

WORKING MEMORY AND THE BRAIN: A REVIEW OF MODELS, AND CLINICAL AND NEUROIMAGING STUDIES

AUGUSTO BUCHWEITZ¹

Universidade Federal de Santa Catarina
abuch@andrew.cmu.edu

Abstract

This paper presents a review of literature aimed at a general discussion on memory, working memory (WM) and the brain, based on a three-pronged source of evidence from clinical, behavioral, and, more importantly, neuroimaging studies. The review is organized following an initial, threefold discussion on (1) the segmentation of memory; (2) WM models; and (3) the prefrontal cortex; in the fourth section it resorts to neuroimaging studies. The objective is to illustrate what possible contributions have already been, and still can be, derived from neuroimaging within the study and modeling of WM, with previous theories and findings as the starting point.

Keywords: working memory; prefrontal cortex; neuroimaging studies

Resumo

Este artigo apresenta uma revisão de literatura que busca incitar uma discussão geral sobre a memória de trabalho (MT) e o cérebro humano, utilizando-se de referências variadas de estudos clínicos, comportamentais e de neuroimagem. A revisão seguirá os seguintes passos: primeiro, uma discussão sobre (1) a segmentação da memória, (2) os modelos de memória de trabalho e (3) o córtex pré-frontal e a MT; em um segundo momento, com base na discussão anterior, parte-se para uma discussão sobre estudos de neuroimagem relacionados à MT. O objetivo do artigo é iluminar as possíveis contribuições que já foram e que ainda podem ser feitas pelos estudos de neuroimagem aos estudos e aos modelos que buscam melhor entender a MT.

Palavras chave: memória de trabalho; córtex pré-frontal; estudos de neuroimagem.

1. The segmentation of memory

Is memory in the brain? Localizationism, a traditional school of neurolinguistics, is named after its arguing for the compartmentalization of memory (Oblor & Gjerlow, 1999, p.9). But it is misleading to state that memory is localized in specific areas of the brain or distributed over the whole brain. It is both. Against localizationism, there is evidence that a single event involves different (but limited) brain systems and pathways. Against distribution, there is no evidence of the brain operating as a single memory center (Squire, 1987, p. 123). Instead of a black-or-white argument, it may be more fruitful to understand memory as a system that engages different and additional cortical tissue, depending on different factors (input, cognitive load, task demand, and others), as the following discussion will try to argue.

To better understand memory as part of a system, it is necessary to understand memory as formed by traces – instead of as a specific file in one area of the brain. In clinical studies, for example, the memory lapses in Alzheimer’s patients are caused exactly by the breakdown in the linking of memory traces. One of the causes of these lapses is a deficit in acetylcholine, a chemical messenger responsible for neurotransmission between brain areas and, thus, consolidation of memories (Rodrigues, 2004, p. 89).

The segmentation of memory approach follows a parts-to-whole manner study of the matter. But “...the hope is to go beyond the simple dissociation of one component of cognition from another. *The ultimate objective is to understand how functions are actually organized in the brain* and how they are related to each other” (Squire, 1987, p. 175) (emphasis added). To this end, behavioral and brain lesion studies have contributed to the study of memory.

Firstly, in terms of behavioral studies, it is well-established that memory has a short-term and a long-term component – notions which, intuitively, stem from our ability to perceive elements in time. But intuition will not suffice. Behavioral studies, in their turn, have challenged the short-term

versus long-term dichotomous view of memory, and help describe how the concepts of short-term memory (STM) and long-term memory (LTM) have evolved.

Behavioral studies with auditory stimulus show that if a string of words, for example, is presented to subjects, subsequent presentation of another string by the same voice and at the same location impairs recall (Squire, 1987, p. 127); hence, there is online interference between processing and storage. The notion of interference between processing and storage, as will be discussed later, is one of the cornerstones of the concept of WM. With time, however, information is represented in an abstract code that is not tied to modality (propositions) and interference disappears. Studies switching between presentation of the same information in the passive and active voices report that, with short intervals of time between auditory presentation of the sentences, subjects have more difficulty identifying that the same propositional information is being conveyed; with longer intervals of time, however, this difficulty caused by active versus passive voice disappears: “The processing systems that *analyze* information also participate and influence the *representation* of that information” (Squire, 1987, p. 129) (emphasis added).

