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A Loop for Speech

Our minds are made of memories. Our past, our present and even our imagined future are memory representations of recent or past events, transformed in different ways by the neural networks that shape our behavior. Everything we do is strongly shaped by the many kinds of memory we have, from recognizing someone familiar, organizing a dinner, driving a car, our consciousness and the image of ourselves, not to mention the memory we need for proper education and the autobiographical memory that gives us a sense of identity. Furthermore, memory is not a single, unitary process but rather is composed of many different mechanisms involved in generating repre- sentations of past events in different sensory modalities. Early researchers in the field of memory recognized that there were at least two forms of memory, one permanent with infinite (or better, unknown) capacity, which remains stable over time, and the other of recent events, which lasts a few seconds and represents a gateway to form enduring memories. Recent memory is vivid, and makes our experiences combine in what seems a continuous stream of events forming the essence of our minds. Eloquently, the Nobel laureate Gerald Edelman titled one of his books on consciousness "*The Remembered Present*" (Edelman 1989).

Memento

Perhaps the first person to recognize the difference between short- and long-term memory was William James at the end of the nineteenth century, who referred to primary memory, which represented "the trailing edge of the conscious present" (James 1890). On the other hand, past memories corresponded to secondary memory, possibly under the assumption that short-term memory is a first stage required to establish long-term memories. In the 1940s Donald Hebb introduced the concept of short-term memory, which was dependent on electrical brain activity, as opposed to long-term memory, which was produced by neurochemical changes (Hebb 1949). Hebb proposed a basic principle for the generation of memories (now called Hebb's rule), based on the maintenance of synapses that successfully exert changes in activity in the next neuron, while synapses that fail to produce a postsynaptic effect are doomed to be eliminated. Hebb's principle has had a tremendous impact on neuro and cognitive science, as it provides a simple mechanism to explain short-term memory, long-term learning and neural plasticity, including the critical periods of neuronal development discussed in the Chapter 1. In the last century, evidence had accumulated that memories decay rapidly if there is no opportunity to rehearse them behaviorally or mentally. The studies by George Miller in the 1950s provided a deeper understanding of the nature of short-term memory, by showing that it has a limited capacity, allowing the storage of no more than about seven separate items in experimental subjects (Miller 1956). One of the earliest tests to assess short-term memory was the digit span test, which requires serial recall of random sequences of digits. As might be expected, the shorter sequence, the more accurate the performance.

What would life be without being able to develop new memories? Guy Pearce provided an eloquent interpretation of this condition in Christopher Nolan's movie "Memento", where the main character has lost his capacity to acquire new knowledge, as his short-term memory vanishes as soon as he changes his focus of attention. This results in a total loss of the sense of continuity and consequent disorientation that deeply affects the subject's daily life. But such profound impairment is not just fiction. In the early 1950s, a patient called Henry Molaison, also

known as HM, underwent profound brain surgery at the age of 16 to treat intractable temporal lobe epilepsy. The surgical procedure eliminated most of his medial temporal lobes bilaterally, including the hippocampus and adjacent structures. Fortunately, this massive surgery alleviated his condition, but on the other hand he was left with severe anterograde amnesia, that is, the incapacity to transfer new information from short-term to long-term memory. Brenda Milner, who had been studying the role of the primate medial temporal lobe in memory, was impressed with this case and made a thorough neuropsychological study of HM (Scoville and Milner 1957). Notably, HM had a preserved short-term memory (evidenced in a normal performance in the digit span test) and procedural memory (the capacity to learn and remember motor programs like riding a bicycle), but was not able to use newly acquired information over the long term. He also had some retrograde amnesia, that is, he could not remember events that happened some 2 years before the surgery, suggesting that these memories were still in the process of being consolidated as enduring long-term memories. By the end of his life in 2008, he was capable of incorporating some new memories and modifying preexisting ones, which indicates a degree of plasticity in the networks controlling his behavior (Banks et al. 2014).

Since the findings by Milner and others, there have been many studies of short-term memory (Baddeley 2007). The earliest formal models of short-term memory, developed in the 1960s, considered in general three stages in memory processing, the first being a sensory memory that could be visual (iconic memory) or auditory (echoic memory). After this, there was a short-term or working memory storage box, which transiently held information, but was also related to direct behavioral control. Finally, there was long-term store of enduring memories. Long-term memories could go back to the short-term store to participate in behavioral responses. It was assumed that the short-term memory store was one and the same for all kinds of memory, and there was no proposal for a specific mechanism involved in transferring memories from the short- to the long-term store. The main determinant of the probability of transfer to the long-term store was assumed to be the length of time remaining in the short-term box. However, several studies showed that the behavioral or cognitive context in which recent memories were acquired is more

important for transfer to long-term memory than time. For example, simple classification of items results in poor long-term acquisition, while items that have to be verbalized are more likely to be retained, and highly meaningful items or ones with emotional content are even more strongly maintained. In addition, assuming that there is only one short-term memory box suggests that short-term memory patients are deficient in all kinds of short-term memory tasks. However, many such patients live relatively normal lives, like running a shop or driving taxi. This means that some types of short-term memory are indeed spared, even though such patients perform poorly on tests like the digit span. Cases like HM are in a way extreme, while most short-term memory patients are not as impaired as he was. The exact process by which short-term memory rapidly decays with time has been a matter of much discussion and is not yet settled. Two main hypotheses have been presented, one is that memory traces spontaneously decay over time, and the other suggests that this decay is based primarily on interference from other sources of activity. In the latter view, inhibitory mechanisms actively repress interfering processes, and control the maintenance of memory traces. Additionally, behavioral rehearsal mechanisms such as vocalizing the remembered items could be an important factor that counteracts the effects of interference or spontaneous decay.

A special case of memory encapsulation was offered by patients with verbal short-term memory deficits. Several papers were published, notably by Elizabeth Warrington and Tim Shallice, describing brain lesion patients with deficits in short-term memory for words and numbers, while visual short-term memory was intact (Warrington and Shallice 1969). Noteworthy, in such patients the lesions were usually located in the left temporoparietal region and not the medial temporal lobe. Furthermore, despite their memory impairment, these subjects were perfectly able to sustain simple routine conversations, and spoke normally, that is, they were not speech impaired. Note that this symptom is very different from aphasia, as in addition to short-term memory deficits; in the latter there is a serious speech condition. Warrington and Shallice interpreted these symptoms as selective disruption of verbal short-term memory (particularly auditory), and spoke of a temporal buffer that maintains perceived speech for a couple of seconds, but was

clearly not necessary for everyday speech. At about the same time, Alan Baddeley and Graham Hitch were working with a model for verbal short-term memory based on motor output, that is, constant vocal articulation of the remembered items to sustain the memory trace. However, the findings of verbal short-term memory patients without speech problems called for a revision of this interpretation. Thus, Baddeley and collaborators decided to include an additional component to their articulatory model of verbal short-term memory, a phonological storage buffer that transiently maintains auditory representation while reverberation of the articulatory loop refreshes the memory trace. As we will see below, this component has turned out to be one of the most controversial in Baddeley's model. In this context, in the 1970s Baddeley and Hitch introduced and popularized the model of working memory, as a limited capacity system that maintains information in the short-term, while one performs cognitively demanding tasks such as reasoning, comprehension or learning (Baddeley and Hitch 1974).

