

Neural Centers and Perceptual Characteristics of Auditory Short-term Memory

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Studies of auditory perception rarely incorporate findings regarding storage of short-term auditory memory. Investigators rarely incorporate auditory working memory into the neural circuits and anatomical regions they hypothesize underlies perception. This review focuses on the brain regions, neural circuits and perceptual characteristics of human auditory working memory, the storage of auditory percepts necessary to perform short-term, trial-by-trial tasks, in contrast to global, permanent memory formation. The neural areas participating in auditory working memory greatly overlap with those implicated in auditory perception, suggesting the importance of incorporating working memory into our understanding of auditory perception.

Investigators interested in elucidating the mechanisms of auditory memory have focused on characterizing the perceptual limitations and neurophysiological responses. Psychophysical studies seek to understand human properties of the representation, single-cell recordings look for responses characteristic of short-term retention and imaging studies implicate the brain regions necessary to perform various short-term memory tasks. In addition, lesion studies have been important in examining the perceptual and neurophysiological defects when a key area implicated in short-term auditory memory has been removed. This review will describe how each methodology has shaped the current understanding of the mechanisms underlying auditory memory. Retention of non-verbal, perceptual information needed in pitch and lateralization discrimination is discussed to allow for comparisons between neurophysiological studies in non-human primates and human perceptual and imaging studies.

Psychophysical studies find parametric segregation of short-term memory stores

Psychophysical studies have explored system storage capacities in delayed performance of tasks with respect to variation in sensory parameters, such as duration, pitch, spatial location and memory load of auditory stimuli. In particular, investigators have discovered that auditory memory has separate stores for important auditory parameters. Anourova et al. (1999) conducted experiments testing whether pitch and location short-term memory can be disrupted with pitch and location-based distracters. Subjects were asked to identify whether two stimuli, separated by a delay, matched in frequency, in cases where either a stimulus of a different pitch or in a different spatial location served as a distracter during the delay. Anourova et al. found that only stimuli of the same modality (pitch or spatial location) degraded performance, concluding that pitch and location are contained in different auditory stores. Findings of Clarke et al. (1999) corroborate those findings. Semal and Demany (1991) suggest that pitch and timbre also have distinctly independent representations in auditory working memory.

Other studies characterize the pitch or location-based stimuli that serve as the most distracting. For instance Deutch (1972) also asked subjects to compare two test tones and played distracter tones between the two test tones. Subjects were told to ignore the distracter tones and indicate whether the two tones were similar or different in pitch. However, as also found by Anourova et al (1999) and Clarke et al. (1999), performance degraded with distracter tones having similar pitches to the test tones. Performance worsened dramatically when the distracter tones were 2/3 tone away from the test tone, regardless of the tone frequency, and improved for distracter tones higher and lower in frequency. These findings indicate that distracter tones are

most effective when they are close in frequency to the test tones. This study and another conducted by the author a year later (Deutsch, 1973) also adds that the auditory memory storage is logarithmically organized, since the errors scaled with tonal distance between the distracter and test tone.

As evidence of further parameter segregation in auditory working memory, Clement et al. (1999) suggested that pitch and loudness memory processing have separate representations and possibly different processing centers. This study measured performance during a frequency and an intensity discrimination task and found that the patterns of performance degradation as a function of delay between the two test stimuli differs substantially, as shown in Figure 1.

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Figure 1: Discrimination performance (d') as a function of separation time between the two stimuli for frequency and intensity discrimination. Results averaged for four subjects in each condition. Results show that working memory degrades at different rates for the two conditions suggesting different underlying storage mechanisms. Adapted from Clement et al. (1999).

This finding is analogous to different working memory domains processing contrast and spatial frequency in the visual system, and provides further evidence of different memory stores for important auditory working memory parameters.

Neurophysiological studies find neural correlates of short-term retention in medial geniculate body and auditory cortex

Relatively few studies have directly recorded neural responses from auditory cortical areas participating in short-term memory tasks. Studies have implicated the auditory cortex in short-term memory processing in cats (Neff et al., 1975), dogs (Chorazyna and Stepien, 1961) and monkeys (Stepien et al., 1960). This relatively primitive stage of cortical processing was thoroughly investigated by Gottlieb et al., (1989) who concluded that the cortical neurons retain information about the first tone frequency during interstimulus intervals (ISI) using a rate code. Gottlieb et al. trained monkeys to discriminate two sounds with a delay in a performance and a passive listening condition, and found that the firing rate during the ISI correlates with the first tone in both conditions. In addition, they found that the firing rate of some units depended on whether the frequency of the first tone matched the frequency of the second tone. This study strongly implicates these neurons in the circuitry of short-term working memory (STWM). Participation of auditory cortex in working memory is also supported by magnetoencephalography study of tone loudness (Lu et al., 1992).

