Dynamics of auditory spatial attention gradients

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ABSTRACT

Auditory spatial attention faces the conflicting demands of focusing on the current task while also rapidly shifting location to unexpected stimuli. We examined the interplay of sustained focus and intermittent shifts in an auditory spatial attention task. Most trials required a choice response from a standard location in virtual space (L-R: −90°, 0°, +90°), but occasionally the location shifted between 45°-180°. Reaction time curves for angular shifts had a quadratic shape, with slowing for small shifts but faster reaction times for larger shifts. The reaction time curves were maintained at faster stimulus rates and usually scaled to fit the range of stimulus locations. However, focus on the right had an attenuated curve, and did not scale to the range of locations. The findings suggest two mechanisms: a top-down bias centered on standard locations that decreases with distance, and a bottom-up bias that under these conditions increases with distance from the standard location.

1. Introduction

Focusing spatial attention on a location pertinent to one's current goals is vital for intelligent behavior. Yet attention must also be capable of rapid shifts to a different location in response to unexpected sounds that may signal opportunities or threats. This is because there is great survival value in being able to orient attention to things happening in the world that are not in the current focus of attention but, nonetheless, may demand immediate action (Bradley, 2009; Erulkar, 1972; Scharf, 1998). Sounds are a potent way to capture attention in this manner, and acoustic orienting, startle, and defensive responses are highly conserved across species (Bradley, 2009; Jerison, 1973; Sokolov, 1963). Moreover, it has been known for decades that the alerting effects of auditory stimuli are generally greater than with vision in attentional cueing tasks (Posner, 1978; Posner, Nissen, & Klein, 1976). Little is known about how the auditory system distributes attentional bias over space to deal with the "stability-flexibility" dilemma (Liljenström, 2003) of maintaining attention to accomplish current goals while also being receptive to attention capture by other events in the environment.

Although the vast majority of spatial attention studies use the visual modality, understanding how auditory spatial attention is allocated over space is important because hearing has a unique advantage among the senses due to its panoramic sensitivity. In contrast, the visual field in humans is not panoramic, which imposes spatial limitations on what can be detected at a given moment. There are also large differences in acuity between foveal, parafoveal, and peripheral areas of the retina,

and the 3-D location of best focus at any one instant is restricted to a particular distance from the eyes (De Valois & De Valois, 1990). To deal with these challenges, specialized motor and short-term memory systems are needed to move the eyes around to sample and retain information about a visual scene.

The situation is less complex in the auditory modality. Although overall spatial acuity is worse in audition vs. foveal vision, processing and representation of stimuli at panoramic locations and distances is more uniform (Blauert, 1997; Middlebrooks & Green, 1991; Mills, 1958). These differences between vision and audition should have implications for spatial attention control because audition does not have to consider the above complexities in 3-D perceptual coding, motor coding for eye movements, and short-term memory coding needed to put-together recently sampled visual information. We next consider in more detail how attention can be distributed over space in vision and audition.

Attention in the visual modality can be concentrated at one spatial location, with graded reductions in attentional benefits with increasing distance (reviewed in Cave, 2013). This "attention gradient" pattern likely reflects limited capacity, although limitations in the number of responses available at a given moment may also constrain attention (Allport, 1989). Spatial attention gradients in the auditory modality have been examined much less often. A few previous studies directed auditory attention with a cue followed by a target, and the locations of the cue and targets varied on a trial-by-trial basis (Mondor & Zatorre, 1995; Rhodes, 1987; Rorden & Driver, 2001; Spence & Driver, 1994).

The overall findings were consistent: there were monotonic increases in target reaction time with increased distance between cue and target locations.

However, some spatial visual attention studies found greater complexity in the topography of spatial attention, such as the possibility of more than one attentional focus when tracking several moving objects (Cavanagh & Alvarez, 2005). Decreases followed by increases in attention bias have been proposed to flank an attended location; a pattern described as a "Mexican hat" or inverted-U shape, that can be fit by a quadratic function (Caparos & Linnell, 2010; Müller, Mollenhauer, Rösler, & Kleinschmidt, 2005). Narrow quadratic-shaped attention gradients are predicted by the selective tuning computational model (Tsotsos et al., 1995), which is based on the biased competition framework (Desimone & Duncan, 1995). Quadratic gradients are an emergent property, and reflect a mechanism for preserving spatial attention selectivity in regions of visual cortex where neurons have very large receptive fields. The possibility of more complex shapes of spatial attention gradients has not been tested in the auditory modality, but is important for advancing theory about spatial hearing and also informs comparisons of attentional processes between modalities.

