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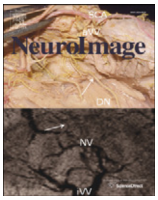

Working memory load modulates the auditory "What" and "Where" neural networks

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ABSTRACT

Working memory for sound identity (What) and sound location (Where) has been associated with increased neural activity in ventral and dorsal brain regions, respectively. To further ascertain this domain specificity, we measured fMRI signals during an *n*-back ($n = 1, 2$) working memory task for sound identity or location, where stimuli selected randomly from three semantic categories (human, animal, and music) were presented at three possible virtual locations. Accuracy and reaction times were comparable in both "What" and "Where" tasks, albeit worse for the 2-back than for the 1-back condition. The analysis of fMRI data revealed greater activity in ventral and dorsal brain regions during sound identity and sound location, respectively. More importantly, there was an interaction between task and working memory load in the inferior parietal lobule (IPL). Within the right IPL, there were two sub-regions modulated differentially by working memory load: an anterior ventromedial region modulated by location load and a posterior dorsolateral region modulated by category load. These specific changes in neural activity as a function of working memory load reveal domain-specificity within the parietal cortex.

Introduction

Working memory refers to the ability to temporarily maintain and manipulate a limited amount of information for goal-directed action (Baddeley, 1986). Neuroimaging studies have consistently reported activation in the prefrontal cortex and the parietal lobule in a variety of visual working memory tasks (e.g., Cabeza and Nyberg, 2000; D'Esposito et al., 2000; Mottaghy et al., 2003; Smith and Jonides, 1998). For instance, Todd and Marois (2004) found load-related changes in the posterior parietal cortex during a visual short-term memory task. Recently, Harrison et al. (2010) further manipulated the amount of object ("What") and spatial ("Where") information of the task and found increased neural activity in the intraparietal sulcus only when increasing the spatial ("Where") memory load, indicating domain specificity in the dorsal pathway. Domain specificity for working memory load was also evident in visual working memory of color and shape (Kawasaki et al., 2008), face (Rissman et al., 2008; Druzgal and D'Esposito, 2001), and kinesthetic information (Fiehler et al., 2008). Using visuospatial *n*-back tasks, Carlson et al. (1998) showed that neural activity in the dorsal pathway, including the medial frontal gyrus, the superior frontal sulcus and the intraparietal sulcus, was dependent on working memory load. Jansma et al. (2000) found that performance of a spatial *n*-back task correlated with neural activity in the anterior cingulate and the right parietal cortex. Altogether, neuroimaging studies of visual working memory have provided strong support for domain specificity, particularly in the dorsal pathway. However, the direct evidence supporting such domain specificity in auditory working memory remains scarce.

A few behavioral studies on auditory processing suggest differential memory systems for sound content and sound localization. For example, Clarke et al. (1998) found that short-term memory for sound content was more sensitive to interference during an auditory recognition task than during an auditory spatial memory task whereas visual interference tasks reduced memory for sound location but not for sound content. In another study, Anourova et al. (1999) manipulated the demand of working memory in auditory spatial and non-spatial tasks by incorporating 1-back and 2-back tasks with and without location or pitch interference. They found that, in the 1-back task, location but not pitch interference impaired working memory for location whereas pitch but not location interference hindered working memory for pitch. In the 2-back task, however, the performance of both the location and the pitch tasks was not disrupted by the interference, indicating that there might be a memory load-dependent neural network responsible for working memory of auditory spatial and non-spatial information. Nevertheless, this memory load-dependent network has never been explicitly tested.

Prior neuroimaging studies (e.g., Alain et al., 2001; Arnott et al., 2004; Kaiser and Lutzenberger, 2001; Maeder et al., 2001) and neuropsychological studies on patients with localized brain damage (e.g., Clarke and Thiran, 2004) suggest that processing sound identity and sound location might be mediated by ventral ("What") and dorsal

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("Where") cortical information streams, respectively. Using a delayed matched-to-sample task, Arnott et al. (2005) found that sound pattern and sound location activated brain regions in the auditory "What" and "Where" pathways, respectively, as well as a common set of brain areas in the frontal and parietal regions irrespective of domain. Kaiser et al. (2003) employing magnetoencephalogram recordings found that memorization of auditory patterns activated the auditory ventral stream comprising the frontotemporal and the prefrontal cortices. In a study focusing on audiospatial working memory tasks, Lutzenberger et al. (2002) showed that working memory of auditory spatial information was associated with synchronization of neural networks in the parietal cortex involving the auditory dorsal stream as well as enhanced activity in neural networks serving the frontal executive systems and the representation of audiospatial information. Rämä et al. (2004) further demonstrated that working memory of voice identity and location modulated activity in the ventral and dorsal auditory pathways, respectively. This domain specificity for remembering sound identity and sound location remained even after controlling for response-related processes and goal-directed action (Alain et al., 2008). These findings suggest domain specificity for auditory working memory. However, as these studies did not manipulate working memory load, it remains unclear whether differences in "What" and "Where" memory tasks are due to memory *per se* or some other processes like perception or attention.

