



Brain activity is related to individual differences in the number of items stored in auditory short-term memory for pitch: Evidence from magnetoencephalography



Stephan Grimault^{a,b,c,*}, Sophie Nolden^{a,b}, Christine Lefebvre^{a,b,f}, François Vachon^{a,b,d}, Krista Hyde^{b,e}, Isabelle Peretz^{a,b}, Robert Zatorre^{b,e}, Nicolas Robitaille^{a,b}, Pierre Jolicoeur^{a,b,f}

^a CERNEC, Université de Montréal, Québec, Canada

^b BRAMS, International Laboratory for Brain Music and Sounds, Université de Montréal, Québec, Canada

^c Centre National de la Recherche Scientifique (CNRS), France

^d École de psychologie, Université Laval, Québec, Canada

^e Montreal Neurological Institute, McGill University, Québec, Canada

^f Centre de recherche de l'institut universitaire de gériatrie de Montréal (CRIUGM), Québec, Canada

ARTICLE INFO

Article history:

Accepted 8 March 2014

Available online 15 March 2014

Keywords:

Auditory
Short-term memory
Working memory
Pitch
MEG

ABSTRACT

We used magnetoencephalography (MEG) to examine brain activity related to the maintenance of non-verbal pitch information in auditory short-term memory (ASTM). We focused on brain activity that increased with the number of items effectively held in memory by the participants during the retention interval of an auditory memory task. We used very simple acoustic materials (i.e., pure tones that varied in pitch) that minimized activation from non-ASTM related systems. MEG revealed neural activity in frontal, temporal, and parietal cortices that increased with a greater number of items effectively held in memory by the participants during the maintenance of pitch representations in ASTM. The present results reinforce the functional role of frontal and temporal cortices in the retention of pitch information in ASTM. This is the first MEG study to provide both fine spatial localization and temporal resolution on the neural mechanisms of non-verbal ASTM for pitch in relation to individual differences in the capacity of ASTM. This research contributes to a comprehensive understanding of the mechanisms mediating the representation and maintenance of basic non-verbal auditory features in the human brain.

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Introduction

Short-term memory (STM) is a central cognitive function that provides an interface between perception, action, and long-term memory. Auditory STM (ASTM) in particular is an important building block for any function that requires the integration of sounds over time, such as the comprehension of spoken sentences, learning a new language, or the appreciation of music. Various models of STM have been proposed (for a review, see D'Esposito, 2007). Early models of STM proposed that specialized subsystems maintain information from different sensory inputs (e.g., Brooks, 1968) and that a central control system coordinates the flow of information through the system (Atkinson & Shiffrin, 1968). Baddeley (1986, 2001) and Baddeley and Hitch (1974) proposed that there are three main components involved in STM: 1) a “phonological loop,” that involves an auditory memory store and articulatory rehearsal process, 2) a “visuospatial sketchpad,” that processes visual-spatial

information and, 3) a “central executive,” that manages and manipulates the information. However, Baddeley's model has several limitations. For example, this model lacks detail with regard to the retention of nonverbal acoustic material, and it may require an ever-expanding number of specialized buffers for different types of information.

More recent models of STM (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) do not rely on separate storage buffers, but rather propose that active maintenance or storage of task-relevant representations occurs in the same brain areas that support the perceptual representation of information. This type of neural system would be more flexible and efficient relative to a system that transfers information back and forth between dedicated storage buffers. Thus, the short-term retention of basic acoustic dimensions, such as pitch, would be reflected, in part, by the prolonged activation of the brain regions that support the processing of pitch. This would be distinct from those processes involved in the memory for attributes of objects perceived through other senses (e.g., for color).

The main goal of the present study was to localize the functional neural correlates of basic non-verbal ASTM for pitch. Most previous

* Corresponding author at: BRAMS – Pavillon 1420 Mont Royal | FAS – Département de psychologie|CP 6128, succ. Centre Ville | Montréal (QC) H3C 3J7, Canada.
E-mail address: stgrimault@gmail.com (S. Grimault).

brain imaging studies have explored ASTM in the context of speech, while relatively fewer studies have specifically investigated non-verbal ASTM for pitch. For example, Zatorre et al. (1994) used positron emission tomography (PET) to investigate the neural correlates of ASTM in the context of melodic perception and memory for pitch. In one task, the pitch of two consecutive notes was compared, and in another task, the pitch of the first and last notes of a six-note sequence was compared. The consecutive-note condition resulted in right frontal lobe activation, whereas the first versus last-note condition implicated various regions including the right frontal and temporal cortices as well as parietal and insular cortices. Zatorre et al. (1994) concluded that pitch comparisons involve a neural network that includes the right prefrontal cortex, but that the active retention of pitch involves the interaction of right temporal and frontal cortices. More recently, Gaab et al. (2003) investigated melodic pitch memory using functional MRI (fMRI). Participants were scanned while they listened to short melodies in which they had to judge whether the last or second to last tone was the same or different as the first tone. As in the Zatorre et al. (1994) study, Gaab et al. (2003) found activity in superior temporal, frontal, and parietal cortices, in response to their pitch memory task. The last authors also found activity in the supramarginal gyrus and the cerebellum. The pitch memory task used in Gaab et al.'s (2003) study above relied more on the left hemisphere versus right hemisphere regions. In an fMRI study, Koelsch et al. (2009) investigated the functional architecture of ASTM for both non-verbal and verbal auditory information during rehearsal and articulatory suppression. Participants were presented with strings of four sung syllables and were asked to recall either the pitches (non-verbal) or syllables (verbal). The rehearsal of both verbal and non-verbal materials implicated a brain network including the premotor cortex, the planum temporale, the inferior parietal lobe, the anterior insula, subcortical structures, and the cerebellum. Overall, the results suggested that the rehearsal and storage of both verbal and non-verbal information rely on largely overlapping neuronal networks, in particular in sensorimotor-related brain areas. The Koelsch et al. (2009) study showed mostly bilateral activations in all tasks. Although Koelsch et al. (2009) used task instructions that asked for recall of only pitch or syllables, it is not entirely clear how the experimental procedure would preclude retention of all attributes in all tasks, which complicates the interpretation of the results.

