Forming and consolidating arithmetical facts in the brain

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Series:
IBRO/IBE-UNESCO Science of Learning Briefings

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Theme/s:

Learning mathematics

This report arises from Science of Learning Fellowships funded by the International Brain Research Organization (IBRO) in partnership with the International Bureau of Education (IBE) of the United Nations Educational, Scientific and Cultural Organization (UNESCO). The IBRO/IBE-UNESCO Science of Learning Fellowship aims to support and translate key neuroscience research on learning and the brain to educators, policy makers, and governments.

Executive summary

- The ability to efficiently retrieve basic arithmetical facts from memory is critical to successfully achieve and master more complex aspects of mathematics.
- Over development, gains in arithmetic problem-solving skills are characterized by a gradual shift from inefficient, effortful counting strategies to direct retrieval of arithmetical facts.
- This shift in strategy-use is supported by the cross talk between different memory systems in our brain, one devoted to short-term replay and multistep manipulations, the other implicated in quasi-permanent long-term storage.
- These systems communicate with each other via characteristic brain rhythms that seem to be orchestrated by the hippocampus, a small seahorse-shaped region, located in the inner layers of our brain.
- The "orchestrating job" of the hippocampus seems to be promoted by appropriate phases of sleep and rest, hinting at the idea that ad hoc recommendations should be developed to promote awareness of the importance of these factors during learning and, where appropriate, their harmonization with educational strategies, particularly for children with mathematical delays or disabilities.

Introduction

The ability to quickly and efficiently retrieve basic arithmetical facts from memory is a critical aspect of successful mathematical skill acquisition[1,2]. Notably, basic arithmetical fact retrieval is foundational for solving more complex math problems. Moreover, deficits in arithmetical fact retrieval represent one of the key impairments among learners who struggle to acquire age-appropriate math skills, such as those with mathematical learning disabilities (MLD)/developmental dyscalculia (DD)[3,4].

Throughout typical development and usually by the age of 10, when asked to solve simple single-digit arithmetical problems (e.g., *3+4 = ?)*, children learn to move away from counting-based strategies (e.g., verbal or finger counting) in favor of less effortful memory-based ones. This transition is a learning process that is anything but effortless. It is slow and involves the "*push and pull*" of multiple brain systems and their dynamic interaction.

When counting on from *3* to *7* to solve the problem *3+4*, an association is slowly formed between the correct solution (*7*) and its addends (*3* and *4*). Several cognitive abilities—and the brain systems supporting them—aid the process by which this association is formed. Specifically, the child needs to first adequately master counting procedures and principles. That is, the child needs to know that *4* is the number that comes immediately after *3*, and that *7* is when the counting sequence "*needs to stop*." Furthermore, when solving this problem, children need to maintain, and dynamically manipulate these rules. They must also update intermediate results "on the fly," an ability defined as *working memory*.

Working memory allows for transient information to persist in the brain as "active representations" (i.e., an active snapshot, if you wish). In this sense, working memory facilitates the active manipulation of information for slightly longer periods of time (i.e., beyond their transient sensory availability). Imagine you are following a set of instructions for a cooking recipe. Being able to briefly glance at a "picture/snapshot" of the recipe held in your mind will certainly help you to efficiently execute the steps required to make it. Working memory essentially enables our brain to hold such "snapshots" (i.e., representations) for a period of several seconds, facilitating mental manipulations on them. Yet, working memory manipulations are effortful, and one of the goals of any successful learning is to "free up" working memory resources in favor of much more efficient retrieval strategies that require minimal mental computations (i.e., arithmetical fact retrieval rather than incremental counting).

How does this transition occur? How do children develop the ability to automatically know that *3+4* is *7*? Neuroscience has recently started to shed light on how this stable association is formed in the brain.

Working memory and memory consolidation in the brain

Working memory is known to be supported by the dynamic interaction of two brain areas of the cortex (i.e., the outer layer of our brain). These are the parietal and the prefrontal cortices (see Figure 1). Specifically, a dynamic cross talk between these two brain areas is known to aid maintenance and updating of information "on the fly."