Secondly, studies of brain lesions to the inferior temporal cortex (TE) area of the brain in monkeys show that such lesions affect visual discrimination abilities (Squire, 1987, p. 122-3). Hence, there is some specialization of brain function over cortical tissue. In humans, classical studies of amnesic patients – such as case H.M., studied for more than 40 years (Paradis, 2003, p. 354) and who became highly amnesic after removal of the hippocampus and medial temporal region, bilaterally, to relieve severe epilepsy – have broadened the knowledge of STM and LTM, and declarative and procedural knowledge (Squire, 1987). In terms of a straightforward definition, Victor (1971, as cited in Kopelman, 2002, p. 2152) defines amnesia as “an abnormal mental state in which memory and learning are affected out of all proportion to other cognitive functions in an otherwise alert and responsive patient.” Let us then turn to the different components of memory and studies with amnesic patients.

STM and LTM, the buffer and the store

STM, conversely to LTM, is spared in amnesic patients. For instance, case H.M., on the one hand, showed normal performance in digit-span tasks (recalling strings of letters), but, on the other, was not able to improve the span with practice, as normal subjects did. Amnesic patients also show normal priming effects, recalling words more easily from the end of a word list (recency effect), but are not aware of this (Squire, 1987). Though STM is spared, amnesic patients cannot recall carrying out a task (reading a word list, for example). Amnesia results from damage to the medial temporal region that spares STM but is important when STM capacity is exceeded (Squire, 1987, p. 145).

Declarative and Procedural knowledge, the what and the how

Continuing to draw on evidence from amnesic patients, LTM is further divided into declarative knowledge (DK) and procedural knowledge (PK), that is, knowledge of what and how, respectively (Paradis, 2003, p. 354). Amnesic patients have the ability to improve motor skills, and even learn new skills (new PK). Researchers found, by accident, that H.M. was able to learn new motor skills (Paradis, 2003, p. 354). However, H.M. could not recall nor explain the process of acquiring the skills (DK) (Squire, 1987, p. 152), he forgot the learning experience: What is available to STM “is different information than what is obtained through intentional learning and later expressed in recall” (Squire, 1987, p. 161).

Lesion studies show the medial temporal region being associated with amnesia, thus operating in consolidating new, long-term memories and declarative memory. The segmentation of memory into STM and LTM, and declarative and procedural knowledge can prove useful not only in terms of understanding the components of memory and memory as a system, but also if it informs the design of neuroimaging studies – in the sense of replicating and improving the findings from behavioral studies with brain imaging – and if it allows for comparison between studies with patients and normals:

The question in all these divisions of memory is not whether it can actually be made or exists, but rather if it is trivial or provides a principle for how memory processes information (Squire, 1987, p. 170).

Are lesion studies trivial? If there were little specialized function for the nervous system, any lesion would affect brain functioning across behaviors (Squire, 1987, p. 176). So the answer is no. Nonetheless, there are shortcomings to lesion studies. First, brain lesions cross anatomical boundaries, and the precise identification of lesion sites is important not only for clinical assessment of severity, but also because the different combinations of damaged structures result in different memory impairments. Second, quantitative information is scarce and comparisons across different cases is difficult (Squire, 1987, p. 183). Neuroimaging techniques may thus unravel these difficulties of earlier lesion studies, allowing for the collection of data from normals and from patients, for more precise lesion site identification, and for the comparison and normalization of data across subjects.

2. Working memory

This section tackles the evolution of WM concepts and important WM models, which are also briefly compared at the end. It draws mainly on chapter 02 of Richardson, Engle, Hasher, Logie, Stoltzfus, and Zacks’s (1996) book, in which Logie describes the “Seven Ages of Working Memory.” The first two ages are interesting in the historical sense, but as the author moves to ages III, IV and so on, the change from a dichotomous view of memory to a more systematic view becomes clear.

1) Age I: WM as contemplation

As early as the late 1600s, John Locke (1690, as cited in Logie, 1996, p. 32) wrote of ideas that are contemplated and ideas that are stored, hence the dichotomous understanding of STM and LTM.

2) Age II: WM as primary memory

The distinction between short and long-term store, in the early 1900s, received new names: primary and secondary memory (James, 1905, as cited in Logie, 1996).

3) Age III: WM as STM

Atkinson and Shiffrin introduced the term WM, but focused on the concept of a short-term buffer for storage and processing information (Logie, 1996, p. 33). The notion of a trade-off between storage and processing and of a limited-capacity STM emerges.

