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The retention of simultaneous tones in auditory short-term memory: A magnetoencephalography study ☆

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ABSTRACT

We used magnetoencephalography (MEG) to localize brain activity related to the retention of tones differing in pitch. Participants retained one or two simultaneously presented tones. After a two second interval a test tone was presented and the task was to determine if that tone was in memory. We focused on brain activity during the retention interval that increased as the number of sounds retained in auditory short-term memory (ASTM) increased. Source analyses revealed that the superior temporal gyrus in both hemispheres is involved in ASTM. In the right hemisphere, the inferior temporal gyrus, the inferior frontal gyrus, and parietal structures also play a role. Our method provides good spatial and temporal resolution for investigating neuronal correlates of ASTM and, as it is the first MEG study using a memory load manipulation without using sequences of tones, it allowed us to isolate brain regions that most likely reflect the simple retention of tones.

Introduction

The ability to retain acoustic items in memory for a short period of time after they are gone from the senses is a key capacity for the integration of acoustic information over time. It is crucial for participating in spoken language and equally important in the non-verbal domain, such as enjoying the aesthetic of a piece of music. In this study, we focused on the retention of non-verbal acoustic items to assess fundamental aspects of auditory short-term memory (ASTM). We aimed to isolate brain areas that are engaged in ASTM with a design that minimized the number of cognitive systems engaged and therefore targeted the retention of pure tones differing in pitch.

Previous studies have suggested that certain brain structures are related to memory processes during the retention of pitch. In a positron emission tomography study (PET) (Zatorre et al., 1994), participants listened to melodies of eight tones and had either to indicate if the first tone had a higher or lower pitch than the second (low memory load), or if the first tone had a higher or lower pitch than the last (high memory load). Thus, in the high memory load condition, participants had to maintain one tone in ASTM for about 3 s (but also to ignore intervening tones). Compared to a passive listening condition, the right inferior frontal lobe was activated in the low memory load condition and the right inferior frontal lobe, the right temporal lobe, the parietal and the insular cortex were activated in the high memory load condition. The authors concluded that the frontal and temporal cortices in the right hemisphere are part of a network that underpins the retention of pitch information in short-term memory.

A more recent study (Gaab et al., 2003) used a similar paradigm. Brain activity was assessed with functional magnetic resonance imaging (fMRI) that used sparse temporal sampling to avoid contamination by scanner noise. Participants listened to a sequence that contained six or seven tones. They compared the first tone of the sequence to the last or second-to-last tone, which was indicated by instruction after the sequence. The authors observed that the superior temporal gyrus, the supramarginal gyrus, frontal regions, parietal regions and the cerebellum were engaged in the retention of tones differing in pitch. Interestingly, they found that the left inferior frontal gyrus was activated whereas Zatorre et al. (1994) found its right hemisphere homolog active in their high memory load condition. Importantly, Gaab and colleagues found that activity in the supramarginal gyrus (especially in the left hemisphere) and the dorsolateral cerebellum was most strongly correlated with individual performance in the memory task.

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In another fMRI study (Koelsch et al., 2009), participants were asked to remember either the pitch or the vowel of sung syllables, with or without simultaneous singing of a well-known song (suppression conditions). The authors argue that a network of activity in premotor cortices, the planum temporale, the inferior parietal lobe, the anterior insula, sub-cortical structures, and the cerebellum was involved in the retention of acoustic items. They concluded that similar structures are involved in the retention of pitch and speech information (see also Schulze et al., 2011a, 2011b, for differences between musicians and non-musicians). However, it is not clear whether participants encoded and retained either pitch or vowel identity rather than treating the presented sounds as a unit and encoding both dimensions simultaneously.

Another fMRI study (Schulze et al., 2011a) addressed mnemonic strategies that could be used when retaining sequences of tones. Musicians and non-musicians retained sequences in ASTM that contained tones of the same musical scale or tones without a tonal relation to each other. Contrasting these two populations can be especially interesting because musicians might use different or additional mnemonic strategies compared to musically untrained participants. The behavioral data suggested that musicians made use of their special knowledge for sequences containing tones of the same scale as their performance was better compared to the other conditions. This sub-group of participants with high expertise showed increased brain activity in the right superior frontal gyrus, the right inferior precentral gyrus, the right premotor cortex, and the left intraparietal sulcus for the tonal sequences. The authors argue that these brain areas might be especially important for strategies that make use of the melodic structure of sound sequences.