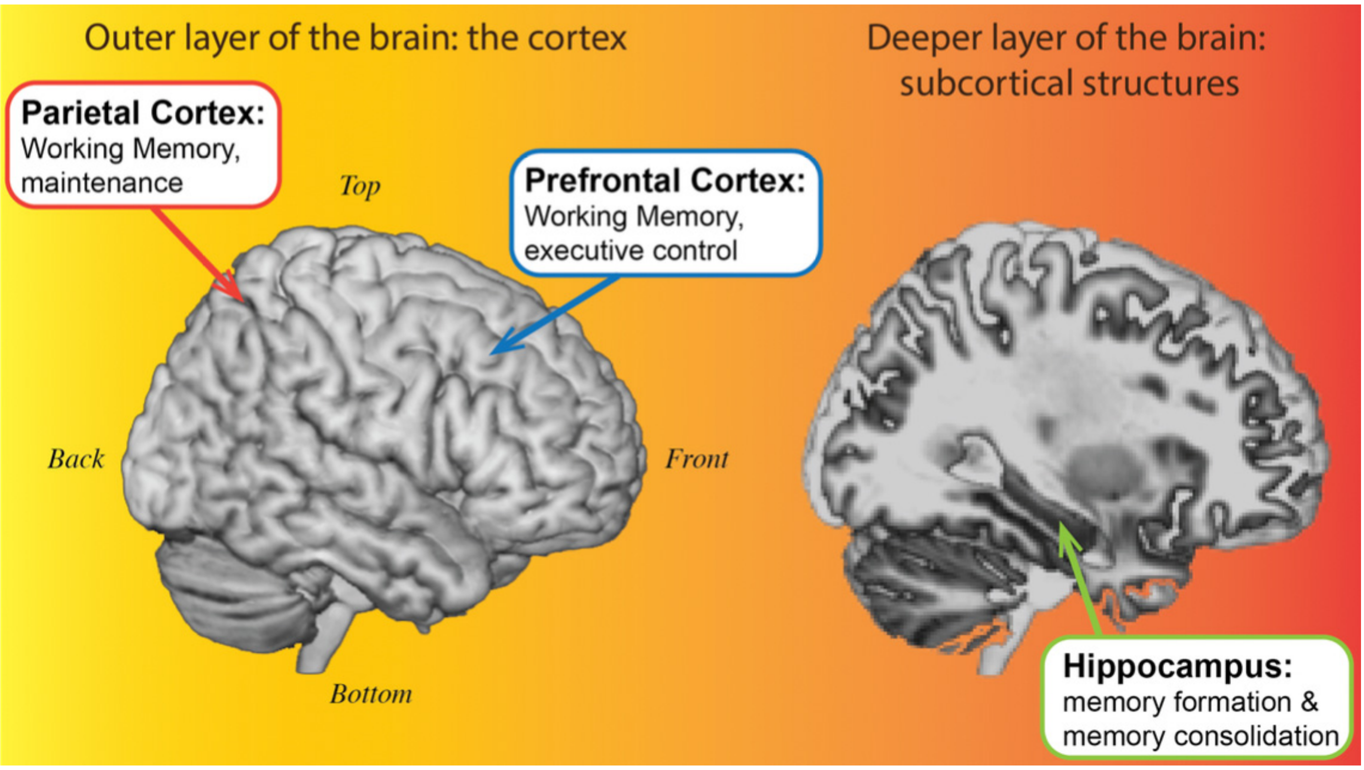

Figure 1. Schematic illustration of different memory systems of our brain. Left: lateral view of the brain. The working memory system is supported by brain regions of the cortex (i.e., the outer part of our brain). Right: medial view of the brain. The memory-formation/memory-consolidation system is supported by the hippocampus, a small seahorse-shaped region of the brain situated in the medial (inner) aspect of the temporal lobe.

