AUDITORY SPATIAL ATTENTION GRADIENTS AND THE IMPACT OF WORKING MEMORY LOAD ON TOP-DOWN GUIDANCE

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BY

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Abstract

Previous studies of visual spatial attention have found that attentional benefits are distributed as a gradient relative to an attended location. Further visual investigations of spatial attention have found that there are important interactions between the contents of a short-term memory (STM) load and the distribution of attention. These phenomena have been much less studied in the auditory domain. The present study aims to investigate the effects of a spatial STM load on attentional distribution in the auditory domain. Attention was directed by auditory targets that required a button-press response, and could appear at one of five spatial locations. Factors of target location, STM load, hemispace, and musical experience were analyzed with measures of accuracy and reaction time in response to targets. Results demonstrated a robust influence of STM load and target stimulus location on how auditory attention was allocated across space. Overall, these results suggest that different attentional profiles under conditions of STM load may be impacted by the type of representations held in STM, the features of these representations, and musical experience.

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1.0 Introduction

Auditory spatial attention refers to the ability to orient towards a sound at a specific location in space. This is vital for successful completion of goal-directed behavior, because it facilitates an attentional bias for auditory information that is relevant to one's current goals. However, attention must simultaneously be susceptible to rapid shifts for sounds at unattended locations. Unexpected events in the auditory environment may signal opportunities or threats that demand immediate action, even if they are not relevant to the task at hand (Bradley, 2009; Erulkar, 1972; Scharf, 1998).

These seemingly conflicting computational demands present the auditory system with a "stability-flexibility" dilemma (see Liljenström, 2003) with respect to the distribution of attentional resources across space. Exactly how the auditory system reconciles the dilemma remains unknown. However, auditory spatial attention is unique to other modalities in that it is sensitive to a wide range of environmental stimuli, and it is susceptible to panoramic capture. Investigations of its computational substrates may lead to important, unprecedented findings that can inform hypotheses regarding attentional distribution mechanisms, and more broadly, cognitive organization in general.

1.1 Spatial Attention Gradients

Despite the unique attributes of auditory attention, most spatial attention research has been conducted in the visual modality. Evidence from visual studies largely favor an attentional gradient to account for attentional distribution across visual space. Support for attention gradients come from convergent findings that show that visual attention can be focused at one spatial location, and graded decreases in attentional benefits occur with increasing distance from the attended location (see Cave, 2013 for a review). Though the idea of auditory spatial attention gradients has been studied far less, some previous studies suggest that the same may be true for auditory attention (Mondor & Zatorre, 1995; Rhodes, 1987; Rorden & Driver, 2001; Spence & Driver, 1994). These studies used an auditory cue to direct attention, then instructed subjects to respond to a target that was presented at various locations across trials. Similarly, they found that increasing distance from a preceding cue led to graded increases in reaction time to targets.

While these results are consistent with those in visual attention research, everyday use of auditory attention often requires it to remain relatively constant at one location. Therefore, interpretations of the results obtained from cue-target studies are limited by the fact that the experimental procedure may not engage auditory processes that are active under naturalistic conditions. One study that more adequately represents natural attentional processing delivered stimuli predominantly from one location, and found that infrequent auditory distractors that demanded shifts to a different location substantially increase reaction time (Roeber, Widmann, & Schröger, 2003). Although this is more representative of attentional processing in everyday situations, the design only included two locations and therefore cannot address more detailed questions about the panoramic distribution that distinguishes auditory spatial attention from other modalities.

1.2 Our Lab

In an effort to address these design limitations, our lab has developed a target detection paradigm that delivers the vast majority (84%) of target stimuli at a single location, referred to as the standard location, while the remaining targets (16%) are delivered from one of four non-standard locations. Since only 4% of target sounds are delivered at each non-standard location, responding to these sounds demands an attentional shift from the attended location. This design is more representative of the auditory events encountered in the real word, because the shift location is unexpected and can come from various locations across space.

A series of experiments that investigated auditory attention gradients with this paradigm revealed that reaction times do increase with distance from the standard location, but only to a certain point (Golob & Mock, submitted).

Reaction times increased substantially when shift locations were near the attended location, but began to decrease for more distal shift locations. These results are summarized in Figure 1A. Notice that the quadratic profile shown in Figure 1A does not support the idea of an attention gradient, because increases in reaction time were not monotonic with increasing distance from the attended location. For comparison's sake, Figure 1B shows what a classic gradient model of spatial attention would predict for these experiments.

The data collected at/near the standard location are consistent with the aforementioned studies that used auditory cue-target paradigms to examine spatial attention (Mondor & Zatorre, 1995; Rhodes, 1987; Rorden & Driver, 2001; Spence & Driver, 1994), as well as visual findings that support graded declines in attentional benefits with distance from an area of attentional focus on measures of reaction time to targets (Cave & Bichot, 1999; Downing & Pinker, 1985; Mangun & Hillyard, 1988), stimulus-response compatibility (Eriksen & Eriksen, 1974), and perceptual sensitivity (Downing, 1988; Hoffman & Nelson, 1981). The novel result of these studies was that reaction times decreased again at larger distances from the standard. Though some visual studies have shown quadratic attention profiles, these tend to occur over a relatively smaller range of locations (Caparos & Linnell, 2010; Müller, Mollenhauer, Rösler, & Kleinschmidt, 2005). That being said, the difference in scope of visual and auditory attention profiles may be due to the fact that visual fields are inherently more limited, and that the receptive fields of auditory neurons are generally very large (Middlebrooks & Pettigrew, 1981; Recanzone, 2000).

In order to interpret these findings, one must consider factors that are known to impact attentional biases and profiles of reaction time. One such factor is the way in which attention is directed to a certain location. Whereas the use of cues in previous studies directed attention to various locations across trials, the attended location in this design was kept constant. While stimuli were occasionally presented at unexpected locations, the likelihood of a target being presented from the attended location remained very high throughout the experiment. Since the formation of attentional biases is known to depend largely on expectations that are generated from probabilities (Itti & Baldi, 2009), top-down expectations that favored the standard could theoretically account for the graded increase in reaction times observed at shift locations surrounding region of attentional focus.

However, this cannot explain why reaction times at the most distal locations were comparable to reaction times at the target location. One possible interpretation of these results is that there exists a separate, but complementary bottom-up mechanism that facilitates stimulus-driven attentional processing at locations outside of the region that is subject to top-down control. Support for this idea comes from the ecologically-based account of auditory spatial attention as an early warning system used to monitor the environment at locations outside of the visual field (Bradley, 2009; Erulkar, 1972; Scharf, 1998), as well as in the context of visual search, where large attentional shifts from an attended area may promote efficient sampling (Bahcall & Kowler, 1999).

This account of two attentional systems is supported by neuroscientific investigations of voluntary/involuntary attention that have revealed a neural basis for distinct, but interactive, attentional mechanisms for stimulus-driven and goal-directed processing (Corbetta, Patel, & Shulman, 2008). Yet, in order to voluntarily focus attention in the absence of unexpected stimuli, attention needs to be directed in a top-down manner (Soto, et al., 2008) based on information held in short-term memory (STM) (Duncan & Humphreys, 1989; Wolfe, 1994; Bundesen, 1990). Thus, the gradient pattern of reaction times at/near the standard location suggest that top-down expectations are formed from active maintenance of the standard location in STM.

1.3 Interaction of Spatial Attention with Short-Term Memory

Several studies confirm that STM contents and attention are automatically linked (see Soto, et al., 2008). In real world scenarios, the connection between STM contents and attention is usually beneficial, because it allows for top-down guidance of attention to goal-relevant information and prevents interference from irrelevant information (Duncan & Humphreys, 1989; Wolfe, 1994; Bundesen, 1990). However, because this connection is thought to be automatic (Pashler &

Shiu, 1999; Downing, 2000; Soto, et al., 2005; Soto, et al.., 2006; Awh & Jonidis, 2001; Soto & Humphreys, 2009), stored STM representations may cause task interference if their contents contain irrelevant or inaccurate information. This sort of top-down interference may account for the increase in reaction times observed at locations near the standard in the results described above.

1.3.1 Different States of Working Memory Representations

One model of load effects on spatial attention comes from visual studies on working memory. Working memory (WM), regarded as distinct from short-term memory (Cowan, 1995; Baddeley & Hitch, 1974; Levin, 2011), refers to the cognitive ability that enables us to retain and manipulate relevant information for the near future (Olivers, et al., 2011). Whereas STM is only involved in the short-term storage of information, WM involves the active manipulation or organization of stored memory representations (Diamond, 2013; Nelson & Cowan, 2008). It has been proposed that not all WM representations have the same status at a given time (Cowan, 2001; Oberauer, 2002; Nee & Jonides, 2011). Instead, WM seems to represent information that is relevant to the current task differently than when information is merely stored for later use. The WM representation that pertains to the current task is actively being used throughout the task, and is therefore thought to be directly available (Olivers, et al., 2011). Information that is not immediately task-relevant but stored for use in the near future is thought to be temporarily peripheral to the active representation, but still available in WM.