Perhaps no one can better tell the genesis of the concept of working memory better than Baddeley. In his influential book *Working memory, Thought and Action*, he provides a very clear account of these developments, which I will succinctly review here (Baddeley 2007). Although Baddeley confessed to having been reluctant to write this book for a long time, many of us are grateful to him for having done so. Moreover, I felt particular empathy with him when he acknowledged his wife at the beginning of the book for her support and encouragement to a husband that wandered about talking to himself instead of doing household chores. Initially, Baddeley and collaborators had shown double dissociation between short- and long-term memory impairments; that is, patients could have deficits in the former and not the latter, or conversely perform normally in short-term memory tests and show long-term memory impairments. An experimental paradigm, called the recency effect well illustrated the difference between the two kinds of memory (Baddeley 1968; Baddeley and Hitch 1993). This phenomenon is seen when subjects have to repeat in whatever order a list of words they have been shown. If recall is immediately after seeing the list, the last items on the list are better recalled than the first ones. However, if there is a short interval between the list and the recall time, this effect tends to vanish, and items presented earlier can

be recalled just as well as the later ones. Long-term memory amnesic patients show a strong recency effect as their short-term memory is good, but tend to fail when recalling the early items. On the other hand, short-term memory patients perform the other way around, doing well with the earlier items and badly with later ones.

Subsequently, Baddeley and Hitch asked normal subjects to continuously rehearse a random sequence of digits while performing a verbal reasoning task like responding true or false to sentences like "A follows B → BA" (true), or "B is not preceded by A → AB" (false), and other combinations (Baddeley and Hitch 1974). Verbally repeating only one digit during the task (say one, one, one, etc.) impeded overt vocal reasoning, while randomly repeating a rising number of digits involved a load on working memory that progressively demanded processing capacity. Notably, as the number of digits to be rehearsed increased from 0 to 8, the time required to respond increased significantly but modestly, from 2.2 seconds to only 2.9 seconds. Moreover, subjects made only about 4% errors in the task regardless of the digit load, that is, this had no effect on the rate of successful trials. Baddeley and Hitch concluded that the observed effect was far less than was predicted from the single unit short-term memory model, and decided to move on to a different, multicomponent model of working memory.

Baddeley's Memories

George Miller and others like Richard Shiffrin used the term "working memory" to refer to a kind of short-term memory used for problem solving. However, Baddeley and Hitch formalized this concept into a model of memory processing involving different components and processing stages. Baddeley and Hitch conceived of working memory as a limited capacity system that maintains information in the short-term while one performs cognitively demanding tasks like reasoning, comprehension or learning. In effect, working memory involves storage and manipulation of elements in the context of a behavioral task, while the more general term short-term memory refers to a passive, short-term

imprinting of events that eventually are extinguished or transformed into long-term memories (Baddeley 2007, 2012).

Baddeley and Hitch's multicomponent model of working memory consists of two modality-specific and limited-capacity storage systems, one for visuospatial behavior, called the visuospatial sketchpad, and the other for auditory-vocal behavior, called the phonological loop (Fig. 6.1) (Baddeley and Hitch 1974). While the former is involved in tasks related to spatial orientation and visual search, the latter keeps vocal and acoustic information online and is involved in inner speech. Maintenance of visuospatial sensory information in these stores partly depends on motor rehearsal involving head, eye, and possibly hand movements, or attentional displacements. Phonological rehearsal involves overt or covert speech (also called inner speech). These sensori-imotor components are in turn supervised by a multimodal attentional
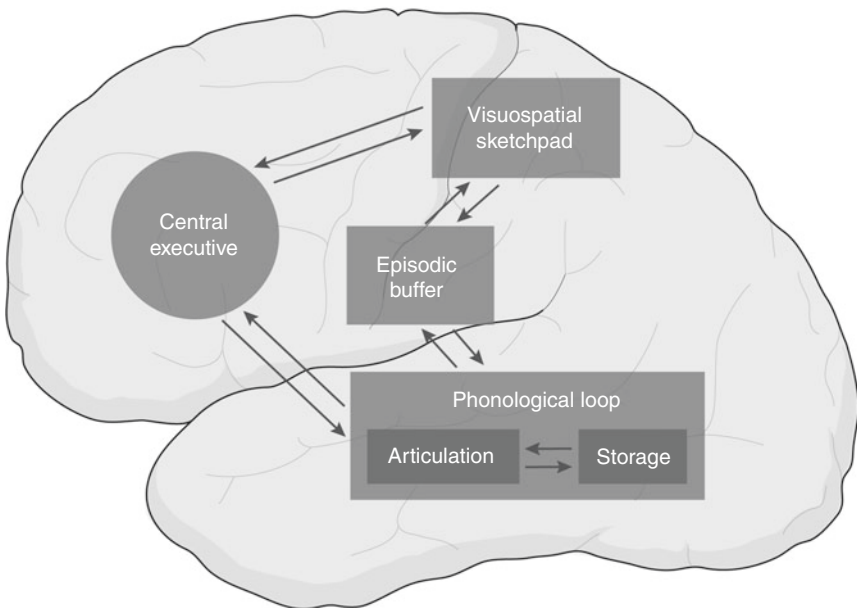
Fig. 6.1 Baddeley's multicomponent model of working memory. There is no precise statement in the model about the anatomical location of the components

control system, the central executive, which manipulates the items in the sensory loops according to cognitive or behavioral demands. The visuospatial sketchpad was initially assessed with a visual orienting task in which there were two alternative ways to recall a path through the university campus, one using rote verbal rehearsal and the other based on visual imagery, recalling relevant points and then mentally connecting them. Subjects performed better in the latter (Baddeley 2007). In a second step, subjects had to complete a visuomotor tracking task parallel to doing the test. With this additional requirement, the advantage observed in the visual imagery task disappeared and performance fell to the level in rote verbal recall. Thus, visuomotor performance impaired visuospatial tracking as it interfered with the rehearsal component of visuospatial working memory.

Baddeley and Hitch assumed that the phonological loop, which is of the utmost relevance for this book, consists of a phonological store and an articulatory rehearsal mechanism. The authors tapped the phonological store with the phonological similarity effect, which is based on the tendency to confuse similar sounding letters like /d/and /t/. Baddeley found that visually presented strings of phonetically similar monosyllabic words were more difficult to recall in the short-term than strings of dissimilar words (Baddeley 1966). This effect was more pronounced than when comparing semantically similar vs. semantically dissimilar word strings. Conversely, in long-term memory tests, semantic similarity impairs recall more than does phonological similarity. This finding underscores the role of phonological processing (as opposed to semantic processing) in short-term memory, even with visually presented stimuli. Basically, visual stimuli have to be first translated into an auditory memory trace that is subvocalized before it is recognized. Another strategy to disrupt phonological storage capacity was to use the irrelevant speech effect, which basically consists of presenting irrelevant sounds while subjects memorize a string of words or letters (Salamé and Baddeley 1982, 1990). These stimuli need not be speech, as they can also be irregular sounds that compete with the phonological trace in auditory short-term memory. According to Baddeley, complex auditory information obliges access to the phonological store, there being no filter to separate relevant from irrelevant input (Baddeley 2000a).