In a similar study, Sakurai (1990) implicated the medial geniculate body (MGB), a processing center downstream from the auditory cortex, in addition to A1 in STWM. In his experiments, rats made discriminatory same/different responses regarding the frequency of two test tones, while Sakurai recorded spiking patterns from the auditory cortex, medial geniculate body and the inferior colliculus. Although many of the cells in each area showed differences in firing rates during the presentations of the two stimuli, some cells in the auditory cortex and the medial geniculate body showed differential, stimulus-dependent activity during the delay between the two stimuli, indicating involvement in retention. Both this and the Gottlieb et al. (1989) study suggest a neural correlate of retention of the two stimuli with a rate code dependent on the first stimulus.

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Figure 2: Responses of a medial geniculate body (MGB) unit to demonstrate the delay correlate between tone presentation periods and the delay period. Left: diagrams represent peri-stimulus time (PST) histograms during a sample tone (3 s), the interstimulus delay (3 s) and the test tone (1 s). Data are presented for six types of trials with tones identified as H=high, L=low, and responses as G=go and NG=no go. Mismatch conditions are H-L and L-H. Right: Bargrams of median spike frequencies (not Hz) during the sample tone, delay and test tone, and for the first and second halves of the delay. The asterisk shows statistically significant differences ($p < .05$) between high and low tones during the sample tone, delay and test tone. Differences in the number of spikes also exist in both halves of the delay for different stimuli. Adapted from Sakurai (1990).

Another non-cortical area neurophysiologically implicated in working-memory in the hippocampus. Although this area is often associated with long-term, reference memory, Sakai (1994) finds that some hippocampal neurons are solely involved in either working or reference memory, whereas other neurons are involved in both types of memories.

Imaging studies (see below) implicate the prefrontal cortex (PFC) in STWM (Romanski and Goldman-Rakic, 2002). The PFC consists of several cytoarchitecturally defined regions and there is evidence that these regions both distinct with respect to sensory modality and

stimulus features (Levy and Goldman-Rakic, 2000; Carmichael and Price, 1995) and integrate information across sensory modalities (Fuster et al. 1990; Bodner et al, 1996). Romanski et al. (1999) find distinct regions in the belt and parabelt regions that have neuronal targets in the frontal lobe of the prefrontal cortex in the rhesus monkey. Since the belt and parabelt regions of A1 have implications of SHTM involvement (Gottlieb et. al, 1989; Sakurai, 1990), these histological studies give further evidence that the prefrontal cortex incorporates auditory STWM neural substrate downstream. Neurophysiological recordings of PFC activity in relation to auditory STWM tasks would shed light on the neural circuitry involving the MGB, A1 and PFC, but such studies are lacking.

Imaging work implicates auditory cortical, frontal, parietal and cerebellar areas in STWM tasks

Functional imaging studies have shed light on neural correlates of perceptual processing and implicate various cortical areas in auditory working memory. These studies suggest that the auditory cortex as well as higher cortical, as well as cerebellar, areas participate in working memory processing, but the degree of activation and the precise neural correlate depends on the type of memory task. Many imaging studies find activation of the prefrontal cortex in STWM tasks (e.g. Romanski and Goldman-Rakic, 2002). Levy and Goldman-Rakic (2000) find “domain-specific” organization of working memory function in the prefrontal cortex, and activation of one or more of several subdivisions of dorsolateral prefrontal cortex, depending on the type of information processed. Romanski and Goldman-Rakic (2002) specifically implicate the dorsolateral and ventrolateral prefrontal cortices in retention of auditory stimuli. Celsis et al. (1999) also suggested frontal and prefrontal regions play a role in auditory working memory in maintenance of tonal patterns.

For pitch comparison memory tasks, Zatorre et al. (1994) found greater activation of the right frontal and temporal lobes, and the parietal and insular cortex in high memory load conditions. Temporal lobe activation is expected, with its recognized role in musical processing, as is frontal activation, known for executive functions. Parietal and insular cortical activation probably played a role in attention. These findings are in line with those of Griffiths et al. (1999) who also found more extensive right lateralized network including the cerebellum, posterior temporal and inferior frontal regions when subjects were making “same/different” judgments while comparing the pitch of 6 tones. This finding may be in sharp contrast with a pitch matching study by Gaab et al. (2003) of greater working pitch memory activation of the left supramarginal gyrus (SMG) and the left dorsolateral cerebellum, as well as other structures in the temporal cortex.

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Figure 3: Brain activation pattern ($P < .05$, corrected) during the initial imaging time points (0-2s after the ends of the auditory stimulation). The pattern is dominated by strong (left>right) activation of the superior temporal gyrus bilaterally including Heschl's gyrus and auditory association cortex; anterior, lateral and posterior to Heschl's gyrus including the planum temporale and the supramarginal gyrus. Activation also includes bilateral posterior dorsolateral frontal regions, superior parietal region on the right side, left>right pre-SMA region and lobules V and VI of the left cerebellum.

Celsis et al (1999) also implicated left SMG and right frontal and primary and secondary auditory cortices in the activation of a task requiring memory judgments between tones of different pitch height or spectral content. Thus, there seems to be some disagreement about the side of the asymmetry of activation patterns in pitch memory tasks.