Olivers has proposed a model that explains this fundamental division between different representational states in WM. The model asserts that the active WM representation, referred to as the ‘search template’ (Wolfe, 1994; Duncan & Humphreys, 1989), is used to distinguish target objects from task-irrelevant objects during selective attention tasks. Consequently, inactive WM representations, are stored in a temporarily dormant state until they are needed. This theory assumes that, while WM as a whole can represent multiple items (Cowan, 2001), only one search template can be active at a time.

Evidence in support of this model comes from visual studies in which storage of task-irrelevant information induces little (Woodman & Luck, 2007; Carlisle & Woodman, 2011; Olivers & Eimer, 2011) to no (Downing & Dodds, 2004; Houtkamp & Roelfsema, 2006) attentional biases, but that storage of task-relevant information can bias attention significantly (Olivers, et al., 2006; Dalvit & Eimer, 2011; Kumar, et al., 2009; Soto, et al., 2007). Neurological studies have shown that the same memory item can be stored in the prefrontal cortex in at least two orthogonal states (Warden & Miller, 2007; Warden & Miller, 2010; Sigala, et al., 2008), and that neurons that code for a search template demonstrate enhanced firing rates (Miller, et al., 1996), activation (Chelazzi, et al., 1993; Tomita, et al., 1999; Bichot, et al., 2005; Jiang, et al., 2000), and precision (Motter, 1994; Moro, et al., 2010) during a visual search task. Furthermore, the idea that only one search template can be active at a time is supported by attentional capture studies that vary the amount of targets required in a visual search task (Huang & Pashler, 2007;Menneer, et al., 2007; Houtkamp & Roelfsema, 2009; Folk & Anderson, 2010; Eimer & Kiss, 2010).

1.3.2 General Load Theory

Alternatively to Olivers' model of different states of WM representations, other visual studies have emphasized more generalized importance of STM load as a mediating factor in the extent of visuospatial attention (Lavie, 2005; Linnell & Caparos, 2011). The general load theory emerged from such studies that sought to examine the interaction of STM and attention (Lavie & Tsal, 1994; Lavie, 1995; Lavie & de Fockert, 2005; Rissman, Gazzaley, & D'Esposito, 2006). General load theory posits that high STM load will negatively impact attentional abilities regardless of content, due to decreased availability of shared processing resources for STM and attention (Lavie, 2005; Lavie, et al., 2004). This view posits that distractor interference during a selective attention task should always increase under high STM load (de Fockert, et al., 2001; Lavie, et al., 2004).

Evidence that supports general load theory comes from studies that show that manipulating the size of STM load has an effect on attentional task performance, even when the information held in STM is task-irrelevant (Brand-

D'Abrescia & Lavie, 2007; Dalton, Lavie, & Spence, 2007; Lavie & de Fockert, 2005). For instance, Lavie and de Fockert (2005) showed that when digits were held in STM during a shape-based visual search task, the extent of attentional capture by an irrelevant color singleton was significantly greater than when there was no load. Similarly, another study used neuroimaging of an attentional task to show that verbal STM memory load caused interference with the suppression of visual distractors (Rissman, et al., 2006).

Together, these results demonstrate that STM load can induce general interference effects on the deployment of attentional processes, suggesting that active maintenance of a STM load may enlist higher-order cognitive processing mechanisms that are shared with those required for selective attention. In line with this perspective, general load effects have been found in studies that use a mixed-trial design requiring task-switching from trial-to-trial (Lavie, et al., 2004; Brand & Lavie, 2005), suggesting that load effects can be caused by increasing overall demands on cognitive control.

Further support for general load theory comes from studies that use cross-modal stimuli to manipulate task performance with and without load. One example used auditory STM items and a visual attention task to show that holding pure auditory tones in STM negatively impacts performance on a visual flanker task (Brand-D' Abrescia & Lavie, 2007). Since auditory pure tones have no extra-modal context that could be associated with representations of visual information, impaired performance on a visual task implies that general processing mechanisms that deal with any sort of STM load are also responsible for general processes required for selective attention. Another cross-modal study produced similar effects by showing that verbal STM load increased interference from tactile distractors on a tactile discrimination task (Dalton, et al., 2007).

1.3.3 Specialized Load Theory

While the previous section reviews evidence in favor of *general* load effects, others have proposed that the effect of STM load is not absolute; rather, it depends on how the features of stored STM representations relate to task-relevant stimuli (see de Fockert, 2013). Contrary to demonstrations of general load effects, some studies have shown that the contents of STM can have differential effects on spatial attention depending on how the STM load relates to the task at hand (Konstantinou, et al., 2014; Park, et al., 2007; Ranganath, DeGutis, & D'Esposito, 2004; Schumacher, Elston, & D'Esposito, 2003; Yoon, Curtis, & D'Esposito, 2006). Such findings have led to the development of a specialized load theory, which is distinguishable from general load theory under the premise that STM processing resources are specialized for specific types of information. According to specialized load theory, STM load will impair attentional processing only when stored items share limited-capacity processing resources with task-relevant targets.

For example, Park, et al. (2007) studied load effects by pairing STM load with a same/different matching task that required focusing on targets while ignoring distractors. The study used two categories of visual stimuli, faces and houses, in order to test whether the specific type of memory load had differential effects on target processing and distractor interference. Consistent with other findings (de Fockert, et al., 2001; Lavie, et al., 2004), when STM load contained items in the same visual category as the target in the attentional task, distractor interference increased. The novel aspect of these findings compared to those in support of Lavie's general load theory is that when STM contained information in the same visual category as the distractor, distractor interference actually *decreased*.

Neuroimaging studies suggest that STM encoding, maintenance, and response selection processes are specific to stimulus type or representations (Ranganath, DeGutis, & D'Esposito, 2004; Schumacher, Elston, & D'Esposito, 2003; Yoon, Curtis, & D'Esposito, 2006). In line with these results, other studies have shown that the perceptual processes for faces and houses are neurally represented in dissociable brain regions (Kanwisher et al., 1997; McCarthy et al., 1997; Aguirre, Detre, Alsop, & D'Esposito, 1996; Epstein & Kanwisher, 1998). Taken together, these findings provide a possible explanation for Park, et al.'s results, which is that STM load may only produce task interference when STM items and attentional task targets (and/or distractors) compete for similar processing resources.

* * *

Altogether, divergent evidence that has been reported and its resulting theoretical discrepancies illustrate the fact that the interaction between STM contents and attentional processing is not fully understood. Furthermore, as with investigations of spatial attention gradients, the vast majority of the relevant literature concerns visual attention. Studies on how the top-down influence of auditory STM affects attentional gradients across space are needed in order to generate a more refined understanding of how attention is distributed across space; how processing resources of attention, memory, and perception interact; and, more broadly, how the functional architecture of shared and distinct processing mechanisms can inform a large-scale understanding of cognitive organization.

1.4 Musical Experience and Spatial Attention

Another way to examine functional architecture and underlying mechanisms of cognition is to look at factors that can modulate structural and functional correlates of cognitive processes. Musical experience is a strong candidate for such a factor. A growing body of literature shows that music training improves the neural encoding of sound and promotes experience-based neural plasticity (see Barrett, et al., 2013). Neural plasticity refers to the capacity of the neural system to change its functional properties after learning (Pascual-Leone, et al., 2005). Evidence suggests that even rapid, short-term plasticity is an essential feature of learning music (François & Schön, 2010), and a huge number of studies have shown that functional and anatomical differences in musicians' brains are accompanied by enhanced cognition in non-musical domains, such as verbal, mathematical and visuospatial skills (e.g. Schellenberg, 2001, 2004, 2006; Brochard, et al., 2004).

Along these lines, Patson and colleagues (2007) demonstrated that, for visuospatial attention, musicians show less lateralization of function than non-musicians. In this study, right-handed adult musicians and non-musicians performed the manual line bisection task with each hand. Consistent with more recent visual findings (e.g., Ishihara et al., 2013), non-musicians bisected the line to the left of the midpoint with both hands. Musicians, however, tended to bisect the line to the right of the midpoint, and the magnitude of their rightward bias was overall less than non-musicians' leftward bias (Patson, et al., 2007). In summary, musicians were more accurate in their line bisection than non-musicians, suggesting that they have a more balanced distribution of attention across space.

This finding is important because a vast amount of visual studies have shown that normal adults bisect lines reliably to the left of the true midpoint

(Barnett, 2006; Brodie & Pettigrew, 1996; Hausmann, et al., 2003a; Hausmann et al., 2003b; and see review by Jewell and McCourt, 2000). This tendency for visual attention to be biased for the left side of space is termed right psuedoneglect (Bowers & Heilman, 1980), is believed to reflect a right hemispheric dominance in the allocation of spatial attention (Foxe, et al., 2003) that results in an overrepresentation of the contralateral (left) side of space (Jewell & McCourt, 2000). Taken alongside evidence of music-induced neuroplasticity and behavioral evidence of more accurate visuospatial processing, this suggests that musical experience may change, and/or enhance, the functional and structural architecture responsible for forming internal representations of external space.