Taken together, the above studies point towards a network of brain regions involved in non-verbal ASTM for pitch, particularly in frontal and temporal cortices. However, none of the previous studies reviewed above investigated which brain areas might respond to parametrically increasing memory load or relate to individual differences in the capacity of ASTM. This is the main objective of the present study. We recently conducted a series of event-related potential (ERP) studies in our laboratory to investigate the time-course of neural activity on an ASTM task in which the memory load was parametrically varied (Guimond et al., 2011; Lefebvre et al., 2013; Nolden et al., 2013). Recently, our approach, described in Grimault et al. (2009a) was also adopted by Albouy et al. (2013). Our experimental protocol was based on three key principles allowing us to focus on the maintenance of objects in ASTM: 1) to isolate brain activity that varies with memory load while keeping other aspects of processing constant; 2) to focus on brain activity during the period of retention in a memory task; and 3) to use stimuli that would engage minimally cognitive or perceptual systems other than those directly involved in ASTM. The ERP results revealed fronto-central brain activity reflected in a sustained anterior negativity during the retention phase of the ASTM task that increased in amplitude (became more negative) with increasing memory load. These ERP studies demonstrated the viability of our ASTM paradigm, and provided valuable information on the time course of functional brain activity related to ASTM. However, the ERP technique did not allow us to localize precisely where in the brain this activity takes place.

In the present study, we used magnetoencephalography (MEG) to localize the brain areas involved in the retention phase of non-verbal

ASTM for pitch. MEG provides a much finer spatial resolution relative to the ERP technique, and also has a much finer time resolution relative to other imaging techniques such as functional MRI. Thus, we were able to examine the time course of ASTM-related brain activity in concert with brain localization. A similar approach using MEG was shown to be very effective in studies of visual-STM conducted in our laboratory (Grimault et al., 2009a; Robitaille et al., 2009, 2010). To our knowledge, the present study is the first to use MEG source-localization analysis to investigate the neural correlates of non-verbal ASTM of pitch as a function of parametrically increasing memory load. Based on previous brain imaging findings on non-verbal ASTM (e.g. Guimond et al., 2011; Koelsch et al., 2009), we expected to find brain activity in frontal and temporal cortices that would correlate with performance in an ASTM task in which memory load was parametrically varied. Importantly, we also examined how brain activity was related to individual differences in ASTM ability, which allowed us to establish a strong link between observed brain activity and its functional significance for maintenance in ASTM.

Methods

Participants

Sixteen university students (6 females and 10 males) participated in the present study. All reported to have normal hearing. Data for three participants were excluded because more than 50% of their trials were rejected due to ocular artifacts (horizontal movements and/or blinks), or excessive head motion. This left a total of 13 participants (5 females, and 8 males) with a mean age of 23 years ($SD = 2.6$ years). All participants were right-handed. All participants gave written informed consent for procedures that were vetted by the appropriate ethics committee.

Stimuli and ASTM task

Participants were presented with two sound sequences separated by a 2000 ms silent retention period. Each sound was 100 ms in duration (including 10 ms rise and fall times) and adjacent sounds were separated by 100 ms of silence. The sounds were pure tones with frequencies selected so as to be 'non-musical' in the sense that intervals between the tones did not correspond to the intervals in the standard Western 12-tone-equal-tempered scale. We determined tone frequencies by dividing a two octave range into seven equal logarithmic steps per octave as follows: 380, 419, 463, 511, 564, 623, 688, 759, 838, 925, 1022, 1128, 1245, and 1375 Hz. The use of these stimuli minimized the potential recruitment of memory structures specialized for verbal or phonological information, as well as the potential contributions from memory for musical structures associated with years of listening to Western music. This approach enabled a better focus on memory for basic attributes of sound. Stimuli were presented at the most comfortable level for each participant.

On each trial, two sound sequences were presented to each participant, and the task was to decide whether the sequences were the same or different (see Fig. 1). The first sound sequence ("memory sequence") consisted of seven sounds, the first of which was always white noise. The remaining six sounds were either all white noise, or included two or four pure tones among the white noise segments. Half of the trials contained "interspersed" sequences, in which the pure tones could appear at any position after the first white noise and in which tones could be separated by one or more white noise bursts (for an example of an "interspersed" sequence, see the sequence for Load 4 in Fig. 1). In the other half of the trials, the "contiguous" trials, the pure tones appeared without interspersed white noises at the last positions of the sequence (for an example of a contiguous sequence, see the sequence for Load 2 in Fig. 1). The second sequence ("test sequence") consisted of only pure tones (no white noise) from the first sound sequence, that were either presented in the same or different orders relative to the first sound sequence. In the case of differences in the first

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