The above studies have examined attention gradients when experimenters cue subjects to frequently shift attention from trial-to-trial. Although purely behavioral studies rarely compare cued and sustained attention, neuroimaging work suggests important differences because distinct neural networks are associated with sustained vs. frequent shifts of attention (Dosenbach, Fair, Cohen, Schlaggar, & Petersen, 2008). In addition, cued attention likely has greater resistance to vigilance decrements (Warm & Parasuraman, 2008), more proactive control (Braver, 2012), and the cues that precede the targets have alerting effects (Posner, 1978). All of these factors suggest that it is important to complement work on auditory spatial attention with cueing methods by instead using a sustained attention paradigm.

As a practical matter, shifting auditory spatial attention every few seconds does not always comport well with everyday life. Auditory attention is often fairly constant at one location, as when carrying on a conversation or listening to music. For example, focus on a partner during an in-depth conversation often lasts many minutes, with intricate attention control such as turn-taking (Levinson, 2016). Thus the generality of conclusions regarding auditory attention gradients based on auditory cued attention tasks have yet to be tested. A previous study that mimicked the more natural situation of sustained attention found that infrequent shifts to a different location substantially increase reaction time (Roeber, Widmann, & Schröger, 2003). However, the Roeber et al. (2003) study was not designed to examine spatial attention in detail because only two locations were tested.

Our research group has developed a computational model to formalize the interactions between top-down attention gradients and bottom-up attention orienting associated with functioning as an early warning system (Golob, Venable et al., 2017). The output is the net effect of two attentional modules. One module is called the "goal map", and roughly corresponds to a typical attention gradient that declines from the currently attended location. The other module is the saliency map, which emphasizes bottom-up processing of sounds and has a bias away from the goal map focus. A major goal of this study was to test the prediction that auditory attention gradients in a sustained attention task would show an inverted U shape, characteristic of two modules, rather than a single-module with a monotonic gradient. Exploratory analysis compared gradients when attending to the left vs. right side of egocentric space, based on the hypothesis that the pronounced right ear advantage in perceiving verbal stimuli in dichotic listening studies (Hugdahl, 2003) may reflect a spatial bias.

The purpose of the current study was to test the hypothesis that auditory attention gradients will have a quadratic function over space when participants attend to one location for several minutes. The experiments will distinguish which of two alternatives derived from the visual literature (linear, quadratic) are operative during auditory sustained attention. In all of the experiments participants consistently maintained attentional focus to a region of acoustic space, termed the "standard location". We used the reaction time costs of occasionally shifting attention to a new location to map-out the spatial distribution of auditory attention. If a stimulus is presented at the currently attended location we, and others, assume that attention will facilitate information processing, with one indication being faster reaction times. When the stimulus is presented at a location that is not the current focus of attention there will be fewer attentional benefits and reaction times will be slower.

2. Methods

2.1. Participants

A total of 85 young adults were tested in three main experiments and one control experiment (Experiment 1: n = 42, age 19 ± 1.4, M/F = 12/30, 38 right handed; Experiment 2 and 3: n = 25, age 20 ± 1, M/F = 8/17, 21 right handed). The control experiment followed Experiment 1 (n = 18, age 23 ± 3, M/F = 5/13, 15 right handed). Three groups of different participants were used, corresponding to Experiment 1, the control experiment, and subjects that performed both Experiment 2 and 3. Based on Roeber et al. (2003) study, 25 subjects would be needed to have 0.80 power at a significance level of p < .05. Experiment 1 was exploratory, and more subjects were tested to examine individual differences in reaction time profiles over stimulus locations, sex differences, and test order, none of which had notable effects (data not shown). Handedness was determined by using the Edinburgh handedness inventory (Oldfield, 1971). None of the participants reported hearing impairment, and all pure tone thresholds were within normal clinical limits. Participants gave written informed consent before testing, as part of a protocol approved by the Tulane University Institutional Review Board.

2.2. Apparatus

Participants sat in a well-lit sound booth with a monitor in front of them. Acoustic stimuli were presented using insert headphones, and a response keypad was held by the subject. Details concerning the sounds that were presented are given in Section 2.3. Participants were instructed to look forward and to not close their eyes while performing the tasks.