Further evidence comes from visual studies on the effects of pitch on the perception and representation of space in musicians versus non-musicians (e.g., Rusconi, et al., 2006; Lidji, et al., 2007; Nishimura & Yokosawa, 2009; Cho, et al., 2012; Ishihara, et al., 2013). These findings show that pitch height (the tonal attribute of being high or low relative to musical scale position, see Miller, 1916), may be represented in a spatial format which interacts with selected manual motor responses. This has been observed in the vertical (Rusconi, et al, 2006; Lidji, et al., 2007; Nishimura & Yokosawa, 2009; Cho, et al, 2012) and horizontal (Rusconi, et al., 2006; Lidji, et al., 2007; Cho & Proctor, 2003) spatial dimensions.

These studies show that when a directional response to a pitched tone is required, both accuracy and response latencies show preferential mapping of high tones to up/right directions, and low tones to down/left locations. A key difference observed in these results, however, seems to be that while preferential mapping is automatically activated for the vertical axis, the association of pitch along the horizontal axis is only automatic in musicians (Rusconi et al., 2006; Lidji et al., 2007; Cho et al., 2012). Thus, there seems to be a unique distinction between the representation of external space in the horizontal dimension for musicians versus non-musicians. This distinction may be related to the observation of less biased visuospatial attention in musicians (Patson, et al., 2007).

Again, however, the majority of these studies have been conducted in the visual modality. Given the unique features of the auditory system detailed above, and the fact that musical experience occurs is predominantly auditory, further research is needed that focuses on the auditory modality. Comparing visual and auditory results could elucidate cognitive features that are modality-specific versus those that are not, providing useful insight into further investigations of higher-order cognition. Furthermore, when considered alongside the conversation of STM and its influence over spatial attention, auditory studies that look at between group differences in musicians versus non-musicians could also provide insight onto some of the unanswered questions in attention research.

1.5 The Current Study

It is clear from the preceding review that (1) task-specific variables affect attention gradients; (2) spatial attention may be distributed by top-down and bottom-up mechanisms; (3) the effect of STM load on attention is not absolute, but dependent on how features of STM representations relate to goal-relevant stimuli; and (4) musical experience may alter the structural and/or functional components of these processes. What is less clear is the computational dynamics of shared and distinct processing mechanisms underlying spatial cognition, and how they will interact with one another under different conditions. Our understanding of these dynamics is limited further by the fact that the vast majority of studies concerning attention, the role of STM, and even musical experience, were conducted in the visual modality.

Auditory spatial attention, however, is the only sensory modality that is able to monitor all locations in space simultaneously. Accordingly, it is also the only attentional system that consistently produces automatic, involuntary shifts of attention in response to unexpected stimuli. These characteristics of auditory spatial attention are not observed in other modalities. Thus, auditory studies are needed to identify shared and distinct mechanisms underlying attention, STM, and music-dependent plasticity across modalities. Such discoveries will not only benefit attention research, but they will also provide clues to overarching principles of cognitive organization.

The main goal of the proposed experiment is to determine if a task-irrelevant STM load will automatically influence the distribution of auditory spatial attention. Participants consistently maintained attentional focus to a region of external space, referred to as the standard location. Occasional shifts to a new location were used to map out the distribution of auditory attention relative to the area of attentional focus (the standard location). Attentional gradients were shown by behavioral measures median reaction time (for correct trials) and accuracy at each target location across a 180° plane.

The connection between attention and STM contents was examined by observing this attentional distribution under two conditions: one where subjects had no STM load, and one where subjects were told to memorize the location of a tone before the attention task and recall it after the task. The magnitude and direction of any changes in attention gradients for the load and no-load conditions could provide insight onto the nature of the interaction between attention and STM. The impact of musical experience was examined with a subanalysis of between-subjects effects. After data collection, subjects were split into two groups, musicians and non-musicians, depending on responses to a musical experience survey. Whereas effects of STM load and target location were looked at within-subjects, the effect of musical experience on attention, STM, and their interaction was examined between groups.

1.6 Hypotheses

Regarding spatial attention gradients, we predict that in the absence of STM load, reaction times will be slowest at ±45° from the standard location, and fastest at the standard location (0°), and intermediate at the far 90° locations. These results would be consistent with our lab's previous investigations of spatial attention gradients using the same target detection paradigm. This study differs from previous studies, however, because previous studies only used spatial attention stimuli. The current study will add the elements of encoding and retrieval during a memory task to the task requiring responses to spatial attention stimuli.

When considering the possible effects of STM load on RT profiles, we predict that in the presence of a STM load, effects of load will be maximal for targets presented at/near the standard (0° and ±45°), because if these are the regions subject to top-down control, then top-down guidance of attention based on STM contents will be less available for target processing. On the other hand, if a bottom-up attention mechanism is responsible for responding to targets that are presented far away from the standard (±90°), we predict minimal load effects at these locations, since resources for target processing at these locations may be exempt from top-down guidance.

For the sub-analysis of musical experience, we predict that musicians will show lower reaction times than non-musicians in all conditions, due to their experience directing attention based on auditory features held in STM. For the load condition, we expect that the reaction time profiles of musicians will be less impacted by STM load than non-musicians, due to the fact that playing music requires storage, maintenance, and flexibility of auditory STM representations while attending to other goal-relevant auditory stimuli. Furthermore, we predict that reaction times on either side of the standard will be more similar for musicians versus non-musicians, due to evidence that suggests that musicians show a more balanced distribution of attention across external space.

2.0 Methods

2.1 Subjects

A total of 23 healthy undergraduates or recent graduates of Tulane University were tested in two conditions (mean age = 20.7 ± 0.6; 11 men and 10 women). Table 1 provides a summary of subjects' demographics. Participants gave written informed consent before testing, as part of a protocol approved by the Tulane University Institutional Review Board.

2.2 Pretest

After providing demographic data and informed consent, subjects participated in brief surveys indexing musical experience, handedness, and cognitive failures. Subjects then underwent audiometric testing to probe for hearing loss. Subjects with hearing loss greater than 25dBs were to be excluded from the study. Pure tone thresholds (0.5– 8.0 hKz) were tested using a Maico audiometer (Eden Prairie, MN) in order to ensure that hearing thresholds and differences between ears are within clinical norms (<25 dB and <10dB, respectively). Handedness was determined using the Edinburgh handedness inventory. Cognitive failures were assessed using the Cognitive Failures Questionnaire (Broadbent, et al., 1982).

2.3 Apparatus

Subjects sat in a well-lit sound booth with a monitor in front of them. Acoustic stimuli were presented using insert headphones. Participants were instructed to look forward and to not close their eyes while performing the tasks.

2.4 Stimuli

For the target discrimination task, five virtual white noise burst sounds were created to generate perceptions of sound sources that originate in the 3-D frontal azimuth plane (left to right: -90°, -45°, 0° midline, +45°, +90°). Figure 2 shows the target sound locations relative to the subject's head. The sounds were white noise (0.1-10 kHz) and lasted 200 ms (5 ms rise/fall times, ~60 dB nHL). For each of the 5 intended locations the appropriate interaural time and level differences and head related transfer functions were applied to the same sample of white noise (Tucker-Davis Technologies, Gainesville, Florida, USA, System II and the University of Wisconsin). For each sound the algorithms employ the same cues that are used for sound localization by the auditory system in the natural environment (Yost & Gourevitch, 1987). Each stimulus was then amplitude modulated at either 25 or 75 Hz (90% depth), which provided a non-spatial cue that was easy to discriminate but also retained for all stimuli the full range of frequencies used for sound localization and had equal energy for the 25 and 75 Hz sounds.

For the stored memory items used in the load condition, five virtual guitar chords were generated using Sibelius First (version 7.1.3, Avid Technology, Inc).

All chords were major triads in root position separated by a perfect fifth. From lowest to highest, the root pitches were B♭3 (233 Hz), F3 (175 Hz), C4 (262 Hz), G4 (392 Hz), and D5 (587 Hz). Each chord was spatialized at each of the five locations using the same algorithm as the white noise bursts, and normalized to 90% depth.

For the no-load condition, spatialized pure tones (260 Hz, because that is near the median frequency of guitar chords) were used as placeholders where remembered items were presented and probed during the load condition, so that the only difference between control and experimental blocks was that subjects were instructed to remember the location of the pitched item during experimental blocks.

The final stimulus set had 40 stimuli: 5 locations x two amplitude modulation rates for white noise, 5 locations x 5 pitches for remembered items, and 5 locations x 1 pure tone for control items. Stimuli were presented with insert earphones (Compumedics-Neuroscan, Charlotte, NC) with a passband > 10 kHz. Insert earphones, rather than free-field speakers, were used in order to minimize potentially confounding effects from indicators of sound sources that can change with visual information and/or head movements.

2.5 Procedures

All subjects were tested in both the load and no-load conditions of the target-detection paradigm. A within-subjects design was used in order to control for individual differences in working memory capacity, which can influence the ability to process information that violates top-down expectations (Yurgil & Golob, 2013).