4) Age IV: WM as processor

Memory as a by-product of cognitive processing (Logie, 1996, p. 34). At this point the short-term buffer of WM starts being understood as the gateway to memory. Later, this model of WM will have difficulty in trying to account for patients with impaired STM and normal learning and retrieval (Logie, 1996, p. 40).

5) Age V: WM as a constraint on language comprehension

Daneman and Carpenter (1980) and Just and Carpenter (1992) are the precursors of the limited-capacity approach to WM and language comprehension, based on WM span measures combining processing and storage (reading span). The limited-capacity approach to WM finds support in correlating WM span and performance on reading comprehension (Daneman & Carpenter, 1980; Tomitch, 1995; 1996; 1999/2000).

Though the reading span measure focused on language processing and storage, others replicated the findings of Just and Carpenter (1992) and devised different types of tasks (counting span, for example) that also correlate with measures of language comprehension (Engle, Cantor, & Carullo, 1992; Turner & Engle, 1989; among others). In comparison to age IV, at this point WM is understood as a system drawing on a pool of common resources for processing and storage.

6) Age VI: WM as activation, attention, and expertise

Cowan (1995) put forth a model of WM as a system with different levels of activation, being the highest level the one involving the contents of WM (focus of attention). The contents of WM help determine the availability of other, related information: Pieces of information unrelated to the focus of attention take longer and require more effort to retrieve; whereas those

that are related are more easily retrieved. The concepts of activation and attention are corroborated by findings of lexical and semantic familiarity helping retrieval, memory span (Logie, 1996, p. 38).

Ericsson and Kintsch's (1995) model of long-term WM also draws on the idea of availability of information just below WM threshold. The authors base their model on cognitive expertise: pieces of information within the domain of expertise of an individual are more readily available to WM (Logie, 1996, p. 38). Hence, the model accounts for familiarity effects. A classical example used by the authors is professional chess players' memory for chess positions. If presented with a chessboard from an ongoing chess game, professional players remember an outstanding number of positions (approximately 20); whereas non-professional players remember approximately seven positions. However, if chess pieces are placed randomly across the board, the effect of expertise disappears (Ericsson & Kintsch, 1995).

7) Age VII: WM as multiple components

At the basis of multiple-component models of WM are the studies of patients with STM impairments (very low digit and word spans, for example) but normal learning and retrieval (normal LTM), such as the well-known case of patient K.F. (Shallice & Warrington, 1970, as cited in Logie, 1996, p. 40), which challenges the notion of WM as a processor (age IV), a gateway to memory. Alternative explanations would have to allow for an alternative route into LTM or different WM subsystems (Logie, 1996, p. 40). Baddeley and Hitch (1974) put forth the multiple-component model of WM, which has evolved since (Baddeley, 1992; Baddeley & Logie, 1999), postulating a visual and spatial, and a phonological component, all regulated by an attentional control system, the central executive. The multiple-component model runs opposite, in terms of its non-unitary nature, to contemporary single-system theories such as those of Just and Carpenter (1992) and Cowan (1995) (Logie, 1996, p. 41).

The models and what do they measure

In sum, though postulating different capacity constraints to WM, the models can be considered consistent in establishing limits on performance of particular cognitive tasks (Richardson, 1996, p. 123). The difference being whether WM limitations are determined by its subcomponents (as in the multiple-component model), by the trade-off between processing and storage, or by activation. At this point, let us draw on the discussion so far and turn to one important area of the brain in the study of WM, the prefrontal cortex.

3. The prefrontal cortex (PFC)

Initially, it is important to establish a foothold on a definition of executive processes, a concept that will appear repeatedly in this section and the next. Executive processes are: (1) focusing attention ("attention and inhibi-

tion”); (2) switching attention between tasks (“task management”); (3) planning a sequence of subtasks to accomplish some goal (“planning”); (4) updating and checking the contents of working memory (“monitoring”); and (5) coding representations in working memory for time and place (“coding”) (Smith & Jonides, 1999, p. 1659). Now to the prefrontal cortex.

While the importance of the prefrontal cortex for ‘higher-order’ cognitive functions is largely undisputed, no consensus has been reached regarding precise specification of these functions (Owen, Schneider, & Duncan, 2000, p. 1).