2.3. Stimuli

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: $-90°$, $-45°$, $0°$, $+45°$, $+90°$). 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 (Miller, 2001). For each sound the algorithms employ the same cues that are used for sound localization by the auditory system under natural conditions (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. The final stimulus set had 10 stimuli: 5 locations × two amplitude modulation rates. Stimuli were presented with insert earphones (Compumedics-Neuroscan, Charlotte, NC) which had a passband > 10 kHz. Insert earphones were used rather than free-field speakers in order to limit the influence of visual indicators of sound sources and avoid changes in the relationship between sound source location and the ears due to any head movements.
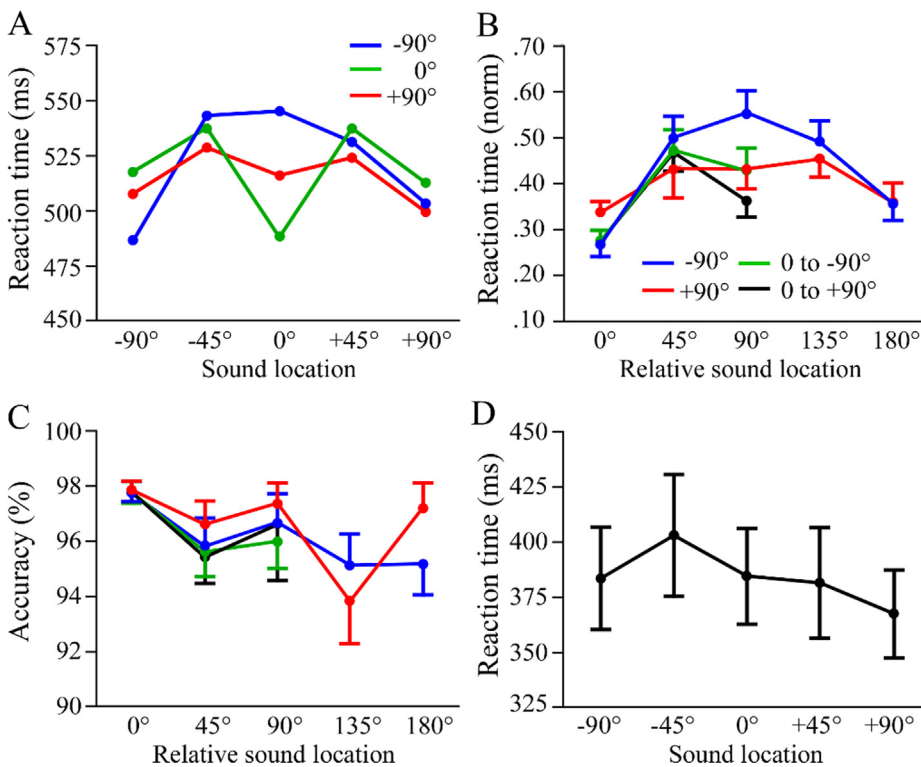
Fig. 1. Behavioral results in Experiment 1 and Control experiment. The left column (A, C) shows Experiment 1 results plotted in absolute spatial positions relative to the participant's head. In B the same results as A are replotted relative to the standard location, to illustrate how reaction time and accuracy were affected by location shifts away from the standard location. Normalized reaction times are shown in B to control for individual differences in overall reaction time. (D) Reaction time vs. stimulus location in the Control experiment. Error bars indicate standard error of the mean. Error bars are absent in A to better view the overlay of the three reaction time × location plots.

2.4. Experimental procedures

Each participant was first tested to verify that they correctly perceived the location of each sound. Stimuli corresponding to each of the five sound locations was repeatedly presented (stimulus onset asynchrony = 750 ms), and participants marked the perceived sound location on a sheet of paper that had perpendicular lines to indicate the midline and interaural axes. As with sounds presented from natural sources there was some variability in perceptual judgments, particularly for the ± 45° locations. However, all participants perceived the sounds at the intended locations in the correct order (e.g. the −90 stimulus was never perceived to the right of the −45 stimulus).

The same basic task was used in all of the experiments. Participants heard a sequence of amplitude modulated sounds that were presented at a fixed rate. For Experiments 1 and 3 the stimulus onset asynchrony (SOA) was 2.4 sec, while Experiment 2 had an SOA of 1.2 sec. Participants responded to each sound by pressing one of two buttons based on the amplitude modulation rate (25 or 75 Hz, 90% depth, p = .50/.50). Each block had an equal number of left and right response trials. The assignment of left/right hand to amplitude modulation rate was counterbalanced across participants.

For each block of 150 trials most stimuli were delivered from a standard location (p = .84). On some trials the location of the sound randomly shifted to 1 of the other 4 locations (p = .04/location), which are termed "shift" trials. Participants were asked to respond to the amplitude modulation rate regardless of sound location. Three standard locations were tested in separate trial blocks: far left (-90°), midline (0°), and far right (+90°). Two blocks per standard location were given, and the six possible orderings of standard location block pairs were counterbalanced across participants.

2.5. Data analysis and statistics

The behavioral measures were accuracy and median reaction time on correct trials. Occasionally participants did not respond; these no response trials were removed before calculating accuracy. Data for left and right hand responses were averaged separately and then averaged

together in order to ensure that any small differences in the number of errors or no responses for trials requiring the left vs. right hand did not affect the results. Normalized reaction times are also presented because our main interest is the profile of reaction time as a function of spatial location rather than individual differences in overall response speed. Normalized reaction times are expressed as values of 0.0–1.0, which are scaled over each subject's range of reaction times in all three standard conditions. All averaged data is publicly available at https://osf.io/ek5u7.