2.5.1 Target-Detection Paradigm

The same target detection task was used in every block. Subjects heard a sequence of ten amplitude modulated sounds, and responded by pressing one of two buttons based on the amplitude modulation rate (25 or 75 Hz) of each sound. Each block required an equal number of right and left responses, and the assignment of right and left responses to amplitude modulation rate was counterbalanced across subjects.

Each block consisted of 150 target detection trials (15 10-item sequences), where 84% of stimuli were presented at center (0°), and the stimulus onset asynchrony (SOA) was fixed at 1.2 seconds. Stimuli were presented at each of the other four locations on 4% of trials, so that attention must shift from the standard location to an unexpected location. Participants were asked to respond to the amplitude modulation rate regardless of sound location.

2.5.2 No-Load Condition

Before any data were collected, subjects were presented with five repetitions of each white noise burst (25 Hz and 75 Hz), and subsequently asked to respond to a brief sequence of randomly mixed bursts using button presses to indicate the amplitude modulation rate of the sound. Subjects were then trained to respond to the noise bursts after three consecutive 250 Hz pure tones[1], and that a single pure tone after a series of bursts signified the end of that trial.

After subjects could consistently respond correctly to a sequence of noise bursts, they completed two blocks comprised of fifteen trials each. These two blocks signified the control, or "no-load" condition. A schematic of a no-load trial is shown in Figure 3. The pure tones used in these trials were spatialized in order to maximize consistency with the experimental blocks, but subjects were instructed to respond only to the white noise stimuli and not the pure tone stimuli.

Each sequence of target detection trials was preceded by three repetitions of the pure tone stimulus, presented at one of the five locations. After ten target detection trials, subjects heard the pure tone stimulus once, at either the same location as the first three or one of the other four locations. The two no-load blocks were always completed before subjects were exposed to the five major triads used as STM items. Furthermore, the no-load blocks were completed first in order to prevent any residual load effects that may carry over between blocks. The order that the control blocks were presented in was counterbalanced across subjects.

2.5.3 Load Condition

After subjects completed both control blocks, they listened to each major triad move across the five locations from -90° (far left) to +90° (far right).

[1] This experiment was designed along with a complementary verbal STM experiment in our lab. In the verbal study, three words were presented as a verbal STM load. In order for the design of this experiment to mirror the verbal experiment, three tones were presented during the encoding phase of each memory trial.

Subjects then verified that they could accurately discriminate between the five locations by listening to five pitched stimuli distributed randomly across the 180° plane, and marking on a sheet of paper where each sound came from. Subjects who could not correctly identify four out of five of the sound locations were excluded from the study.

After marking the sound locations, subjects completed a memory task where they heard a single triad at a single location three times in a row, and, after a five second pause, heard the same triad played once at either the same location or a different location. Subjects were instructed to respond to the single triad with a button press to indicate whether or not it was presented at the same location as before the pause. Subjects were then asked to respond to the triads in the same way, only a sequence of noise bursts that required button pressing replaced the the five second pause. The purpose of these procedures was to verify that subjects could accurately perceive, memorize and recall the triads' locations; no data was collected from these tasks.

After consistently providing the correct response (location match or mismatch) to the memory probe, subjects completed six experimental blocks. The experimental blocks, or "load" blocks, were exactly the same length and design as the control blocks. A schematic of a load trial is shown in Figure 4. Notice that the only difference from the control blocks was that spatialized triads (referred to as "STM items"), rather than pure tones, played at the beginning and end of each sequence of noise bursts, and that the single triad (referred to as the “memory probes”) at the end of a given trial required a match/mismatch response relative to the three triads that played at the beginning of that trial.

All of the probe stimuli had the same pitch as the STM item presented in the same trial, and 50% of the probes matched the STM item’s location. Right and left response assignments to a match or mismatch probe was counterbalanced across subjects. While the six experimental blocks were always presented after the two control blocks, the order that they were presented in was also counterbalanced across subjects.

2.6 Data Analysis

Data were analyzed using repeated measures analysis of variance (ANOVA) tests with factors of load, target sound location, and STM item location. One-way ANOVAs were used to test for simple effects of load at each level of location, and for location at each level of load. Between subjects factors of group and years were included to test for effects of musical experience. Subjects were included in the musician group if they reported that they have received music training for at least ten years, and that they still play their primary instrument. Subjects were placed in the non-musician group if they reported two or less years of formal music training. Subjects who fell in between these criteria were excluded from the between groups analysis. Table 1 summarizes subject demographics by group.

Tests were conducted for dependent measures of reaction time and accuracy on target-detection button responses, as well as button responses to the memory probes. In order to account for sequence effects, reaction time and accuracy data only exclude responses to the first stimulus presented in a group of ten target-detection trials. Only data from correct memory probe responses were entered into analyses of the target detection task, and trials with incorrect responses or no response in the target detection task were removed from the RT analyses. Two subjects were removed from the analysis due to less than 60% accuracy when responding to the memory probes.

3.0 Results

3.1 Analysis of Sequence Effects

Between each STM item encoding and recognition trial, subjects were presented with ten target detection trials between the encoding phase and recognition phase of each memory task trial (Figure 4). Reaction times on the first of these ten trials were consistently slower than the subsequent target detection trials (see Figure 5). Therefore, in order to test for sequence effects, a two-way repeated measures ANOVA was run for reaction time with factors load (no load, load) and sequence (1-10).

Since target stimuli presented at 0° were the only ones presented at each sequence position, the analysis only included data for these target stimuli in each condition. The analysis revealed a significant main effect of sequence position ($F_{(9,180)} = 79.241$; $p < .001$) and load x sequence position interaction ($F_{(9,180)} = 17.276$; $p < .001$). Due to these highly significant effects of sequence position on reaction time in both conditions, all subsequent analyses excluded data from target stimuli in the first sequence position in each trial.

We also collected reaction time and accuracy data for responses to memory probes (the retrieval phase of the memory task). We found the average of median reaction times for each subject to be 1147.9 milliseconds, with standard error of 44.3 milliseconds. Average probe accuracy was 84.6%, with standard error of 1.2%. On average, subjects did not respond to 0.79% of memory probes, with a standard error of 0.28%.

3.2 Load x Stimulus Location

Reaction times are shown as a function of target stimulus location for each condition in Figure 6A, and accuracy (%) of responses to targets are shown as a function of location in Figure 6B. The data shown in Figure 6 were analyzed using a two-way repeated measures ANOVA with factors load (2; no load, load) and location (5; -90°, -45°, 0°, +45°, +90°). For reaction time, there was a significant load x location interaction ($F_{(4,80)} = 4.838$; $p = .002$) and main effect of location ($F_{(4,80} = 14.050$; $p < .001$), but no main effect of load. Accuracy scores also showed a significant main effect of location ($F_{(4,80)} = 4.448$; $p = .003$), but no load x location interaction or main effect of load.

These results taken together with the shape of the curves shown in Figure 6 show that changes in reaction time and accuracy profiles under STM load vary across sound locations. Specifically, they show that load effects are greater at locations that are farther from the 0° standard. In other words, effects of load are greater as sounds get more lateral. In order to analyze effects of load on the left versus the right hemispace, we conducted a 2x2 repeated measures ANOVA with factors load (no load, load) and side (left, right). For the levels of location, data for the left was calculated as the average of all trials where targets were presented at -45° and -90°, and +45° and +90° for the right. The only significant effect generated by this analysis was a main effect of side for accuracy scores ($F_{(1,20)} = 8.268$; $p = .009$).

3.3 Item Location x Stimulus Location

A separate two-way repeated measures ANOVA with factors target location (5) and STM item location (5) was conducted to test for any specialized load effects based on the extent of spatial relation between stored STM item locations and target sound locations. This analysis only included data from the load condition. The analysis revealed only a main effect of location for reaction time ($F_{(4,52)} = 9.160$; $p < .001$) and accuracy ($F_{(4,52)} = 2.943$; $p = .032$), but no significant interaction or effect of item location. See Figure 7 for a summary of these results.

3.4 Sub-Analysis of Musical Experience

To investigate the effects of musical experience on the measures outlined above, the same within-subjects analyses were conducted with a between-subjects factor of group (musician, non-musician). When the factor group was included in the load x stimulus location repeated measures ANOVA, there was a significant load x group interaction ($F_{(1,13)} = 9.908$; $p = .008$) and between-subjects effect of group ($F_{(1,13)} = 15.267$; $p = .002$) on reaction time. No significant effects were shown for accuracy. When between-subjects factor group was included in the item location x stimulus location repeated measures

ANOVA, there was a significant between-subjects effect of group ($F_{(1,13)} = 6.101$; $p = .028$) on reaction time. No other significant effects were found for this analysis. For the 2x2 repeated measures ANOVA that looked at effects of load on each side of the standard, the inclusion of group as a between-subjects factor produced a significant load x group interaction ($F_{(1,13)} = 16.829$; $p = .001$) for reaction time. No other significant effects of group were found for this analysis either. Reaction time data are shown by group (musician, non-musician) and condition (no load, load) in Figure 8.