The articulatory component of the phonological loop can be reflected in a phenomenon called the word length effect, in which the recall of recently presented word strings declines with longer words (after controlling for the different exposure times to long versus short word strings with equal numbers of words) (Baddeley et al. 1975). The short-term auditory memory trace tends to fade rapidly unless it is reactivated by a motor process. Therefore, immediate recall is limited by the decay of the auditory trace and the articulatory speed capacity of the subject. Longer words take more time to be articulated and therefore decay more rapidly than shorter words. However, there is still discussion regarding the exact process involved in the word length effect, whether it owes to the longer rehearsal time per se or to the greater phonological complexity of longer words. Finally, articulatory suppression is an experimental manipulation, consisting of covertly repeating an irrelevant sound during the task while word strings are presented acoustically (Murray 1968). This inhibits motor rehearsal and strongly impairs performance, but suppresses the word length effect. However, the phonological similarity effect is spared, which depends on the phonological store. The effect of articulatory suppression is best observed with visual presentation of verbal stimuli, in which the visual image has to be translated into a phonetic representation. In this condition, articulatory suppression eliminates both the word length and the phonological similarity effects. The latter is eliminated because the translation of the seen stimulus into a sound cannot be readily executed. Thus, neither the auditory trace nor the articulatory speed has any effect on memory maintenance, generating poor performance at all levels. Later in this chapter, I will discuss imaging studies that purport to localize the phonological store and the articulatory system, and criticisms of these findings.

The executive component of working memory was more difficult to tackle, and its conceptualization was derived from Donald Norman and Tim Shallice's schema of attentional control developed in the 1980s (Norman and Shallice 1983). The authors distinguished two attentional mechanisms at work during daily behavior. The first is an automatic habit-based system that one uses to drive home from work, and the second, of more relevance to Baddeley's model, is a supervisory attentional system that involves contextual awareness and permits

circumventing the habit system when it is no longer appropriate or when one is in a novel setting. These two components may be also separated anatomically, the automatic system putting more emphasis on basal ganglia or striatal networks, while the supervisory attentional system is biased to parietal-prefrontal cortical networks. However, Baddeley realized that an additional component was necessary that feeds long-term memory input into the working memory network to address more complex forms of working memory like recalling the elements of a discourse. This was investigated by more complicated studies on working memory span, in which subjects were presented a list of sentences and had to remember the last word of each. This measure is a good predictor of many cognitive capacities, and requires the use of long-term skills in addition to the simple mental manipulation assumed for the initial working memory model. Baddeley conceived the episodic buffer as an interface between the phonological loop, the visuospatial sketchpad and the central executive, which binds incoming information in integrated episodes that can be maintained in the mid-term (Baddeley 2000b). This is different from episodic memory, which is a long-term memory of experiences acquired in a single shot, in that the episodic buffer is transient in nature and related to the specific task. Nonetheless, episodic memory is strongly dependent on the hippocampus, and there is much recent evidence indicating hippocampal involvement in working memory tasks (Baddeley et al. 2011).

Images of Memory

Baddeley's working memory model inspired studies using imaging methods to establish the neuroanatomical regions involved in the different components of this model. Initially many studies concentrated on the phonological loop, which is more amenable to experimental analyses than the visuospatial sketchpad or the central executive. The first of these studies by Eraldo Paulesu, Chris Frith and Richard Frackowiak (Paulesu et al. 1993) used PET to compare brain activation patterns in subjects doing two different tasks, one consisting of short-term memorization of visual letters that supposedly engages both the phonological

store and the subvocal articulatory system. This was contrasted to a similar task using Korean characters, a language that none of the subjects knew. Subtracting the activities in the two conditions highlighted the areas specifically involved in the phonological loop, including both the rehearsal and storage systems, as Korean letters were perceived only as visual stimuli. After this, Frith and Frackowiak applied an additional task requiring rhyming judgments. This was assumed to involve only the subvocal rehearsal mechanism and not the phonological store, as articulatory suppression specifically impairs rhyming judgment capacity. Furthermore, Giuseppe Vallar and Baddeley had shown that in patients with verbal storage deficits there was no deficit in rhyming judgments, indicating that the phonological store is not required for this task (Vallar et al. 1991). By subtracting the activity seen in the letter memorization task from that of the rhyming task, they expected to evidence the locus of activation of the phonological store system only, as it was supposed to be inactive (or less active) during the rhyming task, while the rehearsal system was active in both conditions. The main findings were activation of the left inferior parietal lobe (anterior part, Brodmann's area 40) associated with the phonological store, and activation in posterior Broca's area (pars opercularis, Brodmann's area 44), associated with subvocal rehearsal. These findings provoked a lot of excitement because patients with damage to the inferior parietal area and with deficits in phonological working memory had been reported earlier, although many of the lesions in these patients also involved temporal areas (Baddeley 2007; Vallar et al. 1991; Warrington and Shallice 1969).

Some years later, Bradley Buchsbaum and Mark D'Esposito criticized the report by Paulesu and collaborators, citing evidence that the rhyming task indeed activates the phonological storage system, even if it is not necessary for the task (Buchsbaum and D'Esposito 2008). Therefore, the difference observed in activation does not accurately reflect a phonological store system. It can reasonably be counter-argued that there may be a difference in metabolic activity when a structure is necessary for a task from when the structure participates in the task but is not required for it, and this is reflected in the observed difference between the two tasks. In other words, even if the phonological store is activated during the rhyming task, it may be less active than in the visual letter memorization

task because it may not be critical for rhyming judgment. Nonetheless, this possibility needs to be tested experimentally. Buchsbaum and D'Esposito also made more serious objections to these findings, which I will describe in a few more paragraphs.