Statistical analysis used repeated measures analysis of variance (ANOVA). The left and right side standards were examined together because we were interested in comparing attention shifting from left-to-right vs. right-to-left. The two factors were standard location (−90°, +90°) and sound location (5). In some instances sound location was expressed as the location of a sound relative to the lateral standard location. This permitted a direct comparison of how the behavioral measures were affected as a function of how far away the shift was from each lateral standard location. To illustrate, when using relative locations 0° was always the standard location, 45° was the nearest shift location in absolute space. When the standard was −90° in absolute space the nearest shift was at −45° (a shift of 45° to the right); when the standard was +90° the nearest shift was +45° (45° to the left). The levels of the sound location factor were 0°, 45°, 90°, 135°, and 180°. The omnibus ANOVA was followed by planned contrasts using quadratic functions to assess reaction time as a function of the angular distance between the standard location and the location of the stimulus (0°, 45°, 90°, 135°, 180°). Our computational model, briefly described in the Introduction, predicted quadratic patterns of reaction time as a function of distance from the standard location. When the standard location was at midline (0°) stimuli could shift 90° to the left or right relative to the standard. Having shifts up to 90° in two directions prevented a direct comparison to standards on the left (-90°) or right (+90°), which had shifts up to 180° in one direction. For this reason results in the 0° standard condition were examined separately using one-way ANOVA with the factor of sound location (5). To analyze the left and right hemispaces follow-up planned contrasts for shift locations to the left (0°, −45°, −90°) and right (0°, +45°, +90°). Most of the subjects were

right handed, which prevented a quantitative comparison of handedness. Significance was defined as p < .05, and Greenhouse-Geisser correction was used to control for violations of sphericity. For clarity, the original degrees of freedom are reported below.

3. Results

3.1. Experiment 1

Reaction times as a function of stimulus location for each of the three standard conditions are shown in Fig. 1A. In order to compare the gradient-like effect across standard locations the results are also re-plotted in terms of each stimulus' angular distance from the standard location (Fig. 1B). Reaction times were normalized in B to control for individual differences in overall reaction time, which allows a better focus on the shapes of the reaction time × location functions. The ± 90° standard conditions were analyzed together using ANOVA with factors of standard (−90°, +90°) and stimulus location (5), with planned polynomial contrasts for each standard condition. The 0° standard condition used one-way ANOVA for location, with follow-up planned polynomial contrasts for the left (0, −45°, −90°) and right (0, +45°, +90°) hemispaces.

For the ± 90° standards there was a main effect of stimulus location ($F_{(4,164)} = 9.2$, p < .001, $\eta_p^2 = 0.18$) and a standard × location interaction ($F_{(4,164)} = 3.5$, p < .02, $\eta_p^2 = 0.08$). Polynomial contrasts at each standard location showed that the standard × location interaction was due to a strong, quadratic function for the −90° standard ($F_{(1,41)} = 34.3$, p < .001, $\eta_p^2 = 0.46$) but a much weaker, flatter profile when the standard was at +90° ($F_{(1,41)} = 6.8$, p < .02, $\eta_p^2 = 0.14$). Overall reaction times in the −90 vs. +90 standard conditions were similar. When the standard was located at 0° (midline) there was also a significant effect of location ($F_{(4,164)} = 4.0$, p < .01, $\eta_p^2 = 0.09$). Planned polynomial contrasts showed that reaction time increased for stimuli at the near 45° location and then decreased for the far 90° location in both the left ($F_{(1,41)} = 7.4$, p < .01, $\eta_p^2 = 0.15$) and right ($F_{(1,41)} = 8.1$, p < .01, $\eta_p^2 = 0.16$) hemispaces.

Taken together, when the sound location infrequently shifted away from the standard location reaction times had a quadratic function, evident by increased reaction times at nearby locations which then decreased at greater distances. Comparison of left vs. right sided standards showed a more pronounced quadratic profile when attending to the left relative to the right. This pattern was seen in each subject's first trial block, so is not due to carry-over effects from previous standard locations (data not shown).

Analysis of accuracy for −90 and +90 standards revealed a main effect of location ($F_{(4,164)} = 5.7$, p < .01, $\eta_p^2 = 0.12$), due to a progressive reduction in accuracy as the distance between the standard and stimulus locations increased. Accuracy data are plotted in Fig. 1C with respect to the standard location to more clearly show the gradual decrease with greater distance from the standard location. The effect of location in the 0° standard condition did not attain significance (p > .50), although accuracy was lower for all of the shifts relative to the standard (p < .02). The no response rates were 2.8 ± 0.7%, 3.6 ± 0.6%, and 2.3 ± 0.5% for −90°, 0°, and +90° standards, respectively, and did not significantly differ among conditions (p > .15).