Working memory processes thereby allow the child to remember the rules of the arithmetical operation at hand and, at the same time, hold the intermediate results of their counting. While this happens, the knowledge and application of the rule-to-be implemented (i.e., a mental process called *executive control*) will help the child to correctly update their computations and consequently "stop the counting" at the right number (i.e., the number that represents the end of the counting sequence for that arithmetical operation). As these working memory processes are taking place, memory-formation and consolidation processes coordinated by brain regions located much deeper in our brain (i.e., the medial temporal lobe, and particularly the hippocampus—see Figure 1) slowly pick up on this information, to ultimately generate a stable association between the "start- and end-points" of the aforementioned computations (i.e., the addends and the result of the arithmetic problem).

How does this happen? Or, in other words, how do these brain regions interact with one other to simultaneously maintain and manipulate transiently available information and slowly generate stable arithmetical facts? How do brain regions exchange information? What is their communication-currency?

The "language" of the brain: Neural oscillations

It is well established that the flow of information from one area of the brain to another occurs via spikes of repetitive (and rhythmic) electrical activity (i.e., neural oscillations). In the case of working memory, converging evidence suggests that our transient "snapshot" of information is maintained as an active representation over several seconds in our brain via rhythmic oscillations that have their characteristic frequencies (i.e., rate of occurrence) synchronized. These types of frequencies are mainly generated in the parietal and prefrontal cortices (see Figure 1). For instance, when we see a stimulus that must be remembered over a brief delay (e.g., steps one-to-three of a cooking recipe), electrical activity is first generated from our brain in response to that stimulus. Interestingly, after the stimulus is gone, our brain cells (i.e., neurons) continue to spike at a similar rate, creating a short-term representation of that stimulus (i.e., our transient "snapshot"), allowing for its active mental manipulation[5]. Specifically, it seems that the parietal cortex is the one "in charge" of maintenance, supporting short-term information storage, while updating is achieved with the help of an attentional control system—the so-called *central executive*—which is aided by the prefrontal cortex[6]. The mechanics of this process roughly resemble what happens in an orchestra. Let us see how.

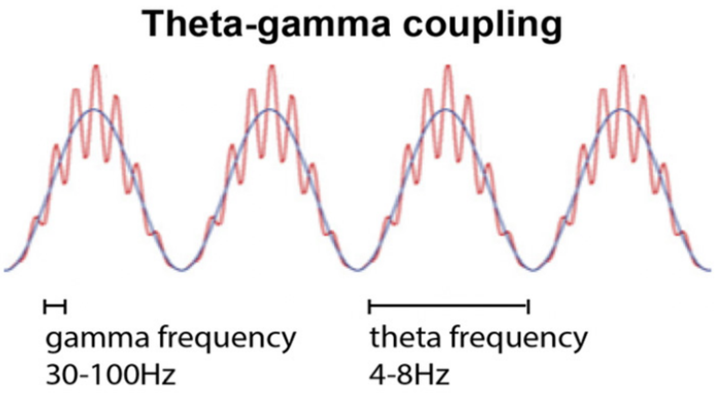

Figure 2. Schematic illustration of theta-gamma coupling important for working memory. Red lines: fast gamma-oscillations. Blue lines: slower theta-oscillations.

The two key frequencies during working memory tasks are gamma—a rather fast frequency spiking at the rate of 30-100Hz, and theta—a much slower frequency whose rhythm is of 4-8Hz (see Figure 2). You can imagine that gamma is like the violins of an orchestra: They carry on the melody of the piece and their tempo is usually quite fast. The melody, in this case, is similar to our transient “snapshot” (i.e., it carries the fundamental characteristics of the stimulus, even after the stimulus is gone). Theta, on the other hand, is more like the cellos: Their melody is less distinct, their tempo is slower, but their function is crucial—they keep the beats and the rhythm of the piece. Crucially, they do so by interacting with the violins, gluing the melody together by representing multiple information in an ordered way[7], allowing for the appropriate steps of the manipulation to occur in the right sequence. As in an orchestra, in our brain, these two types of oscillation-frequencies (gamma and theta) communicate with one another and this occurs when they are “in synch”(see Figure 2). A cross talk between different oscillatory frequencies is typically referred to as “coupling,” so in this case we are talking about a theta-gamma coupling. The theta-gamma coupling (see Figure 2) seems to be at the core of successful working memory performance. In particular, the theta-gamma coupling has been shown to be important for the active (and successful) manipulation of information in working memory[8] which, as we have seen, represents a crucial step during learning of arithmetical facts.