A recent study using magnetoencephalography (MEG, Grimault et al., submitted for publication) localized brain areas that contribute to the retention of tones with a paradigm adapted from event-related potential (ERP) experiments (Guimond et al., 2011; Lefebvre et al., submitted for publication; Nolden et al., submitted for publication). Participants listened to a sequence of tones that they had to compare to another sequence of tones after a retention interval of 2000 ms. To isolate brain activity that was related to the retention of acoustic material specifically, the authors used the following strategies: First, the stimuli were designed to engage auditory short-term memory with as few other cognitive systems as possible. With pure tones differing in pitch, it is very unlikely that these stimuli would engage any verbal process. Further, to avoid memory strategies related to learned melodic contours, the octave was subdivided into 7 equidistant tones and therefore did not correspond to those of any musical scales. Second, the number of tones that had to be retained, and consequently the memory load, was varied. Third, the authors focused on brain activity during the retention period, thereby avoiding activity related to perception, encoding, retrieval, comparison, decision-making, or response selection. Finally, brain activity was correlated to the individual memory capacity of the participants. Participants with a high memory capacity should show increasing brain activity as memory load increases. Participants with a lower brain activity should reach their ASTM capacity limits earlier and, from this point on, brain activity should plateau, even when the set of items to memorize increases. Grimault et al. (submitted for publication) found that activity in the left superior/middle temporal gyrus, the left pre/post central gyrus, the left middle frontal gyrus, the right inferior frontal gyrus, and the right middle frontal gyrus showed a positive correlation with individual ASTM capacity.

Taken together, there are many indications that temporal, frontal, and parietal areas are involved in the retention of pitch information. First, PET and fMRI studies found brain activity in these areas during the retention of tones. The cerebellum is also often activated, although its functional significance for ASTM remains unclear. Second, a MEG study that correlated individual memory capacity with brain activity also points to temporal and frontal areas (Grimault et al., submitted for publication). Even though activity in some brain areas has been repeatedly shown to be a correlate of ASTM, it is still unclear whether and how the retention of pitch in ASTM is lateralized, as there are studies pointing to either hemisphere (Gaab et al., 2003; Zatorre et al., 1994).

Recent models of short-term memory (Cowan, 2008; D'Esposito, 2007; D'Esposito et al., 2000; Goldman-Rakic, 1987; Petrides, 1991, 2005; Postle, 2006; Postle et al., 1999; Ruchkin et al., 2003) propose that the active retention of items makes use of brain areas that are involved in the perception of these items. These models can adequately explain why various studies on ASTM revealed that secondary auditory cortices appear to contribute to ASTM. In these brain areas, representations of the sounds arising from perceptual processes would then be held active during retention. Studies on ASTM have also found activity in the frontal lobe, for which a variety of mnemonic functions have been ascribed. Some models propose that activity in the frontal lobes may reflect executive control over the parts of the brain where the to-be-retained items are represented (e.g., auditory cortex). Areas in the frontal cortex also seem to play a role for memory strategies. During rehearsal of verbal material, the ventrolateral frontal cortex has shown increased activity (Awh et al., 1996; Paulesu et al., 1993) and other frontal areas have been associated with rehearsal that was not exclusively verbal (Courtney et al., 1998; Postle and D'Esposito, 2000). Some authors further argue that the dorsolateral frontal cortex was involved in chunking strategies (Bor et al., 2003; Rypma et al., 2002).

The role of the parietal cortex in ASTM is still unclear and the few studies on the retention of pitch information have not been decisive. Zatorre et al. (1994) found activation in the superior parietal lobe and Koelsch et al. (2009) found activation in the inferior parietal lobe during ASTM tasks. Gaab et al. (2003) reported a correlation between individual memory performance and activation in the inferior parietal lobe, while Schulze et al. (2011a) found that the intraparietal sulcus is more active in the retention of tonal than atonal melodies in musicians. Interestingly, parietal structures have also been discussed as part of a network involved in the retention of visual items (Robitaille et al., 2009, 2010; Todd and Marois, 2004, 2005) and seem to be sensitive to increased memory load, particularly for the retention of spatial locations (Harrison et al., 2010; Sereno et al., 2001). It might thus be that the parietal lobe contributes to processes related to short-term memory in general without being modality-specific, in which case the intraparietal sulcus might have a certain role regarding the relation between the retained items. Another reason for the observation of parietal activity in studies of ASTM could be that participants had to deploy a certain amount of attention to accomplish the task, and parietal structures, in particular the right superior parietal lobe, have been discussed as part of a modality-independent network for attention (Belin et al., 1998; Farah et al., 1989; Pardo et al., 1991; Paus et al., 1997; Zatorre et al., 1999).

It seems, therefore, in the light of recent data and theories, that some of the various areas found to participate in ASTM can be connected to core processes in ASTM, while the functional meaning of other areas remains ambiguous and/or speculative. The activity of keeping sound representations activated, simple retention, is a fundamental mechanism of ASTM. We conjecture that retention requires effortful mnemonic activity and goes beyond sensory memory (Atkinson and Shiffrin, 1968; Neisser, 1967). In particular, retention-specific brain activity is postulated to increase with the number of items held in memory, at least in a number of structures participating in retention, a hypothesis that has been recently confirmed in ERP studies from our laboratory (Guimond et al., 2011; Lefebvre et al., submitted for publication; Nolden et al., submitted for publication).

Many previous imaging studies on ASTM are still ambiguous about the neuronal correlates of retention, as other memory-related processes might have taken place in parallel and might have influenced the results. For example, the use of verbal material might have engaged brain processes related language, the retention of sequences