In the same year as Paulesu's report, John Jonides and collaborators published a PET study assessing brain activation in a visuospatial working memory task that consisted of showing a subject an array of three dots on a screen and after three seconds the subject was presented with a spot that matched or did not match the location of the previous dots. This was contrasted with a similar task that required minimal memory, that is, there was no delay between probe and target (Jonides et al. 1998). In the memory condition, Jonides and team found increased activation in area 40 of the right hemisphere (the same as in Paulesu's study but in the other hemisphere), in left frontal regions and in visual areas. Jonides' group subsequently developed a series of studies aimed at distinguishing the activation patterns of verbal versus spatial working memory processes and confirmed the association between phonological storage tasks with activation of the left inferior parietal lobe, although the precise inferoparietal area activated seemed to depend on the specific task used. Their findings were also consistent with a link between verbal rehearsal tasks and activation of Broca's region. The participation of right inferior parietal and frontal areas in the visuospatial network was also consistently observed. Using more complex designs, such as the N-back task (see Chapter 2), Jonides and collaborators found that verbal material activated the same regions in the left hemisphere as in the previous verbal tasks, but with prefrontal activation that increased with memory load, reflecting the recruitment of executive processes. There were other areas that evidenced activation, like the right cerebellum, and in highly demanding tasks there was also a mild activation of equivalent areas of the right hemisphere. This experiment is open to criticism as the N-back task heavily involves executive processes, and it has been claimed that it does not put increasing demands on phonological storage given that the number of digits in the store is probably constant regardless of the load. However, this assumption has not been verified experimentally. There were other studies that failed to detect left inferior parietal-Broca activation in verbal working memory tasks, but these tasks used semantically meaningful stimuli that confuse the processes being analyzed.

Jonides and collaborators also analyzed the rehearsal mechanisms involved in visuospatial working memory, focusing on attentional direction during the memorization interval (Smith and Jonides 1997). They did not address eye movements, perhaps a more natural effector system for attentional displacement, as these were at the time difficult to monitor and subjects were asked to fix their sight on the center of the screen. Instead, the authors employed a classical design by Michael Posner, who pioneered cognitive studies of attentional mechanisms (Posner and Petersen 1990). Basically, Posner's experiments showed that response to a visual stimulus is more rapid if it coincides with the region where attention is allocated, even if the eyes are not fixed on that position. In the working memory experiment of Jonides' group subjects had to memorize a spatial location, and concurrently a stimulus appeared either within the region kept in memory or outside it, that had to be discriminated. Discrimination evoked a stronger response when the stimulus fell into the patch the subject had to keep in mind, indicating that attention was located in this place. Finally, the central executive proved to be very elusive for imaging studies, as it has been very difficult to design a task that isolates executive processes. Attempts to do so have been inconclusive or contradictory until now. There is general consensus that the central executive probably relies heavily on prefrontal cortex activity, but agreement stops there. In parallel to these studies, several electrophysiological experiments were taking place by other researchers using visual working memory tasks with monkeys, which I will discuss more extensively in the next chapter. These studies revealed two parallel circuits, one via the parietal lobe that processes object location, and the other via the temporal lobe that processes object identity.

Boxes or Networks?

In their critique of imaging studies of working memory, Buchsbaum and D'Esposito referred to a meta-analysis of the data from the group of Julie Fiez (Fiez et al. 1995). The authors emphasized the variability of the activated locus in the inferior parietal lobe, which ranged from area 40 (supramarginal gyrus) to the more posterior area 39 (angular gyrus), and

dorsally up to the intraparietal sulcus bordering the superior parietal lobe. The precise locus of activity was highly dependent on the precise task. For example, activation of intraparietal areas was more evident when using visual-demanding protocols. Furthermore, and perhaps more importantly, Fiez's group noted that if Baddeley's notion of obligatory access to the phonological loop was correct, inferior parietal activation should be observed when subjects listen passively to speech, which had not been reported. Furthermore, studies with monkeys had shown sustained patterns of activation of individual neurons during the delay period of a visual working memory task (see the next chapter). This is the period between presenting a stimulus and response, where sensory information must be kept active as the animal waits for the next response. These neurons were interpreted as memory-related cells. Thus, if a storage system is present, it should be active especially during the delay period, which is when information has to be maintained online. However, previous reports had averaged brain activity throughout the memory task, so it was not possible to determine which areas showed this specific maintained activity. Consequently, Buchsbaum, D'Esposito, Gregory Hickok and others searched for regions of the brain that become active during both the passive presentation of speech sounds and in the memory delay period. In one study, Hickok, Buchsbaum and Colin Humphries used an auditory verbal working memory task with multisyllabic pseudowords (Hickok et al. 2003). They observed only two brain regions that showed persistent activity during both the presentation of the stimulus and the delay period: the posterior superior temporal sulcus, where phonemes are integrated into word forms (see Chapter 2), and a small region in the posterior depth of the Sylvian fissure at the intersection of the temporal and parietal lobes, which they appropriately called Spt (for Sylvian, parietal and temporal). Further studies indicated that these areas also show sustained activation with nonsense speech and musical stimuli. In addition, these areas are active with both visual verbal and auditory verbal stimuli, but the superior temporal sulcus has some preference for auditory stimuli. Activity in these areas decays over time, which is consistent with a fading memory trace. It was also noted that these areas are by no means speech-specific and therefore are not exclusively phonological. These findings

are consistent with aforementioned reports, indicating that many of the verbal working memory-impaired patients also had temporal lobe lesions in addition to damage to the inferior parietal (Baddeley 2007; Vallar et al. 1991; Warrington and Shallice 1969).

Area Spt and the superior temporal sulcus are embedded in the auditory processing circuits and are difficult to separate from early stages of sound analysis. Damage to these areas leads to severe speech deficits, unlike the purely short-term memory condition described by Shallice and Vallar. Considering this, Buchsbaum and D'Esposito argued that the phonological store is a psychological construct, without a neuroanatomical correlate in the brain (Buchsbaum and D'Esposito 2008). They further claimed that the rarity of the pure verbal short-term memory condition, with only 15 reported cases, suggests that these patients are indeed special cases, in which, for example, the right hemisphere may have assumed many language functions, albeit relying on a less robust network that evidences deficits like pure short-term memory. Buchsbaum and collaborators designed a dual-modality continuous recognition task, in which sequences of words were presented simultaneously in the auditory and visual modalities (Buchsbaum et al. 2011a). Subjects had to ignore the auditory stimuli, and discriminate whether each visually presented word had been visually presented before, or if it was a new word. Nonetheless, some of the visually presented words had been presented previously, not in the visual but in the acoustic modality. These visual stimuli were supposedly "new", as the acoustic stimuli had to be ignored. While overall subjects performed well in the task, fMRI-assessed bilateral activation of the inferior parietal lobe decreased with longer distances between the visually repeated words (increasing difficulty). Conversely, areas in the superior parietal and frontal lobes showed higher levels of activity with longer delays between words, which is consistent with their involvement in the difficulty of the task. Furthermore, this study confirmed dissociation between inferior parietal deactivation and activity in area Spt. More recently, D'Esposito and collaborators have criticized the notion that persistent activity in the prefrontal cortex actually represents memory storage, rejecting any claim of a localized storage buffer in the brain (D'Esposito and Postle 2015). As they argue, the only sites that store high-fidelity memory information

are the sensory cortices, which is consistent with many recent findings indicating sensory activity during working memory tasks.