The prefrontal cortex, the outermost surface of the frontal lobe (see, for example, www.brainexplorer.org for illustrations), or the very frontal area of the brain, is ubiquitous in the discussion of WM and the brain. Squire (1987, p. 225) writes that the PFC, though not well-understood, has been assigned higher-order functions of insight, abstraction, and self-awareness. More currently, Levy and Goldman-Rakic, in an *Experimental Brain Research* issue specially dedicated to the PFC, write that it is widely accepted that this area of the brain subserves WM functioning (Levy & Goldman-Rakic, 2000, p. 23). As the quotation above and Squire note, however, there are questions to be answered in relation to the specificity of PFC function: is there a subdivision of functions within PFC areas? If there is such subdivision, is it governed by the type of information or by that of cognitive operation? (Levy & Goldman-Rakic, 2000, p. 23). In this sense, studies with non-human primates and humans alike provide important results.

Studies with monkeys with large prefrontal lesions and delayed alternation and delayed response (DR) tasks show that the performance of PFC-lesion monkeys is profoundly impaired (Squire, 1987, p. 226; Levy & Goldman-Rakic, 2000, p. 24). These monkeys have an impaired ability to maintain information over time (Squire, 1987; Levy and Goldman-Rakic, 2000). Studies with monkeys also report consistent activation of the PFC during the delay period in DR tasks, when information has to be maintained (D’Esposito, Postle, & Rypma, 2000, p. 3). In sum, in primates executive functioning is tied to frontal cortex areas, and this is replicated in humans.

Lesions in humans and monkeys are usually compatible in terms of the impairment that they cause. But in terms of the lesion itself, human lesions are markedly larger and more variable (Squire, 1987, p. 231). Smith and Milner (1984, as cited in Squire, 1987, p. 233) report patients with frontal lobe lesions’ impaired recall of names of 16 objects from memory. According to the authors, frontal-lobe patients apparently lack a strategic approach to the task of free recall. Being strategic, in its turn, is related to the executive functions of planning goals and monitoring, so that tasks are successfully completed. “Forgetting to remember” (Hecaen & Albert, 1978, as cited in Squire, 1987, p. 236) is another characteristic symptom of PFC-lesion patients: they can verbalize a desire, such as to go out for a walk, but in a short period of time simply forget that desire. In unsuccessful progress from desire to action, there is impairment in executive function.

The pieces of evidence presented so far show that whereas medial temporal lesion studies (amnesia) relate this lateral-most area of the brain to general memory deficit, frontal cortex lesion studies, in their turn, relate this anterior-most area of the brain to processing impairments: the PFC is related to the executive processes of WM (Squire, 1987, p. 238). Before the advent of neuroimaging techniques, thus, clinical and behavioral studies already supplied evidence for the notion that the PFC subserves WM functioning.

4. Neuroimaging studies

This final section discusses studies and reviews of studies applying neuroimaging techniques (Positron Emission Tomography, PET, or functional Magnetic Resonance Imaging, fMRI) to tap into executive processes and working memory function in the brain. PET and fMRI provide real-time images of brain areas (regions-of-interest, or ROIs) following specific types of stimuli (reading, listening, for example). The following studies are not organized in chronological order, but rather to facilitate the discussion.

Carpenter, Just, and Reichle (2000)

The authors take the study of WM a step further in relation to lesion studies and frame neuroimaging data, with normals “in light of some classical questions about the organization of working memory and executive processes” (Carpenter, Just, & Reichle, 2000, p. 195). Three questions drive the study of WM and neuroimaging: (1) are discrete regions of the PFC dedicated to particular operations and, if so, what are they; (2) do PFC regions operate conjointly with posterior regions (multimodal networks); and (3) what is the conceptualization of WM capacity constraints in terms of information maintenance (temporal) and problem solving (task complexity) (Carpenter, Just, & Reichle, 2000, p. 195). Table 01 below summarizes the articles discussed in this section in relation to these questions:

Table 01: Neuroimaging and the study of WM

Questions to drive the study of WM and the brain (Carpenter, Just, & Reichle, 2000)			
	(1) Discrete regions	(2) Multimodal networks	(3) WM constraints
<i>D'Esposito, Postle, Ballard, and Lease (1999)</i>	Yes: DLPFC activations according to processing demands	N/A	Executive process tasks requiring both storage (temporal delay) and manipulation (complexity) recruited additional cortical tissue—increased WM demand, increased activations
<i>Allain, Etcharry-Bouyx, and Le Gall (2001)</i>	Yes: FC damage impaired executive processes (dual-tasks)	N/A	When processing and storage were re-

			quired, the FC-damaged patient's WM preferred processing over storage.
<i>Smith and Jonides, (1999)</i>	Yes: DLPFC activations when executive processes are required	Yes: Though the DLPFC was procured only in executive processes, it appears to orchestrate activation to other areas, such as the medial temporal region.	Same as D'Esposito, Postle, Ballard, and Lease (1999)
<i>Hernandez, Martinez and Kohnert (2000)</i>	Yes: DLPFC activation increase in language-switching tasks	Yes: Classical language areas where activated similarly in both languages, apparently orchestrated by the PFC.	Task-switching required additional recruitment of DLPFC tissue.

Carpenter, Just, and Reichle (2000) suggest some reconstruals based on neuroimaging. First, an alternative framework to localizationism emerges. In their own words, “each association cortical region has more than one function, and that the functions of distinct areas might overlap each other” (Carpenter, Just, & Reichle, 2000, p. 196): such as in D'Esposito's (1999) study, in which the same areas were involved in manipulation and maintenance, but manipulation originated greater activation in the DLPFC in comparison to maintenance (executive processing).

D'Esposito, Postle, Ballard, and Lease (1999)

The purpose of the study was to compare a working memory condition that required retention of information (maintenance) with a condition that, in addition to retention, required the transposition (manipulation) of information being held in working memory during a time delay. Applying the fMRI technique, the authors predicted that activation in the PFC would be significantly greater during the delay period in the manipulation rather than in the maintenance condition (D'Esposito, Postle, Ballard, & Lease, 1999, p. 68).

Results indicated that activations were observed in both the DLPFC and VLPFC during the delay period, in both the manipulation and maintenance tasks. Imaging data from subjects show the striking differences in activation between the two tasks, with activation comparatively greater in the manipulation task during the delay period (cue and instruction-probe) (D'Esposito, Postle, Ballard, & Lease 1999, p. 77). The authors concluded that, considering that the manipulation task bears resemblance to executive processes (for example, task management and monitoring), the PFC shows increased activation in comparison to a maintenance-only task (D'Esposito, Postle, Ballard, & Lease 1999, p. 69).

Focusing on the PFC itself, imaging indicated a difference in organization (dorsal/ventral) according to type of processing. Recruitment of cortical tissue changed due to the condition that required manipulation of the information in WM (increased processing demands, increased dorsal PFC activation). This specific finding offers opposition to theories of WM as a unitary system, that is, theories that do not postulate different WM subsystems (D'Esposito, Postle, Ballard, & Lease 1999, p. 83), and it attempts to answer the question presented at the beginning of the previous section and by Carpenter, Just, and Reichle (2000), that is, whether there is a subdivision of functions within the PFC and, if there is, what are its causes. At this point, it is important to note that there is an unclear reference to Baddeley (1992, as cited in D'Esposito, Postle, Ballard, & Lease 1999, p. 83) as the authors mention *unitary* theories of WM. It is clear that the multiple-component model by Baddeley is *non-unitary*. Baddeley and Logie (1999, p. 30) themselves clearly state that their "... model has an inherently *non-unitary* nature in that it comprises several specialized components, *which can be further fractionated if such fractionation is adequately justified empirically*" (emphasis added). Nonetheless, the initial hypothesis of greater PFC activation during the manipulation task was confirmed.

Allain, Etcharry-Bouyx, and Le Gall (2001)

Allain, Etcharry-Bouyx, and Le Gall describe a case study of patient R. C. who, after a motorcycle accident, was submitted to left frontal lobectomy (Allain, Etcharry-Bouyx, & Le Gall, 2001, p. 23). The authors assess the case based on the multiple component WM model (Baddeley & Hitch, 1974; Baddeley, 1992) to try and provide evidence for the existence of sub-components of WM; more specifically, the central executive.