But how do these active manipulations of well-ordered information (and steps) eventually culminate in the formation and consolidation of stable associations between the problem (*3+4*) and its correct solution (*7*)?

One of the key players in this process is a brain region related to memory (and memory formation) par excellence: the hippocampus[9], a small seahorse-shaped area situated in the medial (inner) aspect of our brain in the medial temporal lobe (see Figure 1). How does such a small structure in our brain support the process of building efficient fact-retrieval skills? The hippocampus is known to be particularly important for binding information together[10] and its modus operandi seems to involve theta-oscillations (see Figure 2). It seems that the hippocampus synchs itself (i.e., the technical term is “phase-locks” itself) with regions of the cortex via theta oscillations[11]. By “speaking the same language” of cortical areas, the hippocampus can “access” the information briefly stored and manipulated by these regions and bind it together for more permanent storage. This process culminates in what is known as memory consolidation whereas the information assembled in the hippocampus is “transferred back” to the cortex in the form of a “memory-fact” (*3+4 =7*), which—unless required by another task, such as in the case of more complex calculations or equations—does not need to be manipulated any further.

The hippocampus: The transient player during arithmetical fact learning

As we have seen, the hippocampus seems to be crucial for forming and consolidating memory-facts in the brain. However, its role, while pivotal, is transient: Memories that are originally hippocampus-dependent gradually become hippocampus-independent as they get consolidated in the outer parts of the cortex[12]. This transition was well demonstrated for the specific case of arithmetical fact learning by a recent study[13]. Children of 7-9 years of age were tested as they performed simple arithmetical operations (e.g., *3+4 = ?*) while their brain activity was recorded by functional magnetic resonance imaging (fMRI) scanning. At this age, children showed high prefrontal and parietal activity during problem-solving, possibly reflecting effortful working memory processes taking place in their brains while solving these problems.