What function does area Spt serve? This region is considered an auditory-motor interface that binds acoustic representations with articulatory patterns in Broca's area, possibly via the arcuate fasciculus. Therefore, it represents a core component of the language network. Conduction aphasia, the symptoms of which include naming deficits, impaired verbal repetition and importantly, deficient verbal working memory, was initially believed to be caused by the disconnection between Broca's and Wernicke's areas via the arcuate fasciculus, but more recent studies have shown a significant involvement of gray matter in many patients (See Chapter 2). In an MRI study of 15 patients with conduction aphasia, Hickok, Nina Dronkers and colleagues found that the region of maximal lesion overlap fits the location of area Spt, which according to them explains most of the symptomatology of this condition (Buchsbaum et al. 2011b). This area may be connected to Broca's region, or to the vocal premotor cortex via the arcuate fasciculus or some adjacent tract (Saur et al. 2008). Complementary to this, Angela Friederici and her team assessed sentence processing and verbal working memory performance in a patient with a lesion involving the white matter underlying the left superior temporal gyrus, but sparing gray matter (Meyer et al. 2014). MRI examination revealed the absence of the arcuate fasciculus and the superior longitudinal fasciculus, the latter connecting parietal and frontal areas. Concomitantly, the patient performed poorly in verbal working memory tests, and in memory of sentences involving complex word order and long words, while performing better in tasks requiring long word storage. Another study by Friederici's group with normal subjects revealed that in normal speech, manipulation of phrase ordering (as in subject-first vs. object-first German sentences) primarily involved activation of Broca's area, while storage functions (phrases intervening between object and verb) were more associated with activation of the left temporoparietal junction and tractographic integrity of the arcuate fasciculus/superior longitudinal fasciculus (Meyer et al. 2012). Together, these findings imply that the connectivity of area Spt to

Broca's region via the arcuate fasciculus and other tracts is a critical component of verbal working memory. Likewise, Hickok's group confirmed a role of Broca's region and motor articulatory mechanisms in verbal working memory (Hickok et al. 2014). They assessed short-term verbal memory (assessed with a digit span task), and speech articulation deficits (apraxia of speech) with a series of stroke patients in the very early stages, before the onset of compensatory reorganizations of the damaged neuronal networks. Articulatory deficits were related to damage in posterior Broca's area, motor areas, insula and somatosensory areas, while verbal working memory was related mainly to posterior Broca's and motor areas. This indicates a close overlap in sensorimotor systems involved in speech production and verbal working memory.

So much for the search for a localized phonological store, especially in the inferior parietal lobe. Although the debate has not yet been settled, we will see in the next chapter that animal studies have shown that there no need for a specific storage system in the neural networks underlying visuospatial working memory. More generally, the notion that neuropsychological capacities are encapsulated in modular systems does not fit neuroscientific evidence. Nonetheless, besides the evidence shown here, there have been many other reports that have consistently found involvement of the inferior parietal lobe in verbal working memory tasks. It may be that these areas are recruited because verbal working memory demands attentional capacity, partly controlled by the inferior parietal lobe (as argued by Buchsbaum and D'Esposito), or that the inferior parietal lobe plays some role in rehearsal mechanisms, or that it contributes to the goal-directed component of working memory. For example, Baldo and Nina Dronkers tested patients with either inferior parietal or inferior frontal cortex damage in phonological storage tasks (including auditory rhyming, repetition and digit span), and in articulatory tasks (an n-back task and a visual rhyming task) (Baldo and Dronkers 2006). While inferior frontal patients were specifically impaired in rehearsal tasks, inferior parietal patients showed a deficit circumscribed to storage tasks. Using fMRI, Oliver Gruber and collaborators have done studies using the articulatory suppression condition to eliminate verbal strategies when performing working memory tasks like memory of letter

names, colors or shapes, and found largely overlapping parieto-frontal networks associated with these different modalities (Gruber 2001; Gruber and von Cramon 2001). Furthermore, Gruber showed that during verbal working memory tasks performed under articulatory suppression, activation increased in the posterior inferior parietal lobe (instead of area 44) and anterior prefrontal areas. More recently, Gruber studied two selected patients, one with a bilateral lesion in the frontal pole and the other with a lesion restricted to Broca's area (Trost and Gruber 2012). The former had normal articulatory rehearsal capacity (measured in a subvocalization letter memory task) but impaired non-articulatory phonological working memory (that is, the same task under articulatory suppression), while the Broca's area patient showed intact non-articulatory verbal memory but was highly deficient in articulatory rehearsal tasks. This suggests that phonological storage mechanisms partly depend on networks other than the classical language networks, encompassing parieto-prefrontal systems.

Einat Lienbenthal and collaborators used dichotically presented syllables and chirps in an auditory recognition task with a combined ERP and fMRI protocol (Liebenthal et al. 2013). They found early syllable-specific activations in the auditory areas in the inferior parietal lobe and the ventral motor cortex. Moreover, concurrent left hemisphere activation in the inferior parietal and motor areas preceded the activation of left auditory areas, suggesting an anticipatory role. Dorothy Saur, Cornellius Weiller and collaborators found that the inferior parietal lobe contributed to both the ventral and dorsal language pathways (Kellmeyer et al. 2013). This team investigated the structural connectivity of areas involved in manipulations of segmental (shifting vowels) and suprasegmental (shifting stress placement) elements of pseudo words. The authors reported that connections between the left inferior parietal lobe and pars opercularis in Broca's area (area 44) participated in suprasegmental manipulations (dorsal pathway), while connections between the inferior parietal lobe and pars triangularis in Broca's region (area 45) participated in segmental manipulations (ventral pathway). These findings underscore the supporting role of parietal-frontal networks in phonological processing, even if they are not related to the phonological storage module. In another study of interest, Anne Sophie

Champod and Michael Petrides used an event-related fMRI design to assess the role of the inferior parietal cortex (particularly the intraparietal sulcus) in manipulating verbal information (Champod and Petrides 2010). They presented subjects with lists or abstract disyllabic words that had to be remembered in precise order. Subjects were then required to reorder the list (manipulation task) or to note the occurrence or non-occurrence of certain words from the remembered list when a new list was presented (monitoring task). A control task was simply to recall the words presented in each trial. While they observed increased activity in the prefrontal cortex during both manipulation and monitoring of progressively longer words, increased activity in the posterior parietal sulcus was related to manipulation but not monitoring information. Very recently, Cathy Price and collaborators assessed the participation of the supramarginal gyrus in a variety of phonological tasks, and identified specific subregions involved in articulatory sequencing, auditory short-term memory and lexical processing, which again supports the role of the inferior parietal lobe in the phonological loop (Oberhuber et al. 2016). Other components that have been involved in working memory circuits are the basal ganglia and the cerebellum. Both structures connect intensely with large regions of the cerebral cortex. Christopher Chatham, Michael Frank and David Badre proposed that the corpus striatum participates in input and output stimulus selection during working memory, mediated by contextual information provided by the frontal cortex (Chatham et al. 2014). Jutta Peterburs, Dominic Cheng and John Desmond have recently evidenced involvement of the cerebellum in controlling human eye movement in visual working memory tasks, which are dependent on memory load and independent of eye movements involved in stimulus analysis (Peterburs et al. 2015). While these designs have used mostly visuospatial tasks, it is possible that these systems play similar roles in verbal working memory.