That the cerebellum has non-motor functions is found in several studies, including auditory verbal memory function (Grasby et al, 1993), tone recognition (Holcomb et al, 1998) and musical duration discrimination (Parsons, 2001). Mathiak et al. (2004) also implicates cerebellar involvement in non-verbal auditory memory. Although the latter study suggests that auditory cortex activated early in the delay between the first and second test tones, and that the SMG and cerebellum and activated later, Gaab et al. (2003) finds that the cerebellum activates immediately and sees cerebellar activation through the task. However, both studies agree on cerebellar involvement in STWM tasks.

For audiospatial memory tasks, Martinkauppi et al. (2002) found bilateral activation in superior, middle and inferior frontal gyri and posterior parietal and middle temporal cortices. These areas were similarly found in the Zatorre et al. (1994) pitch study but here with bilateral activation. Martinkauppi et al. (2002) also revealed similar activation in the audio- and visio-spatial tasks, indicating that audio- and visio-spatial performance in STM tasks are located along a common neural pathway.

Lesion studies indicate debilitation in STWM performance with bilateral auditory association cortical lesions.

Lesion studies in monkeys implicate superior temporal cortex, a high-level auditory association area, in short-term memory tasks (Colombo et al., 1990; Colombo, 1996). However, Colombo (1996) suggests that only bilateral lesions impact auditory short-term memory performance significantly. This study used a delayed matching-to-sample task with high-frequency and low-frequency tones. Monkeys had to indicate whether two consecutive stimuli (with 2 s pause) were the same or different. Monkeys received lesions of association cortex with testing after each unilateral operation. The lesions corresponded to cytoarchitectonic area TA, sparing primary (area TC) and secondary (area TB) of auditory cortex. Visual performance after the first operation was unaffected, but auditory performance was affected in some monkeys after many sessions and some were unable to achieve preoperative levels. With bilateral lesions, monkeys were unable to reach preoperative levels with extensive testing, with worse performance deteriorating with delay length.

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Figure 4: Performance (percent correct) on pattern-discrimination task preoperatively and after the second (bilateral) cortical lesion. Top and bottom dotted lines represent criterial and chance levels of performance, respectively. Adapted from Colombo et al., 1996.

This study indicates that good performance is possible with one superior temporal cortex, corroborating findings of greater unilateral activation (Zatore, 1994; Gaab, 2003; Celsis, 1999), and clearly implicates this area in STWM processing.

Conclusion: complex interactions of STWM circuitry

Combined psychophysical, neurophysiological, imaging and lesion studies implicate a complex network of neuronal areas involved in STWM processing. Psychophysical work suggests that different memory representations and processing exists for important STWM parameters such as pitch, timbre, spatial location and loudness, with only slight parametric interaction in memory tasks. Neurophysiological studies find neural correlates of rate-based coding and retention of information about prior stimuli in MGB and A1, but further studies need to map out the connections and coding schemes involving these centers, as well as other center implicated using imaging work. Functional imaging studies suggest a complex asymmetry in pitch and spatial location memory tasks involving primary and secondary auditory cortices,

frontal and prefrontal areas, parietal areas as well as the cerebellum. Studies disagree about the temporal patterns of activation and about the right or left asymmetry of activation. Lesion studies in monkeys suggest that only bilateral auditory cortical lesions significantly affect performance, a finding that may corroborate some imaging studies with asymmetric activation patterns of activity. Because of the wide involvement of many cortical (and sub/supracortical) areas in STWM processing as well as disagreement regarding activated areas, further investigations of perceptual auditory phenomena should keep in mind possible involvement of STWM in designing tasks and evaluating results.

Suggested Papers

Background

Pasternak, T., and Greenlee, M.W. (2005). Working memory in primate sensory systems. *Nature Reviews Neurosci.*, 6: 97-107.

Assigned Papers

Clement S., Demany, L., and Semal, C. (1999). Memory for pitch versus memory for loudness. *J. Acoust. Soc. Am.*, 106(5): 2805-2811.

Gottlieb, Y., Vaadia, E., and Abeles, M. (1989). Single unit activity in the auditory cortex of a monkey performing a short-term memory task. *Exp. Brain Res.*, 74: 139-148

Gaab, N., Gaser, C., Zaehle, T., Jancke, L., Schlaug, G. (2003). Functional anatomy of pitch memory—an fMRI study with sparse temporal sampling. *NeuroImage*, 19: 1417-1426.

Further reading

Colombo, M., Rodman, H.R., Gross, C.G. (1996). The effects of superior temporal lesions on the processing and retention of auditory information in mokeys (ebus paella). *J. Neurosci.* 16, 4501-4517.

Deutsch, D. (1973). Interference in memory between tones adjacent in the musical scale. *J. Exp. Psychol.* 100, 228-231.

Mathiak, K., Hertrich, I., Grodd, W., and Ackermann, H. (2004). Discrimination of temporal information at the cerebellum: functional magnetic resonance imaging of nonverbal auditory memory. *Neuroimage* 21: 154-162.

Sakurai, Y. (1990). Cells in the rat auditory system have sensory delay correlates during the performance on an auditory working memory task. *Behavioral neurosci.* 104(6): 856-868.

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