R. C. is described as showing no problems in functioning of the articulatory component of WM, but dysfunction of the central executive in dual tasks (Allain, Etcharry-Bouyx, & Le Gall, 2001, p. 21). In this sense, the authors hypothesized that the damage to R. C.'s frontal cortex interfered with executive processes (for images of the frontal-lobe abscess in R. C., see Allain, Etcharry-Bouyx, & Le Gall, 2001, p. 24). After lobectomy, R. C. was perfectly able to perform everyday activities and showed none of the behavioral problems commonly associated with frontal lobe damage (perseveration, for example) (Allain, Etcharry-Bouyx, & Le Gall, 2001, p. 24). However, when performing dual-task WM tests (digit span together with onscreen object tracking), R. C. performed poorly, well below controls, and also showed a faster decay in performance as task difficulty increased (speed factor) (Allain, Etcharry-Bouyx, & Le Gall, 2001, p. 31).

Thus, when alternating between processing and storage, processing got the lion's share of WM resources. The central executive dysfunction affected storage capacity, "which could be interpreted as a functional adaptation to the attentional allocation disorder" (Allain, Etcharry-Bouyx, & Le Gall, 2001, p. 36).

Smith and Jonides (1999)

The authors reviewed PET and fMRI studies of the short-term and executive processes components of WM. With the multi-component model as theoretical support, they searched for evidence of separate buffers for verbal and spatial information in neuroimaging data. Studies were selected that subtracted activation from storage tasks from that from storage and processing tasks. Plotting the review results, Smith and Jonides found that dual tasks resulted in more activations (1999, p. 1659). The DLPFC was not activated in any of the verbal tasks requiring only storage. Medial temporal activations were identified in both storage and manipulation tasks, and the DLPFC was activated only in verbal tasks requiring executive processes of task management and selective attention (Smith & Jonides, 1999). The authors concluded that the executive processes activate the DLPFC. Thus, the review corroborates D'Esposito, Postle, Ballard, and Lease's (1999) finding of DLPFC activation with increasing processing demands, and findings from another, more recent, review (Fletcher & Henson, 2001) that correlates activations in frontal cortex with executive processes (p. 849).

Hernandez, Martinez, and Kohnert (2000)

Addressing the issue of bilinguals and language switching, Hernandez, Martinez, and Kohnert present an interesting question, which can be related to WM function and attentional control: "... how is it that bilinguals keep information from one language from consistently interfering with processing of information in the other language." (2000, p. 423). Enter the metaphor of the language switch. To address this question the authors applied the fMRI technique with a group of early bilinguals (EBL) – defined as bilinguals who *acquire* two languages, at the same time, from infancy (Paradis, 2003, p. 352) – naming pictures in Spanish and English. Two block designs were carried out for each language (being the cues "say" and "diga") and one mixed condition, alternating between languages. The regions-of-interest (ROIs) were the dorsolateral prefrontal cortex (DLPFC), the supramarginal gyrus, and the classical language areas: the inferior frontal gyrus (Broca's), and the superior temporal gyrus (Wernicke's) (Hernandez, Martinez, & Kohnert, 2000, p. 424).

Results showed significant activation only in the left DLPFC; with homologous bilateral activation in four of the six subjects. There were no significant differences in activation between languages (Hernandez, Martinez, & Kohnert, 2000, p. 427). In searching for the language switch, thus, the authors found that the DLPFC, among the ROIs studied, is significantly activated in language-switching tasks: apparently executive functions are a determinant factor in successful language switching. As seen above, other studies also related the DLPFC to manipulation tasks (D'Esposito, Postle, Ballard, & Lease, 1999; Carpenter, Just, & Reichle, 2000). It is not by accident, thus, that the DLPFC was importantly activated in switching between two languages.

Conclusion

Carpenter, Just, and Reichle (2000, p. 196) conclude that “multiple activated areas perform different functions but closely collaborate in a distributed processing system.” Activation spreading to multiple cortical sites can, for one, be related to task complexity. A good example can be found in Schneider’s (1999, p. 358) comparison of brain activation, during a learning study, in novice and practiced participants, in which the latter showed decreased brain activation in comparison to novice participants (called “executive dropout with practice”). In terms of computational load, in addition to the studies above, Just, Carpenter, Keller, Eddy, and Thulborn’s (1996) study on brain activation modulated by sentence comprehension also presents findings of increased activation following increased computational load.

Finally, though the PFC, according to neuroimaging findings thus far, appears to orchestrate executive functions, Carpenter, Just, and Reichle (2000, p. 195) and Smith and Jonides (1999) suggest a more dynamic and distributed view of the organization of working memory and executive functions. The clinical case presented by Allain, Etcharry-Bouyx, and Le Gall (2001) corroborates this suggestion in that RC did show normal performance in single-task stimuli and, to some degree, in dual-tasks.