Considering the above, parietal-prefrontal and subcortical networks may contribute to verbal working memory through indirect mechanisms, although they may not contain the memory elements that are kept online. Instead, these networks exert top-down influence over sensory regions in terms of the desired outcome or the motor programs that are to be selected. This view emphasizes a distributed system, encompassing sensory

and higher order areas that support working memory tasks. In this way, activity in sensory regions is modulated, and possibly stabilized against interference by backward inputs from inferior parietal and frontal regions involved in motor programming and goal directed planning. In addition to these supporting components, increasing evidence indicates significant hippocampal involvement in the digit span and other working memory tasks (Baddeley 2000b). As with Baddeley's episodic buffer, working memory depends on the vivid representation of sensory input, which is provided by episodic memory, possibly via theta oscillations that propagate from the hippocampus to the cerebral cortex. A core circuit for verbal working memory therefore contains the arcuate fasciculus, connecting the auditory area Spt with the posterior of Broca's area, but includes surrounding components as subsidiary elements, as Evelina Fedorenko and collaborators have correctly emphasized (Chapter 2) (Fedorenko 2014).

In general, Baddeley's multicomponent model for working memory has been very influential, but it needs to be updated and revisited in the context of new neuroscientific evidence. The model of boxes involved in specific cognitive processes like articulation and storage is too simplistic for neuroscientific work, and will probably be replaced by a network-level model in which overlapping and distributed systems participate in different processes. Nonetheless, we owe Baddeley for introducing the concept of working memory as a kind of explicit short-term memory to be used in the near future, and especially to this book's purpose, for the concept of the phonological loop as a sensorimotor device that allows verbal acquisition, and may be unique to our species.

Tracking Sentences

Baddeley wondered what function verbal working memory serves, especially with subjects with low verbal working memory capacity that do reasonably well in normal life and are able to employ and understand forms of speech used in daily life. One possibility is that phonological memory is needed to understand complex forms of speech that cannot be processed automatically. Baddeley and Giuseppe Vallar worked with PV, a patient who was perfectly able to speak normally, with appropriate

vocabulary and syntax, and normal speed and prosody (which rules out any speech processing deficit) (Vallar et al. 1991; Baddeley 2007). However, she was unable to understand relatively long and intricate sentences, especially passive ones, which required her to keep track of the initial elements to understand their meaning at the end. Linguists refer to these relations between distant elements in a phrase as long distance dependencies, while these are in fact time dependencies as whether in speech or reading, the relation between distant components is mediated by time and necessarily invoke some kind of memory. During reading, one can come back to the original words above on the page to help in understanding, while in speech one has to rely exclusively on memory, or else say, "Could you say that again?"

Thus, one possibility is that the loop serves to integrate complex sentences and track elements in memory phrases that are needed to understand the phrase as it is unfolding. This resembles the N-back task described in Chapter 2. However, this is not a simple retention memory task, as it requires manipulation of the items as they enter and exit the attention window, keeping their order in sequence. Thus, it also involves executive processes that may be at work during natural speech processing. Furthermore, there are additional elements in complex sentences that go beyond a mere string of concatenated elements. Steve Pinker argued that this is a critical element for language, requiring a special kind of memory that allows for keeping the first elements of sentences active as new words arrive (Pinker 1994). Some years ago, Eleanor Saffran went beyond the phonological dimension of working memory, putting forward a model that includes several parallel but interacting working memory systems involved in phonological, syntactic and semantic processing (Saffran and Marin 1975). Likewise, David Caplan has argued the existence of separate working memory systems for semantic and for syntactical processing (Caplan and Waters 1999). These ideas agree with Joaquín Fuster's notion that memory is a property of cognitive circuits, rather than a separate system in the brain (see Chapter 7). Circuits involved in different linguistic processes like syntax, semantics and phonology, may have their own memory capacities, even if they show significant overlap. In a similar line, Aniruddh Patel analyzed two existing models for syntactic and harmonic processing of

music, the Dependency Locality Theory (DLT) and the Tonal Pitch Space Theory, respectively (Patel 2003). In both theories, distances between items (words or chords) have to be computed and stored while the sequence is still being perceived. In his words, "in DLT, integration can be understood as activating the representation of an incoming word while also reactivating a prior dependent word whose activation has decayed in proportion to the distance between words. In TPS, integration can be understood as activating an incoming chord while maintaining activation of another chord which provides the context for the incoming chord's interpretation" (Patel 2003, p. 678). Although Patel does not mention a memory system involved in this process, this is quite similar to the online management of information during working memory tasks.

Therefore, phonological, syntactical and semantic circuits may use different but overlapping short-term memory processes that contribute to creating a contextual framework in which linguistic elements are organized into a coherent whole. In this sense, an algorithm may be necessary to translate a sequential phonological working memory code into a visuospatial working memory code provided by lexical and semantic contents. Some of my students and I have argued that this algorithm is contained in the hierarchical organization of phrases that transforms the sequential auditory code into a visuospatial code. In this sense, syntax works as an interface between phonology on one side, and the lexicon and semantics describing actions or events, on the other (Aboitiz et al. 2006a, b). Furthermore, this interface may be represented by the nested time scale organization of oscillatory activity during speech processing, as the group of David Poeppel has recently found (Chait et al. 2015; Ding et al. 2016; see Chapter 2). In this, our brains are probably unique, as no other species is known to make translations of this kind in the context of short-term memory.

In Broca's aphasia there seems to be a specific difficulty in keeping the memory traces that connect phrase components in special verb tenses like passives, in which the canonical order of a sentence is reversed (for example, "The boy kissed the girl" → "The girl was kissed by the boy"). Something similar happens with some

interrogative sentences, as in "Where did you go?" This operation is called "syntactic movement", and it is believed to be a consequence of the recursive property of language, in which components can be inserted within others, or moved from place to place, as if they were Leggo blocks. In order to recompose the canonical structure of the sentence, phrasal constituents keep connected with traces that bind them to their canonical place. As I said above, such traces have to be mnemonic in nature, as the brain processes sentence structure over a time interval. Yosef Grodzinsky, who first noted that Broca's aphasics have difficulty with syntactic movement, proposed the "trace deletion hypothesis", claiming that in Broca's aphasia, traces of syntactic movement are specifically erased (Grodzinsky 2000). As expected, the longer and more complex the dependencies, the more trouble patients have to understand them. Grodzinsky did not mention any memory deficit in these patients, and specifically referred to the elimination of formal syntactic operations. However, as I told Josef at one time, no matter what formal elements are missing, the main problem is the neurocognitive process by which the brain keeps these traces. Grodzinsky has responded that a direct connection between formal syntactic elements and working memory has yet to be demonstrated, which is correct but for now seems to be a reasonable neurobiological and cognitive explanation for these findings. However, I am not saying that working memory explains syntactic movement or long distance dependencies in complex grammars. Clearly, there is a lot more to these processes than short-term memory, like hierarchical organization and appropriate labeling and ordering of the phrasal components. But these syntactic operations are probably limited by short-term memory capacity, which, if impaired, results in a restriction of the syntactical operations that can be performed.