4.0 Discussion

The overall goal of this experiment was to map out auditory spatial attention gradients during a sustained attention task in order to examine how they are impacted by a concurrent, task-irrelevant STM load. The main findings that reaction times increase when a STM load is imposed confirms our initial hypothesis. In the no load condition, attentional shifts to the left of the standard produced graded increases in reaction time (RT) with increasing distance from the standard, which unlike previous results was more consistent with a gradual spatial attention gradient. Shifts to the right, however, did produce a curve that was more reminiscent of the quadratic reaction time profile found in our lab's previous studies (see Figure 1A).

The most important finding was that when there was a STM load present, attentional shifts in either direction produced a monotonic increase in reaction time that became greater with increasing distance from the standard. STM load also produced an overall increase in reaction time at all shift locations, but not at the standard. Contrary to our initial hypothesis, these results prove that maximal effects of load occur at locations at greater distances from the standard.

Finally, when subjects were split into groups based on musical experience, the musician group showed overall lower reaction times for all stimulus locations. Reaction time profiles were also flatter for the musician group, except for when the targets were presented to the right of standard in the load condition. The reaction time profiles for musicians were also more stable than non-musicians when a STM load was added, as well as more balanced on either side of the standard.

4.1 Impact of STM Load on Spatial Attention Gradients

The main result of this study was that load effects increased with greater distance from the standard location at center. Figure 5C shows that reaction times are almost identical at the standard location for each condition, and that, while reaction times increase for all shift locations, the change in reaction time for shifts to the right of standard is far less than for those to the left of standard. The sub-analysis for asymmetrical load effects on the left versus right sides of standard provided a preliminary finding well worth looking into in future studies. These results suggest that load may not always affect attentional processing, and that its impact may depend on the task procedure, task stimuli, and direction of attentional shifts.

4.1.1 Dual-Task Coordination

The finding that reaction times do not change at the standard location when there is a STM load disproves our initial hypothesis that predicted load effects to occur only at/near the standard. This was based on the assumption that top-down guidance of attention from STM contents shares processing resources required to generate top-down expectations based on task-relevant information processing. The task conditions inherent to the design of this study may have been a source of variability for attentional performance, as well as for results seen here compared with other studies on STM load and attention.

For instance, the fact that ten target detection trials were embedded between the encoding and retrieval phases of the memory task renders the overall procedure a dual task paradigm. Although the focus of this work is to understand effects of STM load on auditory spatial attention, it may be worth considering potential performance detriments attributable to dual-task coordination. Indeed, previous studies show increased distractor interference in dual- versus single-task conditions (e.g., Lavie, et al., 2004, Experiments 4 and 5).

In fact, the effects of dual- versus single-task coordination for tasks that impose a low memory load, or even no memory load at all (Brand-D'Abrescia & Lavie, 2008; Burnham, et al., 2014; Lavie et al., 2004). Importantly, this has been proven not only for tasks requiring executive control, but for STM maintenance tasks (e.g., Burnham, et al., 2014). Thus, dual-task coordination may have placed additional demands on the cognitive resources involved in maintaining stimulus-processing priorities. Since the memory task was added in the load condition only, these results may, in part, reflect effects of dual-task coordination.

4.1.2 Categories of Task Stimuli

As noted earlier in this section, task stimuli may have also played a role in our pattern of results. Subjects were asked to selectively remember the location of STM items, and STM items differed considerably from target stimuli. Previous studies of load effects on visuospatial attention have emphasized the importance of considering how stimuli from different visual categories can selectively affect target processing in a response competition task (Kim, et al., 2005; Park, et al., 2007). These studies demonstrated that if a task selectively engages resources involved in either target (but not distractor) processing or vice versa, then processing of the unloaded stimulus will increase. In other words, if task processing recruits overlapping resources with target processing, then distractor processing would increase (or vice versa).

While the neural correlates recruited in response to different visual categories are well understood for certain stimulus categories (ie: faces and houses), the same cannot be said for auditory categories. For one thing, categorization of auditory stimuli, even those that are clearly distinguishable from one another, is far more ambiguous than for visual stimuli. Consequently, far less is known about shared and distinct neural correlates of processing different types of sounds.

The current study overtly directs attention to the spatial location of major chords played on a guitar, and to amplitude modulation rates of white noise bursts. Furthermore, as shown by plotting our behavioral measures as a function of location, attention is covertly directed to the spatial location of target stimuli. Covert attention may also have been directed at the pitch of the STM items. Unlike the visual categories used in the studies mentioned above, differentiation of noise bursts and major triads has not been clearly defined. The same is true for the auditory features of stimuli that are relevant to the current discussion, including pitch, amplitude modulation rate, and spatial location. Thus, while visual studies provide the possibility that stimulus type influenced processing of task stimuli, we cannot presently assess if there were any selective effects on target processing due to stimulus categories.

4.1.3 Different States of Working Memory Representations

The results of the current study could be interpreted as consistent with Olivers' proposed model of visual WM. Cognitive control over information processing is limited to prioritization of relevant over irrelevant information, and these priorities are actively maintained in WM so that processing capacity is preferentially allocated to high-priority information (Konstantinou, et al., 2014). Since the majority of targets occurred at the standard location for all trials, perhaps a WM representation of the standard was used as a search template, causing spatial attention mechanisms to prioritize that location.

According to Olivers' model, only one search template can be actively represented at one time. Our results show that attentional benefits are greatest at the standard location in both conditions, suggesting that a spatial representation of the standard is assigned as the active search template during all target detection trials, regardless of load. It follows, then, that the spatial representation maintaining the STM item location would be stored in a dormant state during target detection trials if it is not being used as the search template.

This account is consistent with the absence of any significant effects of STM item location for the load condition of the current study.

The graded increase in reaction time observed with increasing distance from the standard is compatible with this interpretation, indicating that attentional benefits decrease with increasing distance from the search template. Attentional benefits diminished with distance from the standard location even when there was no STM load, and these effects were exacerbated by the addition of a STM load. These findings are consistent with Olivers' account of an active search template that guides attention, because in both conditions the standard was the only location at which targets appeared with regularity. Additionally, the fact that there was no significant effect of STM item location or item x target location interaction supports the idea that the STM item representation assumed a dormant state during target detection, when it was task-irrelevant.

4.1.4 Load Theory: General versus Specialized Load

Research on load theory interprets changes in attentional profiles as a consequence of shared or distinct resources required for target processing and a concurrent memory task. Thus, rather than differentiating between states of WM representations, comparing our results to previous research on load theory may provide an alternative explanation for what we found. Recall that general load theory (Lavie, 1995; Lavie, et al., 2004) posits that STM load will negatively impact attention regardless of its contents. STM load caused an increase at all shift locations, regardless of the spatial location represented in STM during a given target detection trial (Figure 6C, Figure 7). However, behavioral measures of attention remained relatively constant at the standard location. These two observations provide conflicting evidence with respect to load theory. On the one hand, load produces a general effect at shift locations regardless of when the location held in STM contents matched target stimuli. This supports general load theory if the criteria for congruence between a STM item and target stimulus is spatial location. At the standard location, on the other hand, load does not produce any significant effect on attention. When considered alongside findings at shift locations, these results may favor specialized load theory if criteria for congruence is based on whether load shares processing resources with target versus non-target stimuli. Since the latter account includes load effects at all five locations, as opposed to just shift locations, the present results may be best explained when considered alongside specialized load theory.

The specialized load theory depends on the assumption that there is overlap between processing resources dedicated to maintaining STM representations and task-relevant target processing (Park et al., 2007; Woodman & Luck, 2004). However, when we looked at the reaction time data for target processing when each STM item location was held in memory (Figure 6), we did not find any significant effects of item location in memory on the pattern of reaction times across the five locations. This finding could be taken as evidence against selective load theory, because selective load theory would predict that load effects will vary depending on whether the stored STM item matches the target on a given trial. Perhaps, then, it is best to differentiate between processing conditions at each target location rather than processing resources of STM representations. To the best of our knowledge, this is the first study that looks at a parametric manipulation of load, rather than manipulations of representation type. This presents a novel strength of the current study, because comparisons of load effects between types of representations is limited by the fact that they are blind to variability within different types of representations. The fact that a *spatial* STM load had differential effects on a *spatial* target detection task proves that there are more detailed factors that contribute to load effects than simply type of representation.

Priority-based processing and maintenance of STM representations have been shown to be dissociable functions of WM (Konstantinou, et al., 2014; Konstantinou, et al., 2012; Konstantinou & Lavie, 2013). Support for this idea comes from studies that show that these functions activate different cortical areas (see Repovs & Baddeley, 2006; Smith & Jonides, 1999 for reviews), and that the sensory visual cortex is recruited during visual STM maintenance (Ester, et al., 2009; Harrison & Tong, 2009; Malecki, et al., 2009; Munneke, et al., 2010; Serences et al., 2009; see Pasternak & Greenlee, 2005 for a review). In addition, there are neuropsychological reports of patients that show deficits in STM storage but not in priority-based WM processes and vice versa (Baddeley, 2012; D'Esposito & Postle, 2000).