Returning to the models and animal studies discussed in the beginning of this paper, neuroimaging techniques can corroborate and help inform our understanding of WM and brain organization of WM functions. This, in its turn, should help develop better empirically-based models of WM. For example, neuroimaging studies systematically continue to find evidence for subcomponents of WM spread over different brain regions. Fletcher and Henson (2001) in a review on neuroimaging and frontal lobe function, conclude that the fact that since fMRI studies include normal subjects (and not only brain-lesion patients), they

... can elucidate different stages of a memory process. For example, they can examine separately the encoding and retrieval of memories, a dissociation that cannot be made with confidence from anterograde memory deficits following frontal lobe lesions (Fletcher & Henson, 2001, p. 850).

Moreover, discrepancies that may arise from neuroimaging findings and neuropsychological data (Fletcher & Henson, 2001, p. 850) (as the neuroimaging techniques become increasingly fine-grained), and current cognitive models of WM may point to flaws in how we understand executive functioning, task performance, and storage, calling for improved modeling of human cognition and WM (Fletcher & Henson, 2001).

The segmentation of memory proves useful in its motto of dividing-and-conquering. Whereas there is interaction between processing and storage, and there are areas of the brain that operate conjointly in different functions, combining the understanding of the pieces, which are not trivial, as Squire (1987) cautioned, with imaging of the whole can help understand the implementation of memory and WM function in the brain.

In specific terms of function, neuroimaging studies with patients indicate that the PFC specializes in executive processes, with regional dissociation for type of processing (verbal, spatial, for example). Thus, they specifically corroborate Baddeley and Hitch's (1974) multiple component model of two slave systems for the processing of visual and spatial information. The model, since its early developments, has been consistently supported by clinical data.

The initial general discussion on the segmentation of memory and WM (models and ages), in addition to the final discussion on neuroimaging data point in the direction of some specialization in brain areas for WM components. However, all roads seem to lead to a more dynamic modeling of WM functions across the brain. Previous clinical and behavioral findings are not replaced by the contribution from neuroimaging; rather, the new techniques provide new insights into WM modeling and theories across different areas. Neuroimaging allows research to go beyond simple dissociation of memory components and thus to study the organization of its functions in the brain.

NOTE

- 1 Doutorando, programa de pós-graduação em inglês e literatura correspondente (PPGI), Universidade Federal de Santa Catarina. Orientado pela professora doutora Lêda Tomitch (UFSC) e co-orientado pelo professor doutor Fábio Alves (UFMG), Augusto Buchweitz tem sua pesquisa voltada para a área de leitura e cognição e memória de trabalho. Trabalhos recentes incluem participação e apresentação no Summer School of Cognitive Sciences sobre memória de trabalho, em 2003, em Sofia, Bulgária.

REFERENCES

- Allain, P. Etcharry-Bouyx, F., & Le Gall, D. (2001). A case study of selective impairment of the central executive component of working memory after a focal frontal lobe damage. *Brain and Cognition*, 45, 21-43.
- Baddeley, A.D. (1992). Working memory. *Science*, 255, 556-559
- Baddeley, A.D., & Hitch, G. (1974). Working memory. In G.H. Bower (Ed.), *The psychology of learning and motivation*, vol. 8 Academic Press.
- Baddeley, A.D., Logie, R.H. (1999). Working memory: the multiple-component model. In A. Miyake & P. Shah (Eds.) (1999). *Models of working memory: Mechanisms of active maintenance and executive control*. UK: CUP.

