

5

Discussion

The results showed several important findings. The present discussion attempts to pinpoint the most important findings based on the data that were gathered. The major result of this entire work was confirmation that the prefrontal cortex is a center of neural activity during working memory tasks. Although this result was expected, the most important region of the prefrontal cortex was its left anterior portion. Brodmann area 10, more specifically the fronto-polar prefrontal cortex, is responsible for controlled attention and task switching. The prefrontal cortex has been suggested to account for the central executive (D'Esposito & Postle, 2015). The results of the present study also suggest core activation of the anterior portion of the PFC. Thus, attentional control and task switching appear to be dimensions of the central executive as suggested by Baddeley (2012).

Dove, Pollman, Shubert, Wiggins, and von Caron (2000) performed a task switching experiment and found that the fronto-polar prefrontal cortex, combined with the anterior insula and left intraparietal sulcus, was activated when the participants tried to keep in mind one task and execute another. In another experiment, Braver and Bongiolatti (2002) tested the involvement of the entire prefrontal cortex in working memory tasks. They found a triple dissociation of function within prefrontal cortex regions, including the anterior, dorsolateral, and orbitofrontal portions, and further

indicated that the anterior prefrontal cortex is selectively engaged by the requirement to monitor and integrate subgoals during working memory tasks. Koechlin, Basso, Pietrini, Panzer, and Grafman (1999) assigned secondary tasks to participants at the same time they executed a working memory task. They found that the fronto-polar prefrontal cortex selectively mediated the ability to hold subgoals in mind while exploring and processing secondary goals, a process that is generally required in planning and reasoning. Simple working memory tasks are believed to not require planning or any kind of thinking. In fact, Collette and Linden (2002) reviewed neuroimaging studies in an attempt to find a center for the central executive. They found that controlled attention and supervisory systems are actually very widespread in different neural networks, mainly in frontal and parietal regions. Thus, our results that showed activation of the anterior prefrontal cortex may be unrelated to the central executive because the participants were trying to think of strategies and alternatives to perform well on the diverse tasks.

We compared the results of overlapping activation between words>syllables and the three types of stimuli together. When the participants had to use an abstract phonological code, such as syllable phonemes and word semantics, they tended to use similar regions. Rottschy et al. (2012) reported similar results of an ALE meta-analysis using verbal, non-verbal, and visual working memory tasks. The only difference between the present results and the results of Rottschy et al. (2012) was significant activation of the anterior prefrontal cortex.

Another major aspect of the present results is the unexpected activation of the left fusiform nucleus. Lesions of this region can lead to color-phoneme synesthesia and visual hallucinations. However, the activated portion of the fusiform nucleus in the present study also corresponds to the visual word form area. The visual word form area

is an hypothesized functional region of the fusiform gyrus, and there is concrete evidence of a separation within this region. It seems to be related to identifying words from lower-level shape images prior to associations with phonology or semantics (i.e., shape-related identification; Dehaene & Cohen, 2011). According to these authors, the written language is relatively new in human evolution. Thus, this region unlikely developed as a result of natural selection related to word recognition. Nonetheless, the visual word form area of the fusiform gyrus may be specialized for certain types of shapes that occur naturally in the environment and are likely to resemble human handwriting. fMRI studies usually use written instructions and written stimuli during the tasks which can explain this area activation. Another possibility is participants may attempt to imagine a shape for the tones and sounds that reminded them of a letter to facilitate the execution of tonal working memory tasks (Baddeley, 2003a). Further studies are needed to test these possibilities.

Another overlapping region was Brodmann area 42 (the left anterior transverse temporal gyrus at the surface of the temporal lobe). This region functionally corresponds to the primary auditory association cortex, which executes two main functions in the brain: processing sensorial auditory information and creating associations between sounds and auditory memory (Petkov et al., 2004; Weinberger, 2007). One could argue that memory is spread throughout the entire brain, but evidence indicates a role for the auditory cortex as the first storage site for sound information. Primate studies showed that the representation of known sounds, such as a bird singing or a known song, is associated with activation of the primary auditory cortex together with the hippocampus, medial geniculate complex, and other parts of the thalamus (Kaas, Hacket, & Tramo, 1999). In humans, the anterior transverse temporal gyrus is linked to the recognition of familiar sounds (Petkov et al., 2004) and identification of

the human voice when voice-like sounds arrive in the cortex (Weinberger, 2007). Interestingly, primary visual areas are also responsible for storing visuospatial information (Mance & Vogel, 2013). The activation of this region is consistent with the models of both Baddeley, Allen, and Hitch (2011) and Cowan (1999, 2010). The results suggest the existence of sensory memory that is located within the neural circuit that is formed by the primary auditory cortex, which is responsible for storing this information until it is encoded. After encoding, this region stores represented information in the same way the activated portion of memory allows information to be manipulated. Petkov et al. (2004) suggested that the primary auditory association cortex plays an important role in auditory attention. He argued that automatic attention should be activated in the same region where it is stored for faster responses to the environment. Evidence suggests that individuals with any kind of lesion of the primary auditory cortex exhibit impairments in automatic auditory attention, whereas voluntary auditory attention and visual attention, regardless of modality, remain intact. Therefore, auditory inhibition could be the opposite of automatic attention, which would go against Diamond's (2013) claim of an independent special feature of executive functions called inhibitory control.

Our main results raise two different hypothesis: (1) Cowan's (1999) theoretical model makes more sense than the others due to significant differences between types of stimulus and (2) the complexity of tone tasks requires planning and reasoning for execution, whereas syllable and word tasks require the further integration of information.