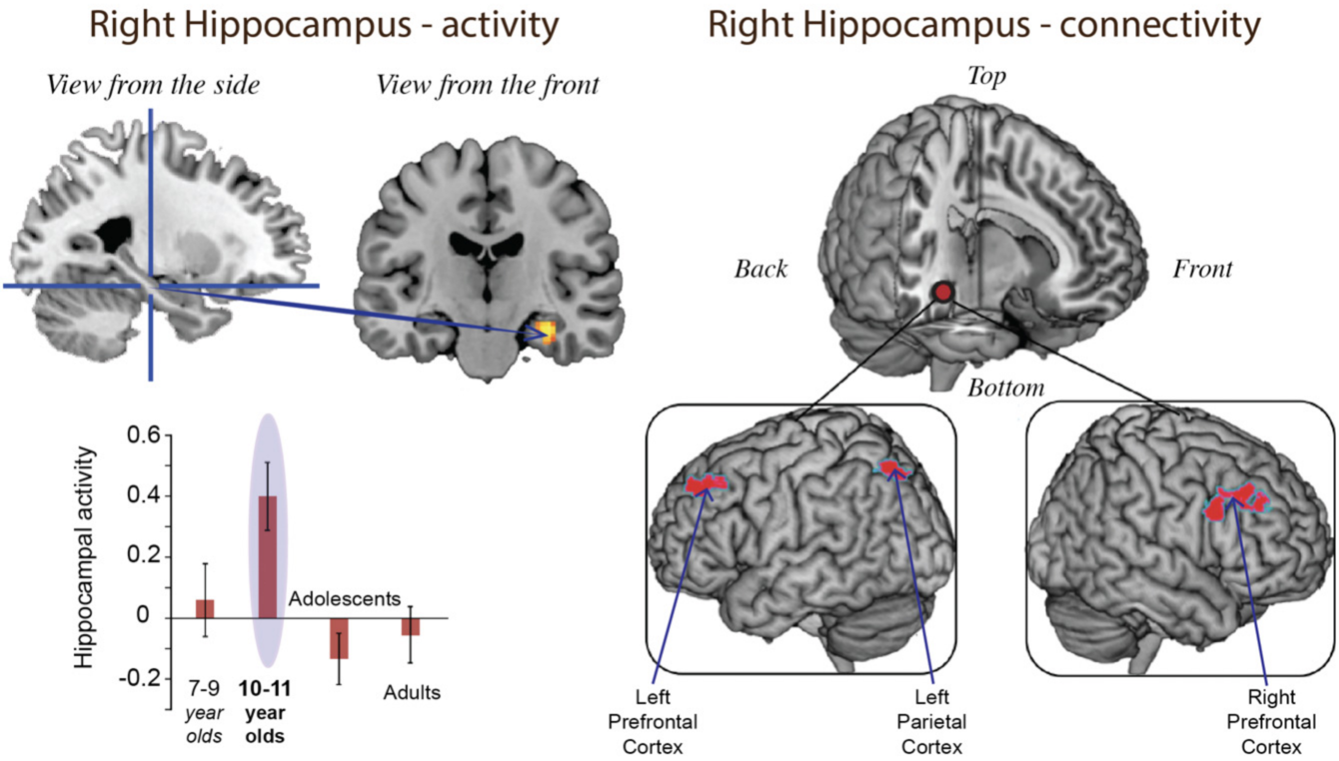

Figure 3. Left panel: During arithmetic problem-solving, activity of the right hippocampus increases in 10- to 11-year-olds. Right panel: Connectivity of the right hippocampus with regions of the prefrontal and parietal areas in the outer cortex increases with increases in arithmetic fact retrieval (Adapted from Qin et al., 2014).

When tested at the age of 10-11 years, however, the same children showed decreases in prefrontal and parietal activity and increases in hippocampal activity (see Figure 3—*left panel, top*). Critically, the increase in hippocampal activity when children were older was accompanied by higher use of fact-retrieval strategies. The latter aspect was tested by asking the children—outside the scanner at this point—to report the strategy used to solve the problem. Example of strategies varied from "just knew it!" (i.e., retrieval) to "I counted in my head" or "I counted on my fingers" (i.e., both examples of counting). Even more interestingly, the authors found that gains in fact retrieval—that is, increasingly reporting retrieval strategies during arithmetic problem-solving—from when the children were 7-9 to when they were 10-11 years old were related to increases in brain connectivity (i.e., brain cross talks) between the hippocampus and prefrontal and parietal regions of the cortex (see Figure 3—*right panel*). This data suggests that a reciprocal dialogue between the hippocampus and the cerebral cortex underlies successful memory consolidation for arithmetical facts. As facts get stored in a more permanent way, the hippocampus is no longer needed. And indeed, the authors found that groups of adolescents and adults, while continuing to show increased retrieval-rates, did not show any hippocampal engagement while solving the same arithmetic problems that were given to the children[13](see Figure 3—*left panel, bottom*). The findings of this study point to a developmentally specific role of the hippocampus in the acquisition of arithmetical facts. Interestingly, lack of hippocampal activity during arithmetic problem-solving has been reported in a group of 10- to 12-year-old children with MLD[14]. This suggests that one of the possible developmental deficits in these children may derive from a failure to appropriately engage the hippocampal system during crucial phases of arithmetic learning.