Broca's area has been considered critical for complex syntactic processing, as evidenced by studies showing activity changes associated with grammatically correct sentences compared with ungrammatical sentences. Notably, this area is also active during harmonic musical processing and mathematical calculations (both involving a sort of grammar). Disengaging the syntactic and mnemonic processes

in these instances can be very difficult, as has been discussed by several authors (Fiebach et al. 2005). Michiru Makuuchi, working in Angela Friederici's laboratory, made an fMRI study in which they compared German sentences with two manipulated variables: hierarchical organization, tapping grammatical processing; and long distance dependencies that put a preferential load on working memory (Makuuchi et al. 2009). For example, phrases like "*Maria, die Hans, der gut aussah, liebte, Johann geküsst hatte*" ("Maria, who loved Hans who was good looking, had kissed Johann") vs. "*Maria, die weinte, Johann geküsst hatte und zwar gestern abend*" ("Maria, who cried, had kissed Johann and that was yesterday night"). Both phrases are highly hierarchical but the former has more long distance dependencies than the latter, as shown by the distance between the main subject "*Maria*" and the verb "*hatte*" in each of them (8 words in the former, 4 in the latter). On the other hand, phrases like "*Achim den grossen Mann gestern am späten Abend gesehen hatte*" ("Achim saw the tall man yesterday late at night") and "*Achim den grossen Mann gesehen hatte und zwar am abend*" ("Achim saw the tall man at night and that was late") are simple in hierarchical organization but again the former sentence has a longer distance dependency than the latter (8 words as opposed to 4 between "*Achim*" and "*hatte*"). Makuuchi found that hemodynamic activity in the left pars opercularis correlated more with structural complexity, while a slightly more ventral region (the left inferior frontal sulcus) was more sensitive to long distance dependencies. However, there was a very strong overlap between the activated regions for each variable, as well as a significant functional connectivity between these areas. Thus, they were able to partially segregate these two functions, but in my opinion the most important finding is the strong interconnectivity observed between the involved regions, which increased with higher syntactic complexity. This argues in favor of a tight relationship between syntactical processing and working memory load. As judged by the images presented, the activated areas in this study do not exactly fit the restricted notion of Broca's area, which involves only the inferior frontal gyrus (located just ventrally to the sites of activation). This underscores the point I made in Chapter 2, that

Broca's region may be functionally more extended than the pars triangularis and pars opercularis of the inferior frontal gyrus. Furthermore, the subtracting design of fMRI experiments emphasizes differences in activity but tends to eliminate areas that may be very necessary but coactive under different conditions (see also Chapter 2).

The Loop is for Learning

Interesting as the evidence and theories above may be, Baddeley correctly argued that it is difficult to think that the main benefit of the phonological loop is that we can understand complex and unusual sentences. My students and I have also argued that the development of complex syntax may have benefited from the acquisition of a sufficiently robust phonological loop, but clearly this does not explain its initial development (Aboitiz and García 1997; Aboitiz et al. 2006a, b). More than complex language processing in adults, the ease for learning a language may represent a more critical process for human development, and must have been a critical selective factor in early humans. Baddeley then focused on language acquisition, first with adults learning a second language, and later with children learning their mother tongue.

Baddeley asked the aforementioned patient PV to associate Russian words (a language that PV did not master) with their Italian translations (her native language), as opposed to learning associations between semantically and structurally distinct Italian words (Baddeley 2007; Vallar et al. 1991). PV was especially impaired in learning Russian-to-Italian associations, while Italian-to Italian pairs were recalled perfectly well. Control subjects did well in both tasks. The same findings were obtained when a graduate student with poor phonological working memory was assessed. Vallar described a patient with Down syndrome that had an outstanding verbal working memory capacity and had mastered three languages despite having a low IQ, (Vallar and Papagno 1993). Other studies successfully used articulatory suppression to interfere with learning foreign words,

while the same procedure had no effect on associations between native words (Baddeley 2007).

Baddeley and colleagues then moved on to children with specific language impairment. This is a partly hereditary condition characterized by delayed language development in otherwise normal children that do not suffer hearing loss, vocal deficits or other developmental delays. Baddeley and colleagues observed that these children had a notable impairment when it came to repeating spoken non-words of different lengths (something reminiscent of conduction aphasia, although not the same, where the deficit consists of repeating spoken phrases or words). Baddeley and colleagues tested 8-year-old patients that performed at the level of normal 4-year-old children (Baddeley and Hitch 1993; Baddeley et al. 1998; Baddeley 2007; Gathercole et al. 1994). The non-word repetition test proved more reliable than other measures of phonological working memory, as it relies on novel phonological combinations that have not been overlearned as real words and numbers have. It has also been found that tests of non-word recognition, instead of repetition can be useful in assessing phonological storage capacity, especially with subjects with speech production problems. Returning to our point, the next step was to test non-word repetition capacity in normal children and find whether it could predict aspects of speech and language development. As expected, with children of a given age, verbal IQ significantly correlated with non-verbal IQ. However, non-word repetition was a better predictor than non-verbal IQ of verbal IQ performance. Furthermore, Baddeley and colleagues did a follow-up study that initially assessed vocabulary levels, and performance with two kinds of non-words, one type similar to English words, like "prindle", and the other dissimilar to English words like "stikicult". A year later the same children were evaluated for vocabulary richness again. Acquisition of new words during the year strongly correlated with earlier performance in the less English-like non-words but did not correlate with performance in the more English-like non-words. The point here is that children with more capacity to keep and repeat novel utterances are able to learn new words more rapidly.

But as many say, correlation does not mean causation. To get stronger evidence that better phonological working memory was indeed causing

the difference in vocabulary acquisition, Baddeley and his group made what is called a cross-lagged correlation study, in which 4-year old children were tested on non-word repetition and on vocabulary (as had been done before), and after 1 year were tested again on both non-word repetition and vocabulary (Baddeley et al. 1998; Baddeley 2007). The point of this design was to determine which variable better explains the changes in the other. They found that non-word repetition at 4 more strongly correlated with vocabulary at 5 than vocabulary at 4 with non-word repetition at 5. This rules out the possibility that vocabulary itself is the main factor increasing phonological working memory. In fact, there is a positive effect of increasing vocabulary on working memory capacity, but it is much weaker than the effect that working memory capacity has on vocabulary acquisition. Finally, Baddeley and colleagues looked for evidence of the influence of working memory on grammatical development in children. They found indirect support for this, such as a study of two highly intelligent bilingual siblings, one with deficits in phonological memory accompanied with slow vocabulary and syntactic development, while the other was good at both (Baddeley 2007). Other studies have found correlations between phonological working memory capacity and the mean length of utterances, and grammar learning in a second language. Further studies of working memory and syntax development, as well as on working memory and other aspects of language and speech are strongly needed.