- Carpenter, P. A., Just, M. A., & Reichle, E. D. (2000). Working memory and executive function: evidence from neuroimaging. *Cognitive Neuroscience*. 195-99.
- Cowan, N. (1995). *Attention and memory: An integrated framework*. Oxford Psychology Series, No. 26. New York: Oxford University Press.
- D'Esposito, M.D., Postle, B.R., Ballard, D., & Lease, J. (1999). Maintenance versus manipulation of information held in working memory: An event-related fMRI study. *Brain and Cognition*. 41, 66-86.
- D'Esposito, M.D., Postle, B.R., & Rypma, B. (2000). Prefrontal cortical contributions to working memory: evidence from event-related fMRI studies. *Experimental Brain Research*. 133, 3-11.
- Daneman, M., & Carpenter, P.A. (1980). Individual differences in working memory and reading. *Journal of Verbal Learning and Verbal Behavior*. 19, 450-466.
- Daneman, M., & Green, I. (1986). Individual differences in comprehending and producing words in context. *Journal of Memory and Language*. 25, 1-18.
- Engle, R.W., Cantor, J., & Carullo, J.J., (1992). Individual differences in working memory and comprehension: A test of four hypotheses. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 9, 972-992.
- Ericsson, K.A. & Kintsch, W. (1995). Long-term working memory. *Psychological review*. 102 (2), 211-245.
- Fletcher, P.C., & Henson, R.N.A. (2001). Frontal lobes and human memory: Insights from functional neuroimaging. *Brain*. 124, 849-881.
- Hernandez, A.E., Martinez, A., & Kohnert, K. (2000). In search of the language switch: An fMRI study of picture naming in Spanish-English bilinguals. *Brain and Language*. 73, 421-431.
- Just, M.A., & Carpenter, P.A. (1992). A capacity theory of comprehension: Individual differences in working memory. *Psychological Review*. 99(1), 122-149.
- Just, M.A., Carpenter, P.A., Keller, T.A., Eddy, W.F., & Thulborn, K.R. (1996). Brain activation modulated by sentence comprehension. *Science*, 274, 114-116.
- Just, M. A., Newman, S. D., Keller, T. A., McEleney, A., & Carpenter, P. A. (2004). Imagery in sentence comprehension: An fMRI study. *NeuroImage*, 21, 112-124
- Kopelman, M.D. (2002). Disorders of Memory. *Brain*. 125, 2152-2190.
- Levy, R., & Goldman-Rakic, P. (2000). Segregation of working memory functions within the dorsolateral prefrontal cortex. *Experimental Brain Research*. 133, 23-32.

- Logie, R. H. (1996). The seven ages of working memory. In J.T.E. Richardson, R. W. Engle, L. Hasher, R.H. Logie, E.R. Stoltzfus, & R.T Zacks (Eds.) (1996). *Working memory and human cognition*. New York: OUP.
- Obler, L. & Gjerlow, K. (1999). *Language and the Brain*. Cambridge: CUP.
- Owen, A.D., Schneider, W.X., & Duncan, J. (2000). Executive control and the frontal lobe: current issues. *Experimental Brain Research*. 133, 1-2.
- Paradis, M. (2003). Differential use of cerebral mechanisms in bilinguals. In M.T. Banich & M. Mack (Eds.) (2003). *Mind, Brain, and Language: Multidisciplinary perspectives*. London: Lawrence Erlbaum.
- Richardson, J.T.E. (1996). Evolving concepts of working memory. In J.T.E. Richardson, R. W. Engle, L. Hasher, R.H. Logie, E.R. Stoltzfus, & R.T Zacks (Eds.) (1996). *Working memory and human cognition*. New York: OUP.
- Rodrigues, C. (2004). A dissolução da linguagem na demência do tipo Alzheimer. In C. Rodrigues & L.M.B. Tomitch (Eds.) (2004). *Linguagem e Cérebro Humano*. Porto Alegre: Artmed.
- Schneider, W. (1999). Working memory in a multilevel hybrid connectionist control architecture (CAP2). In A. Miyake & P. Shah (Eds.) (1999). *Models of working memory: Mechanisms of active maintenance and executive control*. UK: CUP.
- Smith, E.E. & Jonides, J. (1999). Storage and executive processes in the frontal lobes. *Science*. 283, 1657-1661.
- Squire, L. R. (1987). *Memory and Brain*. New York: OUP.
- Tomitch, L.M.B. (1995). *Reading: Text organization perception and working memory capacity*. (Unpublished doctoral dissertation). Florianópolis: UFSC.
- Tomitch, L.M.B. (1996). Individual differences in text organization perception and working memory capacity. *Revista da ANPOLL*. 2, 73-93.
- Tomitch, L.M. B. (1999-2000). Individual differences in working memory capacity and the recall of predicted elements in the text. *Lenguas Modernas*. 26-27, 31-51
- Turner, M.L., & Engle, R.W. (1989). Is working memory capacity task dependent? *Journal of Memory and Language*, 28, 127-154.