3.2. Control experiment

The above reaction time results showed an inverted u-shaped, quadratic curve as a function of the distance between a stimulus' location and the standard location. However, across all conditions the most lateral sound locations (−90°, +90°) tended to have fast reaction times. What if participants respond faster to lateral locations regardless of where they are attending? The precision of spatial hearing is greatest at the midline, and decreases for more lateral locations (for example, Jeffress, 1948; Makous & Middlebrooks, 1990). The specific pattern

depends on a host of variables such as stimulus bandwidth, frequency, task, and whether testing is in the horizontal plane or included elevation too (Blauert, 1997). Further, in addition to spatial acuity differences across locations there may be other nuisance variables that relate to the sounds themselves rather than attention factors. We note that if the patterns of different reaction times as a function of stimulus and attended locations in Experiment 1 were due to bottom-up processing of the sounds themselves, it would not matter where the subjects were attending in space. Instead, for Experiment 1 the pattern of reaction times as a function of location strongly depended on where subjects were attending in space (i.e. the standard location).

Nonetheless, in an effort to rigorously define how stimulus features relate to reaction time, we next recruited a new group of participants and had them perform the same amplitude discrimination task as in Experiment 1. The only difference was that all locations were equally likely (p = .20/location). Reaction time results are shown in Fig. 1D. A one-way ANOVA across the 5 stimulus locations did not have a significant effect of location (p > .07). As additional protection against insufficient power, ten more subjects were added from preliminary testing (total n = 28), but the effect of location was still non-significant (p > .10), and there was no trace of a quadratic fit ($F_{(1,27)} = 0.02$, p > .85). This shows that the quadratic reaction time profiles in Experiment 1 were not influenced by faster overall reaction times for stimuli presented at the ± 90° locations. Comparison of overall reaction times among the control and experimental groups (pooled across standard locations) had a significant group difference ($t_{(58)} = 2.3$, p < .03, $\eta_p^2 = 0.09$), with faster reaction times in the control (432 ± 31 ms) vs. experimental group (518 ± 20 ms). Analysis of accuracy in the control group showed a significant effect of location ($F_{(4,68)} = 3.8$, p < .02, $\eta_p^2 = 0.19$), due to greater accuracy at midline (96.8 ± 1.4%) relative to the four lateral locations (range = 92.5–94.2%). Accuracy was comparable among the control and experimental groups (96 ± 1% vs. 94 ± 2%, respectively; p > .10).

3.3. Experiment 2

One potential mechanism for the quadratic spatial profiles in Experiment 1 is that slower reaction times to shifts reflect orienting responses that are weighted by distance from the standard location. Relatively automatic orienting to sounds that occasionally differ from what is expected has been shown to slow reaction time (Parmentier, 2014). The slower responses are presumably due to additional time needed to shift attention to the deviant sound or sensory feature, process the deviant information, and reorient back to the primary task. Occasional shifts in the location of a target sound is one way to slow responding, relative to the expected location (Roeber et al., 2003). If the quadratic reaction time profile observed in Experiment 1 is due to orienting responses to occasional shifts in location, then the shape of the profile may be sensitive to stimulation rate. Previous work shows that repeated and/or more rapid presentation of stimuli induces greater habituation of the orienting response (Barry, 2009; Sokolov, 1963), which is particularly evident with auditory event-related potentials (Golob, Miranda, Johnson, & Starr, 2001; Naatanen & Picton, 1987). We therefore ran a new group of participants but reduced the SOA from 2.4 sec down to 1.2 sec, and compared the fast SOA group (1.2 sec) to the slower SOA group (2.4 sec) from Experiment 1. The prediction was that if the orienting response drives the quadratic profile across locations then the profile would become flatter with a faster stimulus presentation rate. In addition to testing temporal aspects of the attention effects Experiment 2 also serves as an opportunity to replicate the basic findings of quadratic-shaped curves seen in Experiment 1.

