approach also has been actively misleading researchers in their empirical work. For instance, in a recent study using a relatively new technique called near-infrared spectroscopy (NIRS), Baird, Kagan, Gaudett, Walz, Herslag and Boas [10] measured activity-dependent changes in the infant brain during a task that involved retrieving a hidden object. Here recordings were made *only* from the frontal lobe, so the possibility of discovering any involvement of other areas was excluded from the start. Additionally, the behavioral test in this study involved reaching and means-ends analysis and, as was shown more than fifteen years ago, this classic task underestimates infants' knowledge of hidden objects [6,7].

## 5. Conclusions

In summary, our behavioral studies showed that 9-month-old infants are capable of tracking *what* object (as identified by shape) went *where* (as defined by separate screen locations). The infants' object representation can, therefore, integrate featural information with location information. These data present evidence for functional integration between the object recognition and the object localization systems in humans by 9 months of age. In this paper, we have investigated the putative neural system underlying this function and suggested that, while the prefrontal cortex is often regarded as essential in working memory tasks in general, it might not play a central role in object-location memory in infants: instead, we have argued for the involvement of the medial temporal structures in perception and visual working memory.

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