To end, the analysis related to errors in the digit span task has provided further insight into the mechanisms of verbal working memory. It has been known for some time that if a sequence of numbers increases beyond storing capacity, all the items are still remembered but are recalled in the wrong order, typically transposing two adjacent digits. Likewise, in studies using consonant-vowel-consonant (CVC) non-words like /wux/- /caz/, a common error is to transpose the consonants and retain the vowel order intact, for example, recalling /cux/- /waz/ after presentation of the above non-words. Furthermore, lists of CVC non-words similar in vowel sounds (/dah/, /fah/, /gah/) are more difficult to recall than non-words differing in their vowels (/di/, /dah/, /doh/). Baddeley and colleagues found that closed item sets (that is, using the same words in different trials), resulted in complete word transposition

deficits, while with an open set (that is, new words in each trial), words themselves were often misreported, with a predominant shift of consonant order (for example /hat/- /pen/to /pat/- /hen/) (Baddeley 2007). These experiments make an important point, which is that order information tends to be carried by vowels instead of consonants, while consonants can be seen as the "junctures" between vowels (see Chapter 10).

Amplified Working Memory

There are about 37,000 articles in the scientific search page PubMed on working memory, the majority of which involve human subjects. In fact, the concept of working memory was conceived as a human trait, and initially there was little interest in its evolutionary development. Peter Carruthers recently published an interesting review of the comparative issues raised by working memory research (Carruthers 2013). Many objections have been raised to the idea that other animals display working memory capacities, including the incapacity to maintain sensory information for a relatively long period (2 seconds or so), the incapacity to resist interference, the inability to generate top-down control of memory traces, and the absence of rehearsal mechanisms that refresh working memory. Traditionally, it has been argued that if animals have any working memory capacity, it is very limited (no more than two objects) and they are unable to manipulate items in memory. Furthermore, animals only use working memory in contingent behavioral situations and not during mind-wandering and inner speech, as human commonly use it. And finally, only in humans does working memory operate in a communicative context. Although there has been little research directly comparing memory capacities in humans and non-human animals, there is evidence at least in higher vertebrates and especially monkeys and some birds, which challenges many of these assumptions. Studies have shown higher than expected memory spans and capacities in non-human species, as well as evidence of the capacity to resist interference in certain tasks (even in mice), and crows have been described as performing "mental travels", which is the capacity to recall one's past or future, a function dependent on episodic memory that is

activated in working memory (see Chapter 9). Basically, tests involved in assessing this capacity rely on the animal's being able to forecast a complex future event, or to accurately recall the three W's of an event: what, when and where did something happen. Crows perform admirably well in these tasks, which implies that they can create vivid images of past or future events. Likewise, chimpanzees have shown the ability to rehearse actions mentally and plan strategies for cognitively complex behaviors. For example, Carruthers refers to a case of a captive chimp in an open-plan zoo that amused itself by collecting stones that he would later throw at the human visitors. Zookeepers then started removing his stone stashes, to which the chimp responded by concealing his projectiles and using new materials to throw. In this context, a very recent article by Hjalmar Kuhl Ammie Kalan and collaborators reported widespread stone accumulating behavior in wild chimpanzees (Kuhl et al. 2016). Notably, some chimps have the habit of throwing stones at certain trees, or tossing them inside tree holes, which result in piles of stones inside or around apparently targeted trees. Moreover, several species have shown the ability to mentally manipulate volumes, being able to recognize among other alternatives a three-dimensional object after it has been rotated to hide its initial appearance. The notion that animals engage little in daydreaming (or mind-wandering) and are more limited in the ways they use working memory capacities seem to be better sustained at the moment, as there is an apparent relationship between speech and mind-wandering in humans. Cerebral patterns of resting state activity similar to humans have been reported in chimpanzees, macaques and rodents (Rilling 2014), but whether these involve any mental imagery is still a big question. In my opinion, these patterns do not necessarily involve working memory capacity, as the phonological loop, using inner speech, may be an important element in maintaining the stability of mental contents. As I have said before, the language circuit may have a double role, connecting with executive networks for problem solving but also engaging with the default network at rest, providing continuity to our daydreams.

Working memory is directly related to mechanisms of cognitive control, which is a key element for appropriate social behavior. Executive function, which depends on working memory, is critical to

revisit judgments that may be produced automatically but can be repressed or controlled by top-down mechanisms. In this line, Baddeley refers to Donald Norman and Tim Shallice's supervisory attentional system as a key element inhibiting automatic behavioral patterns in order for individuals to behave appropriately in social contexts. This system may have undergone strong selective pressure in human evolution (Norman and Shallice 1983). Nelson Cowan and others have argued that working memory has been expanding in response to increasing social and technological demands, but it is not clear whether this alleged increase is due to genetic selection or to learning or brain plasticity mechanisms, including epigenetic factors (Cowan 2005, 2009). Another proposal by Michael Vendetti and Silvia Bunge attributes relational thinking capacity, that is, the ability to represent relations between several items, to the lateral frontoparietal networks (Vendetti and Bunge 2014). In human development increased connectivity among these areas is associated with better relational thinking. Other authors, including Richard Passingham, have highlighted the role of dorsal prefrontal-parietal networks in foraging behavior in different species, by integrating information about metrics, distances, proportions and order (Genovesio et al. 2014). In the next chapter, I will mention additional functions of the parieto-frontal pathway that very likely played a significant role in the origin of speech and vocal communication. Finally in this line, working memory is intimately linked to attention, and increasing working memory capacity is dependent on a concomitant enhancement of attentional systems. In human evolution, both functions must have interacted closely, and the case of language origins and the generation of the phonological loop may not be exceptions to this. We still need to disentangle better the participation of attentional mechanisms in verbal working memory, to envision their role in the evolutionary origin of speech. In my opinion this is a highly promising direction for future research.

Perhaps no one has more explicitly pursued the amplification of working memory in human evolution than Fred Coolidge and Thomas Wynn, who proposed that an expansion of working memory capacity was a key event in late human evolution, separating modern

humans from Neanderthals (Coolidge and Wynn 2007). It is supposed that working memory expansion was associated with expansion of the inferior parietal lobe and globularization of the brain, facilitating planning behavior and the development of progressively sophisticated technologies and social organization. Coolidge and Wynn put special emphasis on abilities like communicating in the subjunctive mode, referring to events that are not real and may never occur, and the capacity to understand metaphors or jokes, which has been associated with inferior parietal lobe activation. As I said in Chapter 3, the associations between gross brain anatomy or cranial features and cognitive abilities still require empirical support, and are highly reminiscent of Franz Galls's phrenology doctrine. The archaeological evidence of less sophisticated technology may however give us clues about early human behavior, and indicates that the technological revolution only took place in modern humans, which implies that a profound change in cognitive development was occurring at that time. I will come back to these issues at the end of the book (Chapter 11), while in the next chapter I will focus on a more restricted aspect of working memory, which is the phonological loop, and of evidence suggesting its possible evolutionary history. This, however, will bring us far back from the Neanderthal-modern human split, and we will have to look for evidence in non-human primates to get a glimpse of its neural underpinnings.

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