The data were analyzed as in Experiment 1, with separate ANOVA tests for the ± 90° standards and 0° standards using factors of standard (2) for the ± 90° conditions and location (5). A between subjects factor of group was also included (slow SOA, fast SOA). A plot of reaction time
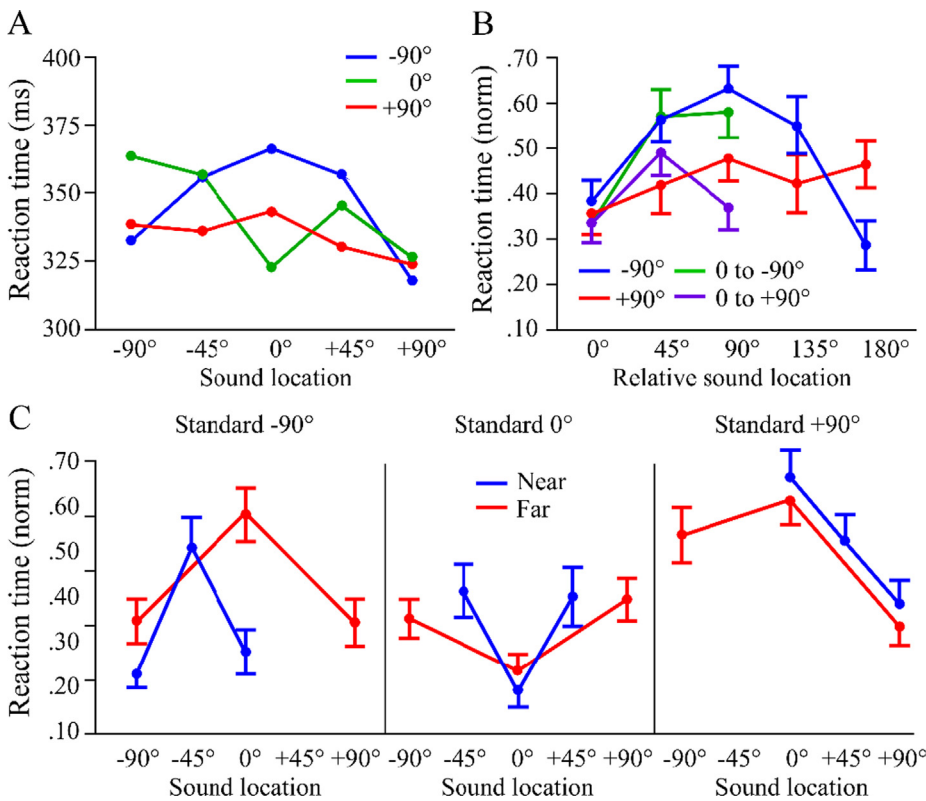
Fig. 2. Reaction time as a function of shift distance in Experiment 2 and Experiment 3. Experiment 2 reaction times as a function of location (A), and the same data plotted relative to the standard location using normalized reaction times (B). (C) Normalized reaction time results from Experiment 3 in all three standard locations. Error bars indicate standard error of the mean.

data in the 1.2 SOA condition is shown in Fig. 2A and 2B. The most important result was that in both ANOVA tests (± 90° standards, 0° standards) there were no significant group interactions (analysis of ± 90° standards: non-significant group × standard; group × location; group × standard × location; analysis of 0° standards: non-significant group × location). There was a main effect of group in both the ± 90° standards ($F_{(1,65)} = 41.1$, $p < .001$, $\eta_p^2 = 0.39$) and 0° standard ($F_{(1,65)} = 38.2$, $p < .001$, $\eta_p^2 = 0.37$) analyses, which was due to shorter reaction times in the fast SOA group.

Although there were no group interactions above, to independently examine replicability the same ANOVA tests as in Experiment 1 were performed on only the new subjects in the fast SOA group. The reaction time findings replicated those of Experiment 1. Comparison of the ± 90° standards had significant effects of stimulus location ($F_{(4,96)} = 6.8$, $p < .001$, $\eta_p^2 = 0.22$) and a standard × location interaction ($F_{(4,96)} = 4.0$, $p < .02$, $\eta_p^2 = 0.14$), while the 0° standards had a significant main effect of location ($F_{(1,41)} = 5.1$, $p < .01$, $\eta_p^2 = 0.18$).

Examination of accuracy in the ± 90°conditions revealed a significant effect of group ($F_{(1,65)} = 49.7$, $p < .001$, $\eta_p^2 = 0.43$) because accuracy was higher in the slow SOA group (96 ± 1% vs. 86 ± 1%). There were also significant effects of standard, location, and interactions of location × group and standard × location, all of which were subsumed under a group × standard × location interaction ($F_{(4,260)} = 5.8$, $p < .000$, $\eta_p^2 = 0.08$). The three-way interaction reflected the above effects of group and location, except accuracy was relatively high (94%) at the 0° location in the 1.2 sec SOA group in the +90° standard condition. The no response rates were 4.0 ± 0.9%, 5.6 ± 1.3%, and 3.6 ± 1.1% for −90°, 0°, and +90° standards, respectively, and did not significantly differ among conditions ($p > .10$). For the 0° standard condition accuracy was also greater in the slow SOA group ($F_{(1,65)} = 30.0$, $p < .001$, $\eta_p^2 = 0.39$; 96 ± 1% vs. 89 ± 1%). There was also a main effect of location, indicating greater accuracy at the 0° standard location relative to the other four locations ($F_{(4,260)} = 38.2$, $p < .03$, $\eta_p^2 = 0.04$). Taken together with the reaction time data, the main accuracy finding was that a speed-accuracy tradeoff existed among the groups; the fast SOA group had shorter reaction times but was less accurate relative to the slow SOA group.