Taken together with these findings, the current results may be interpreted as a consequence of distinct processing resources. Visual studies support the claim that priority-based processing and STM maintenance are dissociable, and that STM maintenance enlists the same processing resources as perceptual representation resources. When targets are presented at standard, performance is facilitated by the fulfillment of top-down expectations, which are generated by priority-based WM processes that maintain higher processing priorities for task-relevant information. Violation of these expectations may generate a feature non-specific signal that recruits an alternative processing strategy in response to any non-target location, because shift locations are not actively represented in priority-based WM. In the absence of an attentional representation to guide selection, the alternate process should rely on stimulus-driven, perceptual processing resources. Thus, if target sounds presented at shift locations activate perceptual processing (as opposed to priority-based processing at standard), and STM maintenance recruits sensory representation resources, then STM load would share processing resources with targets presented at shift locations, but not the standard.

4.2 The Role of Musical Experience

The results shown in Figure 7 demonstrate that load effects can also vary with musical experience. In the absence of STM load, musicians showed lower overall faster reaction times than non-musicians. With a STM load, musicians showed a more stable and bilateral profile of reaction time than non-musicians. These results may seem counterintuitive when considered alongside the account of pseudoneglect given earlier. Pseudoneglect, again, refers to the tendency to bisect leftward of a true midpoint (see Jewell & McCourt, 2000). Pseudoneglect is believed to arise as a consequence of right hemisphere dominance for allocation of spatial attention (Foxe, et al., 2003), leading to overrepresentation of the contralateral (left) side of space (Jewell & McCourt, 2000). In line with the current results, previous findings that show an absence of pseudoneglect in musicians but not non-musicians (Patson, et al., 2007), musical experience is thought to affect the hemispheric representation of external space (Patson, et al., 2007; Patson, et al., 2007a; see Patson, et al., 2007b for neurophysiological evidence).

Why, then, should non-musicians' performance be at its worst for targets presented on the left side of space? As shown in Figure 7, non-musician reaction times in the load condition drastically slowed down on the left, but not the right side of space. One might expect the opposite to occur if, according to evidence for pseudoneglect, non-musicians are expected to show an attentional bias for the left side of space. However, more careful consideration of the mechanisms responsible for STM load maintenance may provide an explanation for why this was not the case.

If pseudoneglect is, in fact, a result of spatial representation regions being lateralized to the right hemisphere, then perhaps these right-hemisphere processing resources were loaded by the STM item location regardless of its hemispace. In line with previous accounts of load effects on shared processing resources, increased demands on right hemispheric processing may result in disproportionate load effects on the contralateral (left) side of space. This interpretation is consistent with behavioral (Patson, et al., 2007; Patson, et al., 2007a) and neurophysiological (Patson, et al., 2007b) evidence that musicians do not exhibit pseudoneglect, because musicians' reaction time profiles in the current study remain relatively stable, as compared with non-musicians, across load conditions and horizontal space.

4.3 Limitations and Future Directions

The current study was not without its limitations. First, the sample size for every condition. Overall, subjects performed twice as many load trials as no-load trials, which may have produced carry-over effects of fatigue or boredom. There needed to be six load blocks in order for all combinations of STM item pitch and location to be included. Practical constraints on time needed for each testing session prevented us from being able to counterbalance load trials with no load trials.

Furthermore, subjects were grouped after data collection, and no special consideration was given to musical experience during recruitment. Therefore, the musician group ended up with only eight subjects and the extent to which those subjects practiced music was not matched. Since a few subjects had some, but not much, musical experience, the non-musician group only had seven subjects. Both of these samples are too small to draw conclusive evidence for between groups differences, but our results still show promise for future studies that are more controlled on the basis of musical experience. Greater sample sizes would not only enable greater statistical power, but more subjects also provides more opportunities to analyze effects of more specific aspects of musical experience. These might include differential effects of reading musical notation, playing certain instruments, extent of practicing alone, playing in groups, extent of improvisation, musical styles, or having perfect pitch. It is also worth mentioning that the musician group only contained one female. Future studies might also control for an equal distribution of sex differences between groups.

Despite our limitations, our results extend investigations of load theory to the auditory domain and provide promising directives for future research on auditory load effects. To examine the effects of STM load, we used spatial location as the remembered identifier. Future studies should look at how load effects could vary with the exact same design, except instructing subjects to attend to pitch instead of spatial location. This paradigm could be extended to vary load with information about verbal, intensity, amplitude modulations, or frequency content. The same design could also be used to examine magnitude effects of load, where the same manipulations could be done with varying numbers of objects to be memorized. Such studies could provide more detailed insight onto the determinants of how load affects attention. Furthermore, cross-modal studies that expound upon auditory findings, rather than visual, could provide unique insight on these same issues.

* * *

The current study demonstrates that load effects on auditory spatial attention gradients during a sustained attention task are not constant for every location in space. Factors such as task processing conditions, load-dependent STM maintenance mechanisms, and musical experience could all influence profiles of reaction time in response to auditory targets. We attribute these differences to overlapping processing mechanisms for STM maintenance of spatial information and target detection, and changes in the hemispheric lateralization of spatial representation that result from musical experience.

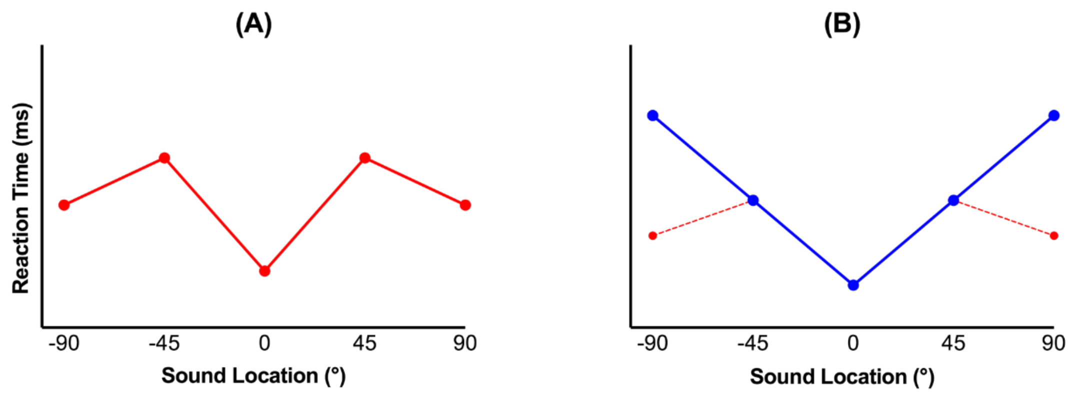

Figure 1. Reaction time as a function of sound location from our lab's findings (A) juxtaposed with what would be expected from a classic attention gradient (B). The red dotted line in (B) shows where the function in (A) diverges from the classic gradient model.

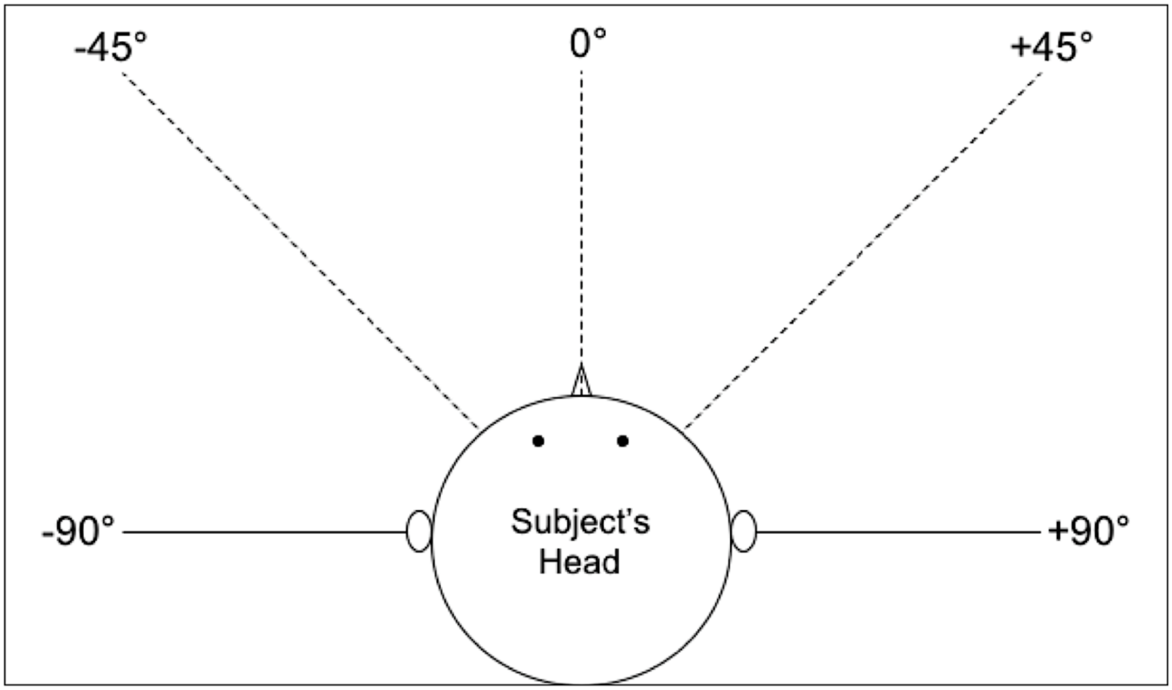

Figure 2. Target sound locations as presented across a 180° plane relative to the subject's head. Targets at 0° (the standard location) sounded from directly in front of the subject. ±90° represent the subject's far left (-90°) and far right