To our knowledge, the effects of auditory working memory load have been examined for sound location (e.g. Alain et al., 2010; Martinkauppi, 2000) or sound identity only (e.g., Kirschen et al., 2005), making it difficult to determine whether changes of neural activity as a function of working memory load reflect domain generality or domain specificity. The present study aimed to investigate the effect of working memory load on the auditory "What" and "Where" neural networks. Similar to Alain et al.'s (2008) study, the present study adopted a mixed-block and event-related design so that the sustained neural activity was analyzed with minimal contamination by transient response-related activity associated with target detection. The novelty of this study was the manipulation of working memory load for both category and location of sound objects in an fMRI paradigm. This design allowed us to delineate the functional significance of the ventral and dorsal pathways with regard to auditory working memory load and to unveil particular brain regions, if any, that might be modulated by the working memory load. We used an *n*-back task (1-back, 2-back) in which the same stimuli were used during working memory for sound identity and during working memory for sound location. We sought to determine whether variation in working memory load for sound identity and sound location would modulate specific regions in the dual pathway. We anticipated domain specific activities in the parietal cortex to correlate with performance during working memory for sound location. We also sought to examine the pattern of neural activation induced by working memory load of sound category and sound location using a conjunction analysis (conjoining working memory load of sound category with working memory load of sound location). We expected an increase in neural activity in the ventral and dorsal pathways corresponding to an increase in working memory load for sound category and sound location, respectively.

Methods

Participants

Sixteen right-handed young adults aged between 18 and 30 years (M = 25.19, SD = 5.13 years, nine women) gave written informed consent and participated in the study. All participants had pure tone thresholds below 30 dB HL for octave frequencies from 250 to 8000 Hz. None of the participants had a history of neurological or psychological illness and were not taking medication at the time of the experiment. The study was approved by the Research Ethics Board of the Toronto Academic Health Sciences Network and the University of Toronto and Baycrest Hospital Human Subject Review Committees.

Stimuli and task

Stimuli consisted of meaningful sounds that were unambiguously allocated to one of the following three categories: human (e.g., laughing, crying), musical instrument (e.g., piano, flute), and sounds that were neither human nor musical instrument (e.g., flushing, splashing). There were 40 different exemplars for each sound category. Onsets and offsets of the sounds were shaped by two halves of an 8-ms Kaiser window, respectively, such that all sounds had durations of 1005 ms. Digital stimuli were converted to analogue using an RP2 converter with a 16-bit resolution and 12.21 kHz sampling rate (Tucker-Davis Technology, Gainesville, FL). They were presented at three possible azimuth locations relative to straight ahead (i.e., +90°, 0°, −90°) using head-related transfer functions that replicate the acoustic effects of the head and ears of an average listener (Wenzel et al., 1993). During fMRI scanning, the stimuli were delivered to the participants at about 88 dB sound pressure level (root mean square) by means of circumaural, fMRI-compatible headphones (Avotec, Jensen Beach, FL), acoustically padded to suppress scanner noise by 25 dB.

The experiment comprised four different conditions that resulted from the orthogonal combination of task (Category vs. Location) and working memory load (1-back vs. 2-back). There were a total of six fMRI runs each containing six blocks of 20 trials including on average five target stimuli (i.e., number of targets ranging from four to six stimuli per block). Prior to a block of trials, participants were presented with a visual prompt (e.g., Category 1-back) on a screen indicating the target type. The prompt appeared 10 s prior to the start of the block and remained on until the start of the first stimulus. Participants were asked to press a button as quickly as possible using their right index finger when the target appeared. For example, when the phrase "Category 1-back" was presented, participants were required to press a button whenever a sound from the same semantic category was repeated. Participants' responses were registered using an fMRI-compatible response pad (Lightwave Technologies, Surrey, SC, Canada). In the category task, participants responded whenever a semantic category was repeated, regardless of changes or repetition in sound location. In the location task, participants responded whenever a stimulus occurred at the same location, regardless of changes or repetition of sound category. For both the 1-back and the 2-back tasks, most of the targets (on average 90%) were randomly distributed within the blocks such that at least one non-target appeared between targets (i.e., number of non-targets between targets ranging from one to six stimuli for the 1-back task and one to ten stimuli for the 2-back task). Occasionally two consecutive targets (on average 10%) were embedded in some of the blocks. For example in the 2-back category task, there were situations in which stimuli from two of the three categories were interleaved in four trials so that participants were expected to respond to two consecutive targets. In the 1-back task, consecutive targets occurred when three consecutive stimuli belonging to the same sound category during the category task or the same sound location during the location task were presented. Aside from the prompt, the set of stimuli used were identical in both the category and the location tasks. Moreover, the presentation of the three sound locations and the three sound categories were balanced across tasks, i.e., there were same number of sound stimuli coming from each of the three locations during the category task and same number of sound stimuli for each of the three sound categories during the location task. This ensured that participants were not biased towards any of the three locations during the category task or any of the three categories during the location task. Each block lasted 40 s, with a 2 s inter-