Both hypotheses may likely be true. Cowan suggested that encoding is the ability of the human mind to create a code to mentally represent environmental information (Cowan, 2010), and codes can be divided into two categories: abstract and sensorial. If

we categorize our results based on this classification, then tones would probably require sensorial codes to be represented, whereas syllables and words would require abstract codes, such as phonological codes or semantic codes, to be mentally represented. Our results suggest minor overlap between tones and other types of stimuli, whereas syllables and words show significantly more regions of overlap. Because of the different types of encoding, the neural network of phonological working memory can be divided into abstract and sensorial codes.

Humans tend to use such strategies as naming and chunking to perform better in working memory tasks (Cowan, 1999; Engle, Kane, & Tuholski, 1999). In olfactory tasks, the performance of participants in a 2-back span task was 20% higher when participants were able to name the odor when compared to unnamed odors (Jönsson, Moller, & Olsson, 2011). Whenever we deal with a new task, we tend to constantly plan and try to execute the task accordingly. The familiarity of sounds may lead participants to try to name or chunk similar sounds to facilitate encoding. We did not see activation in Broca's or Wernicke's areas. These areas are associated with language, and sounds do not seem to require any kind of spoken language to be stored. While the participants were executing auditory tasks with merely sensorial stimuli, they may have attempted to plan and actively execute the task in such a way that they could perform better than chance while not consciously being aware that they were doing this. If so, then Diamond's (2013) proposition of the inseparability of higher cognitive functions even during simpler tasks appears to be true. Diamond suggested that executive functions indeed have pure measures, but they tend to work simultaneously. Activation of the fronto-polar prefrontal cortex may be evidence that participants attempt to use higher cognitive functions to deal with simpler working memory tasks.

The main results of the present study appear to support Cowan's (1999, 2010) theoretical model, with evidence of the existence of sensory memory and significant differences between the neural bases of different types of encoding within the same modality (i.e., phonological working memory). Nonetheless, we did not find any evidence of separation between voluntary and automatic attention, despite some suggestions of such in the literature (e.g., Petkov et al., 2004; Weinberger, 2007). We cannot assume that mere activation of the primary auditory cortex is attributable to both attention and memory. Additionally, no activation of regions that are responsible for voluntary attention was seen, which does not corroborate Cowan's model. The strongest claim in favor of Cowan's model is the difference between types of stimuli and thus the difference between encoding processes.

Evidence of the model of Baddeley, Allen, and Hitch (2011) was almost nonexistent. First, the overlapping regions were minor, suggesting significant differences between core phonological working memory neural networks. Second, no evidence was found in the literature regarding the role of the anterior prefrontal cortex as the central executive. We cannot say that fronto-polar prefrontal cortex activation is caused by attentional control. The only support for this model is activation of the primary auditory association cortex, which is likely attributable to auditory storage. However, if we look at words>syllables contrast (while excluding tones from the analysis), then we can see the core network of working memory as Baddeley (2000) suggested. One possibility is that other neuroimaging meta-analyses neglected tone-and sound-related working memory tasks because they do not corroborate the model of Baddeley, Allen, and Hitch (2011). For example, Rottschy et al. (2012) reported results from both visual and auditory working memory imaging studies. They presented 113 articles, but only two of these used tones. They also did not utilize any algorithm to

correct possible bias. Our results of the words>syllables analysis were very similar to those reported by Rottshy et al. (2012). However, when we include tonal working memory using the new ALE algorithm (Eickhoff et al., 2009), which attempts to reduce bias, we found completely different results. Despite the results of the present study, Baddeley's model appears to be the most adequate for explaining behavioral data (Allen, Baddeley, & Hitch, 2014).

Working memory is argued to be one of the most important cognitive functions of humans. It serves as a foundation for cognitive flexibility, language, writing, logical thinking, abstract thinking, planning, and learning (Diamond, 2013). The present results suggest that working memory is indeed a complex cognitive function that is based on the architecture of our contemporary brain. The most important conclusion that we can make is that the prefrontal cortex is responsible for the central executive as suggested in the literature, but there are significant differences between semantic, phonological, and auditory encoding in the brain that can be explained by different storage sites, depending on the code type. These storage sites appear to be both sensory- and code-dependent. One interesting hypothesis is that primary cortices can also account for long-term memory, as suggested by Cowan (2010) and D'Esposito and Postle (2015).

5.1

Limitations and future directions

The present study has limitations but also leads to future directions in the study of working memory. Two main limitations should be highlighted. First, although Cowan's framework explains a little better the found results, working memory is still a psychological construct and theoretical model that aims to explain behavioral

performance. No evidence suggests that working memory is a scientific law, such as gravity or relativity. Different tasks tap into different neural networks during working memory tasks. All fMRI meta-analyses seek to discover intersections between regions of activation in working memory tasks, but the neural networks are clearly distinct and strongly rely on the type of task. Thus, it is possible that none of these theoretical models can fully explain or prove the existence of working memory.

Second, the methodology of the present study has limitations. The ALE method of meta-analysis utilizes only significant activation results from other studies. This means that possible differences in voxels that are not significantly activated are ignored. For example, if a voxel does not present a significant difference in particular studies, but instead only presents marginal significance, an author who performs a meta-analysis may reanalyze those nonsignificant results such that statistical significance becomes evident. In ALE meta-analyses, nonsignificant results are not considered because the database consists only of articles that present significant differences in contrast. Thus, the present study was limited by relying solely on significant results.

Future studies can fill the gaps that remain. One interesting line of investigation would be to perform meta-analyses that include other sensorial inputs, such as visual, olfactory, and tactile. fMRI meta-analyses can also utilize raw data by asking the authors of previous studies to share their data. This would allow previously nonsignificant results to be further analyzed. Another frontier of working memory studies would be to develop theoretical and computational models to explain neuroscientific results rather than solely behavioral results.