3.4. Experiment 3

Previous work on visual attention has shown that the probability of stimulus presentation at a given location has a strong impact on performance (e.g. Chun & Jiang, 1998; Miller, 1988; Posner, Snyder, & Davidson, 1980). The spatial range of attentional bias, subject to task factors, has also been explored in the context of visual search (Belopolsky & Theeuwes, 2010) and perceptual or cognitive load manipulations (Lavie, 2005; Linnell & Caparos, 2011). Related work shows that cueing can be used to define a spatial range (or 2-D area) where stimuli can occur (Greenwood & Parasuraman, 1999). Cueing thus defines a region of space where stimuli may be presented from a region with zero probability of stimulus occurrence. In effect, range is implicit in nearly all studies of spatial attention because task-relevant stimuli are presented within the range of, for example, a computer monitor or a set of speakers in a room.

In Experiments 1 and 2 the range of space where sounds can occur, and the locations where sounds were never presented, define regions of space with, respectively, non-zero and zero probability for stimulus presentation. Within the range of locations tested in these experiments the reaction time × location curve adopted a quadratic shape to varying degrees, depending on the standard location. The purpose of Experiment 3 was to determine if the quadratic reaction time profile observed in Experiments 1 and 2 is adjusted to fit the range of sound locations that are used in a given trial block. Alternatively, the spatial reference frame for attention gradient effects could be fixed in egocentric space, in which case the reaction time profile over space would not be affected by the range of possible sound locations. To distinguish these two possibilities compared performance over a wide range of sound location (180°, as above), with a narrower range spanning 90°.

The same task was used as in Experiments 1 and 2, with the exception that there were three stimulus locations in each condition instead of five. In the wide condition the three locations were separated by 90°, while in the narrow condition the locations were separated by

45°. For example, when the standard was at $-90°$ the wide condition delivered stimuli from $-90°$, $0°$, and $+90°$ while the narrow condition presented sounds from $-90°$, $-45°$, and $0°$. The SOA was 2.4 sec.

The reaction time measures as a function of spatial range (narrow, wide) for each of the standard locations are shown in Fig. 2C. Normalized data are shown to better assess the shape of the reaction time functions for narrow and wide ranges by taking into account any overall differences in reaction time between the narrow and wide ranges. Results in the $-90°$ and $0°$ standard conditions suggest that the quadratic profile scaled to the range of locations. The most lateral locations had comparable, fast reaction times while the middle location was much slower even though the physical location of the shift stimuli were different in the narrow and wide conditions. In contrast, for the $+90°$ condition reaction times nearly overlapped with respect to the physical sound locations in the narrow and wide range conditions. Thus, reaction times scaled to the range in the $-90°$ and $0°$ conditions but were relative to absolute space in the $+90°$ condition.

We quantitatively tested these impressions using 2 (range) × 3 (location) ANOVA tests. Each standard location was tested separately because visual inspection suggests different scaling effects (relative vs. absolute space) for the $-90°$ and $+90°$ conditions. For $-90°$ standards there was a main effect of location ($F_{(2,48)} = 18.3$, $p < .001$, $\eta_p^2 = 0.43$). Critically, both the range effect ($p > .30$, $\eta_p^2 = 0.04$) and the range × location interaction ($p > .50$, $\eta_p^2 = 0.02$) were not significant. Similarly, for the $0°$ standards there was a main effect of location ($F_{(2,48)} = 6.9$, $p < .01$, $\eta_p^2 = 0.22$), but the range × location interaction ($p > .30$, $\eta_p^2 = 0.05$) and range main effect ($p > .80$, $\eta_p^2 = 0.001$) were not significant. The lack of range × location interactions shows that the shape of the reaction time profile over locations was comparable for the narrow and wide location ranges. For the $+90°$ standard there was a significant range × location interaction ($F_{(2,48)} = 5.0$, $p < .02$, $\eta_p^2 = 0.17$). The interaction was due to a progressive increase in reaction time over locations in the narrow range, while an increase and then a small decrease was evident in the wide range.

Analysis of accuracy data showed that when the standard was at $-90°$ or $+90$ there were no significant effects of range or location, and the range × location interaction was also not significant. For standards at $0°$ there was a significant main effect of location ($F_{(2,48)} = 6.2$, $p < .01$, $\eta_p^2 = 0.21$), which was due to greater accuracy at $0°$ relative to either of the lateral locations. There were no significant effects or interactions for no response rates ($p > .20$; $2.2 \pm 0.6\%$, $3.7 \pm 1.1\%$, and $2.5 \pm 0.8\%$ for $-90°$, $0°$, and $+90°$ standards, respectively).

4. Discussion

This study used occasional shifts in sound location to map-out spatial attention gradients in a sustained attention task. The main results were that occasional shifts led to a quadratic profile of reaction time when plotted as a function of distance from the standard location. Reaction times increased for nearby shifts, and then decreased for shifts to more distant locations. This profile was evident in all three standard conditions but was attenuated in the far right standard relative to standards at the far left and midline. Data from a control experiment showed that the quadratic reaction time profile was not due to differences in sound location per se. These findings were then replicated at a faster stimulus rate, which did not support a classic orienting response as a mechanism underlying the quadratic reaction time profile. Finally, reducing the range of sound locations caused the reaction time profile to contract and fill the range, but only when the standard was at the left or midline location. The differential impact of the range manipulation suggested that spatial attention bias when focusing at left and midline locations was relative to the range, but centered on absolute space when attending to the right side.