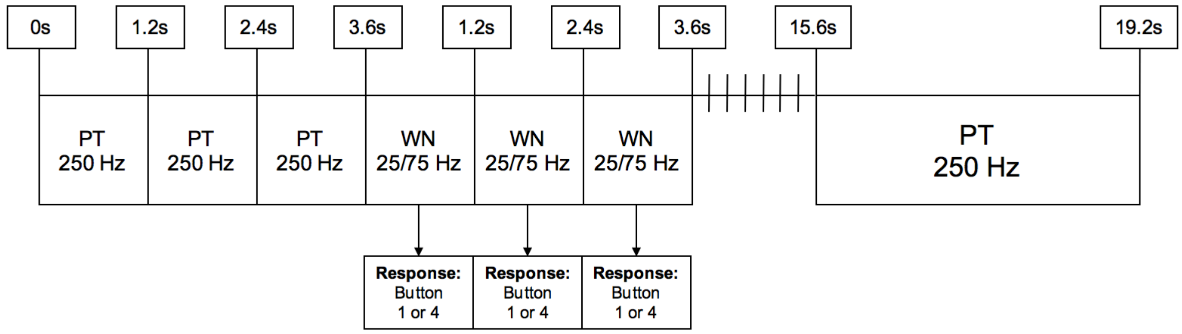

Figure 3. Example schematic of a given trial under the no-load (control) condition, where PT=pure tone and WN=white noise.

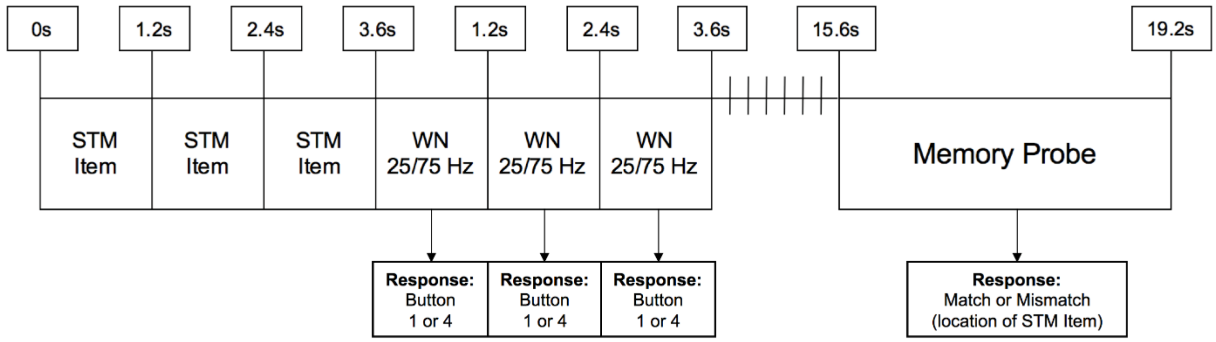

Figure 4. Example schematic of a given trial under the load condition, where STM item=sound whose location is held in STM, WN=white noise, and memory probe=same sound as STM item at either the same/different location.

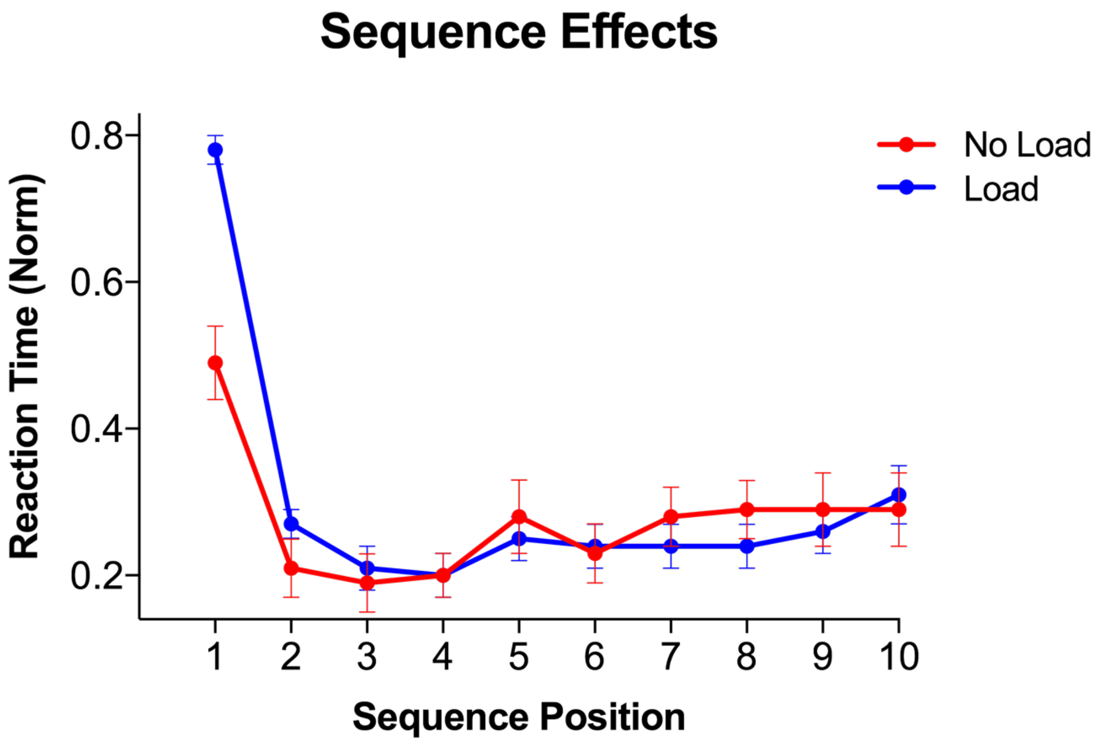

Figure 5. Reaction times plotted as a function of sequence position for target detection trials presented between the encoding and retrieval phase of the memory task. Since every group of target detection trials began with targets presented at the standard (0°), only target stimuli presented at 0° were able to assume every sequence position (1-10). Therefore, plotted data reflect reaction times only to target stimuli presented at 0°.

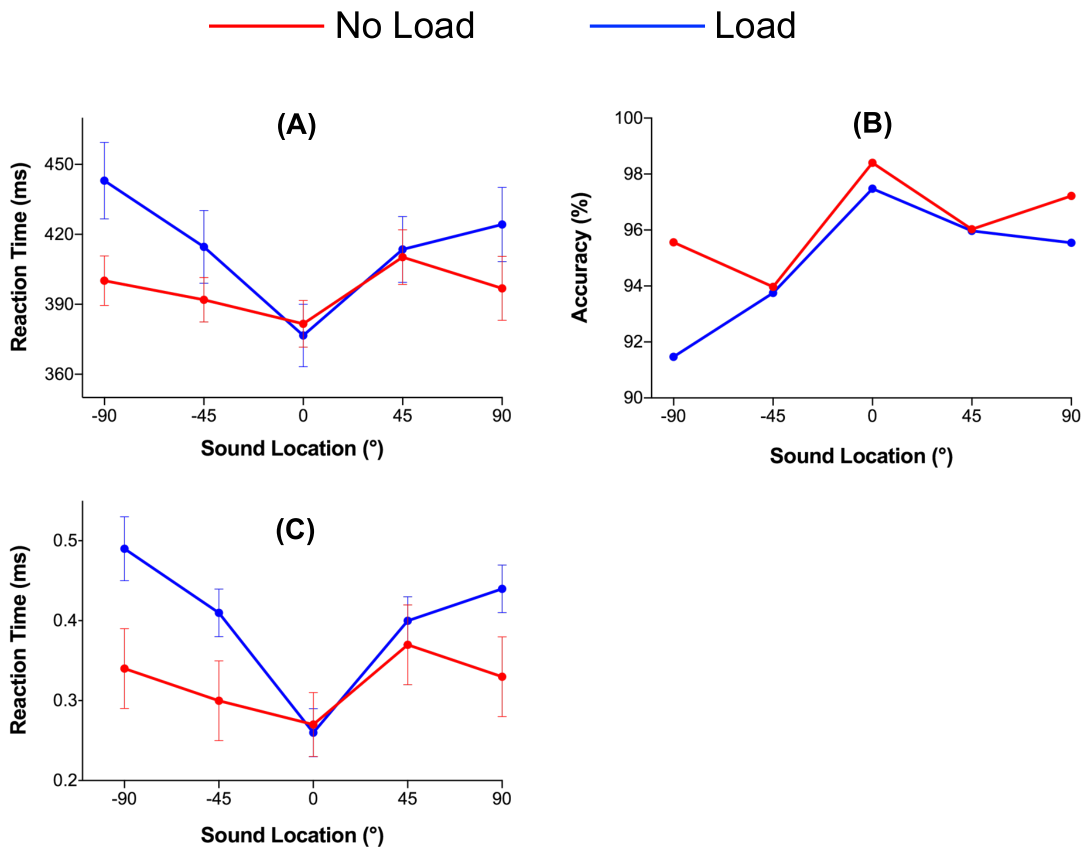

Figure 6. Behavioral results as a function of target sound location. Reaction time (A) and accuracy (B) as a function of location. (C) shows normalized results for the same data in (A), in order to control for individual differences in overall performance.