Facilitating memory consolidation: The active role of sleep and rest

As discussed, when children start acquiring arithmetic problem-solving skills—first through the application of effortful multistep rules and counting procedures, and later through increased implementation of efficient retrieval strategies—a dynamic dialogue is established between the cortex (i.e., the outer layer of the brain) and the hippocampus (see Figure 1). The hippocampus tunes to the frequencies of the cortex and, in this way, the cortex can send information to the hippocampus which is in charge of elaborating them by binding them together. Yet, at this point, the information held in the hippocampus is not securely stored. Fortunately, this is not the end of the story. As previously described, memory consolidation—which is at the core of successful fact retrieval—occurs via a further (and reciprocal) cortical-hippocampal dialogue. This dialogue is two-stage and, as we have seen, occurs *via* brain frequencies. Stage one takes place during the waking phases of learning and, as previously described, is characterized by a set of relatively higher frequency signals (including theta) conveying information between the cortex and the hippocampus. In contrast, during stage two—which occurs when we are asleep—information travels also in the reverse direction, from the hippocampus to the cortex *via* much lower frequency bands (< 1Hz). Such "outbound-flow-of-information" has been shown to occur during what is known as slow-wave sleep (SWS). SWS constitutes one of the two core sleep phases—the other is rapid eye movement (REM) sleep. SWS is predominant during the early part of the night and decreases both in intensity and duration across the sleep cycle, whereas REM sleep becomes more intense and extensive towards the end of the sleep cycle[15]. In terms of rhythm, SWS is characterized by very slow brain oscillations (< 1Hz), while REM sleep predominantly shows theta-like (4-8Hz) frequencies/oscillations that have been extensively studied in animal models[15]. The order in which SWS and REM sleep occur across the sleep-cycle (i.e., SWS precedes REM sleep) is very aligned with their hypothesized role in fostering the cortical-hippocampal dialogue that is at the core of memory-consolidation. In fact, it has been proposed that during SWS, recently acquired hippocampal information is first reactivated and then transmitted to the cortex where it becomes part of a more permanent memory-storage[16]. In turn, ensuing REM sleep may help stabilize this "hippocampally-reshaped-information" into a consolidated fact within the permanent memory-storage[17].

To date, no studies have systematically assessed the contribution of sleep (either SWS or REM sleep) to the acquisition of arithmetical facts in children (nor adults). Yet, evidence seems to suggest that sleep is indeed important to memory formation and consolidation, particularly in children. In a study that asked 9- to 12-year-olds to learn novel word-pairs and assessed their performance either after a full night's sleep or after a similarly long lag of wakefulness, it was reported that performance was significantly better after sleep. Specifically, when children were examined after a full night's sleep (i.e., they learned the word-pairs in the evening and were tested the next morning) their retrieval-rate was higher compared to when they learned the word-pairs in the morning and were tested the same evening (i.e., no full-sleep cycle between the learning and test phase)[18]. Daytime sleep—in this case in infants—has also been related to better performance during learning of novel object-word-pairs associations: Performance in the "nap group" was significantly better than performance in the "non-nap group"[19].

Together with sleep, wakeful rest periods have also been related to better learning. Studies indicate that moments of unoccupied rest immediately after learning can help memory consolidation, possibly through mechanisms of enhanced theta oscillations that are likely orchestrated by the hippocampus. In a study of word-list learning in 13- to 14-year-olds, it was shown that the word list that was followed by a period of 10-minute rest was much better retrieved (i.e., remembered) compared to a word list that was followed by a 10-minute problem-solving session. This effect was particularly evident in individuals who performed at the lower end of the distribution for word recall[20]. Notably, another study exploring the learning of lists of word-pairs found that hippocampal theta power was significantly higher during conditions when eyes were closed[21]. As mentioned, these studies have mainly looked at verbal tasks, and remembering a list of novel words may not necessarily involve the same exact computations taking place during arithmetic learning. Yet, the mechanisms of action may be very similar, demanding the support of the hippocampus and hippocampal-cortical connectivity as we have seen[13] (see Figure 3).

In the math domain, more studies are needed that specifically assess the contribution of different phases of sleep and rest to the successful acquisition of arithmetical facts. With this in mind, the next challenge will be to start taking these aspects into consideration in the dialogue between different educational stakeholders (including mainstream teachers, teachers of children special needs, clinicians, policy makers, and parents), particularly when trying to foster better learning environments for children falling at the lower end of the distribution for mathematical abilities.

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