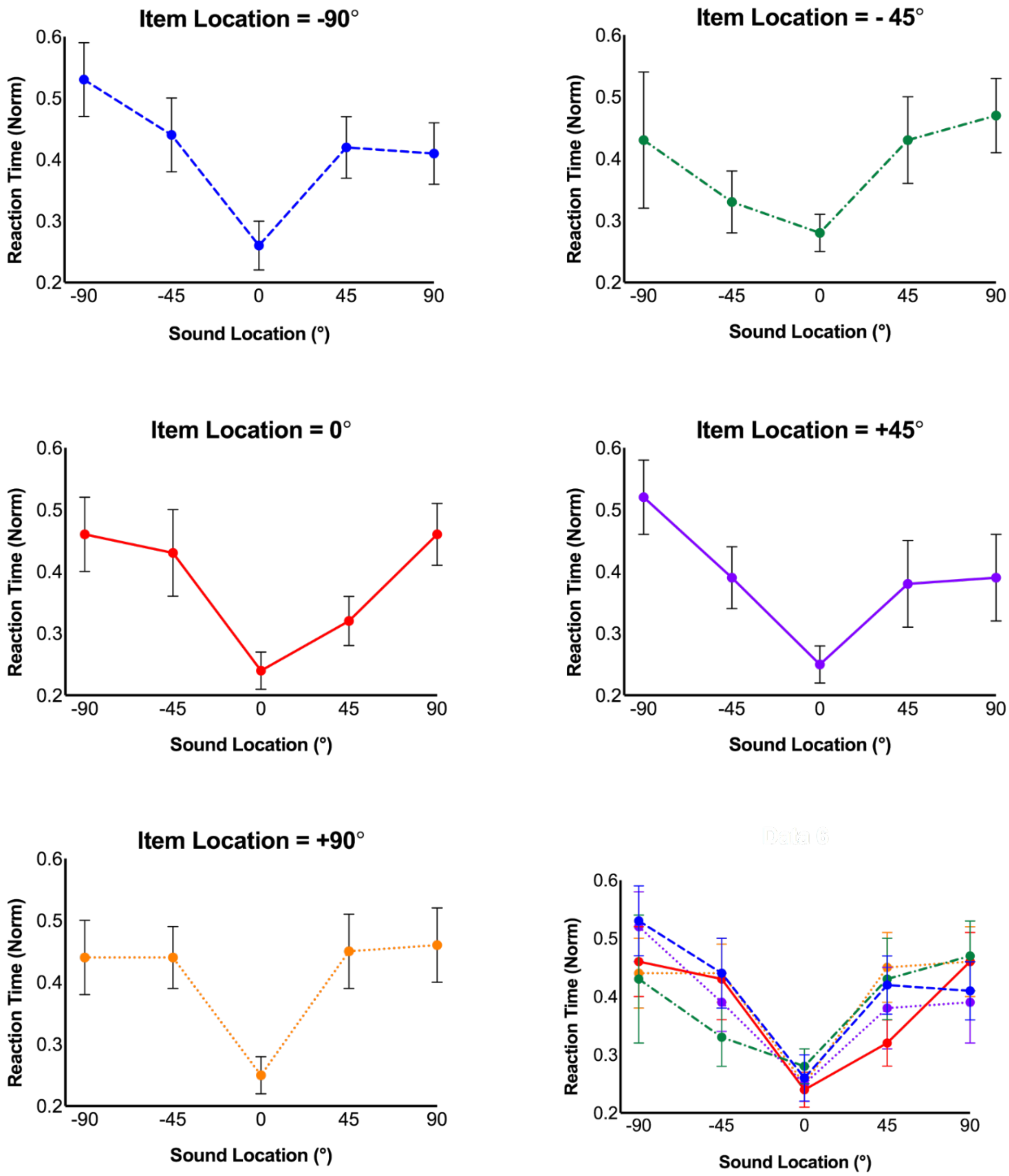

Figure 7. Reaction time as a function of target location for the load condition only. The separate plots represent reaction time data from load trials during which the same STM item location was stored. For example, the curve labeled -90° represents reaction times to all target-detection trials where the remembered location was subjects' far left.

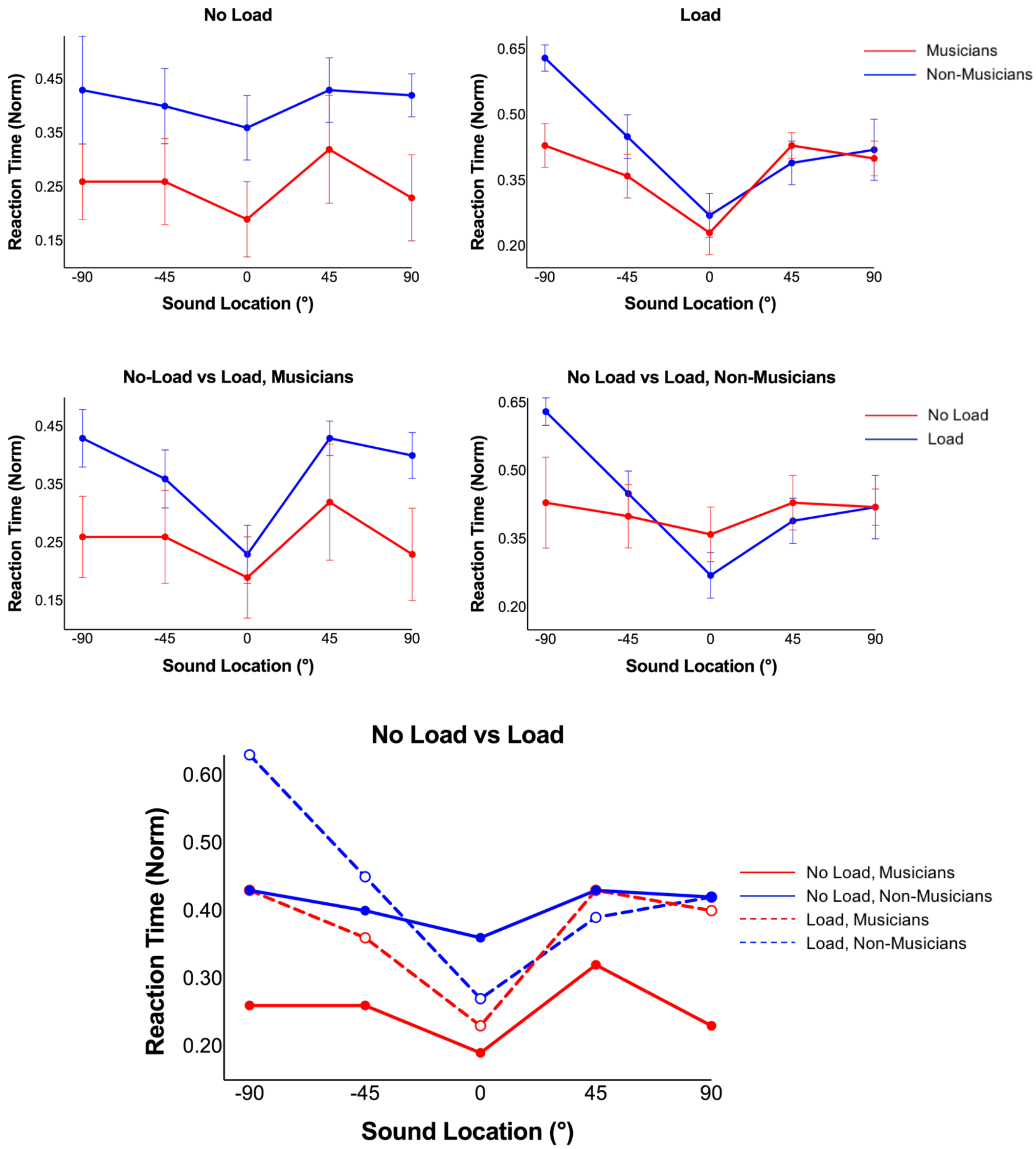

Figure 8. Between subjects reaction time data plotted as a function of sound location.

Group	n	# Male	# Female	Hand	Mean Age	Within Subjects	Between Subjects
Experimental	21	11	10	18 Right 2 Left 1 Mixed	20.7	✓	
Control	21	11	10	18 Right 2 Left 1 Mixed	20.7	✓	
Musician	8	6	2	6 Right 1 Left 1 Mixed	22.9		✓
Non-Musician	7	2	5	7 Right	19.1		✓

Table 1. Subjects' demographic information organized by group.

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