4.1. Spatial attention & quadratic gradient shape

The finding that reaction times increase when sounds shift to a position near the standard agrees with previous work where attention focus was manipulated with a cue whose location varied across trials (Mondor & Zatorre, 1995; Rhodes, 1987; Rorden & Driver, 2001; Spence & Driver, 1994). Progressive declines in attentional benefits with greater distance from the attentional focus is well documented in visual studies using 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). An important difference here was that for even larger spatial shifts reaction times sped-up, which falsified a simple gradient model as applied to this task. A control experiment ruled-out factors related to the stimuli themselves that might relate to the main results, such as differences in spatial acuity among locations.

There are a host of factors that may be influence whether reaction time progressively increases away from an attended location or, instead, has a quadratic-shaped profile. Most previous studies varied the attended location across trials by using a cue, while in the current study the expected target location was invariant across trials. Thus the standard location is highly probable, and attentional bias is known to strongly depend on expectations based on probability (Itti & Baldi, 2009; Shaw & Shaw, 1977), which can interact with attentional cueing (Geng & Behrmann, 2005; Klein, 1994). Overall, the findings here suggest auditory spatial attention gradients may adopt different shapes in cued vs. sustained attention tasks, although a direct comparison would be needed to test this possibility.

Task-specific variables known to affect attention gradients in the visual modality are also relevant, such as the type of task (e.g. detection vs. discrimination), the specific type of stimulus features that are task relevant, such as brightness or form (Downing, 1988), and the ecological significance of stimuli (New, Cosmides, & Tooby, 2007). Perceptual and short-term memory load are also important factors in the spatial extent of visual attention (Lavie, 2005; Linnell & Caparos, 2011). Some electrophysiological studies suggest that the range of auditory attentional focusing depends on whether perceptual load is low (Golob & Holmes, 2011; Mock, Seay, Charney, Holmes, & Golob, 2015) or high (Teder-Salejarvi, Hillyard, Roder, & Neville, 1999). The impact of short-term memory load has not been extensively investigated in the auditory modality. We recently found that loading short-term memory with spatial, but not verbal, information narrowed presumed attention gradients in the same task used in the present study (Golob, Winston et al., 2017). Here we show for first time that the extent of an auditory attention gradient has pronounced asymmetries depending on whether subjects focus on the left vs. right side, with a more pronounced gradient when attending to the left.

There is some precedent in visual studies for quadratic attention profiles, sometimes termed "Mexican-hat" shaped gradients, which occur over a relatively small range of locations (Caparos & Linnell, 2010; Müller et al., 2005). The Mexican hat pattern may reflect a mechanism for inhibiting input from neurons that have receptive fields close to the attended location, particularly for higher levels of the visual system in response to cluttered visual arrays (Tsotsos et al., 1995). Receptive fields of neurons in the auditory system are generally very large, typically encompassing much of the contralateral hemispace (Middlebrooks & Pettigrew, 1981; Recanzone, 2000), which may explain why the quadratic profile observed here is much wider relative to observations in the visual modality. However, additional complexities are evident in the spatial tuning of auditory neurons in marmosets, with reference frames centered on contralateral-ipsilateral, medial-lateral, and front-back egocentric directions (Remington & Wang, 2018). In addition, the asymmetries seen when attending to the left vs. right sides, as well as the impact of the range of locations in Experiment 3 also suggest that quadratic shaped gradients are not fully explained as a

result of fixed receptive fields.

4.2. Time and spatial range effects – Experiments 2 and 3

To test for a role of orienting responses that may vary as a function of stimulus location, the stimuli in Experiment 2 were presented twice as fast as in Experiment 1. The rationale was that if reaction times to the far shifts speed-up because of an orienting response then the faster rate would induce some habituation of the orienting response (Sokolov, 1963) and flatten-out the reaction time profile across locations. This idea was not supported by the data because the reaction time profiles in Experiments 1 and 2 did not significantly differ. This one comparison is not decisive because there may not have been enough of a difference in SOA between conditions, and key aspects of orienting responses may be best examined using psychophysiological measures (Barry, 2009; Bradley, 2009). Alternatively, the profile of reaction times may not reflect an orienting response, and is instead a consequence of inhibiting input from regions near the attended location, as suggested by some visual attention studies and the selective tuning model discussed above.

The spatial extent of attention gradients in the visual modality has been difficult to pin down because depending on the task demands attention can be tightly focused or diffusely spread-out (Anton-Erxleben & Carrasco, 2013; Hughes & Zimba, 1985). Here we found that the reaction time profile contracts to fill the space of sound locations in the left and midline standard conditions. The narrower reaction time profile in the left and right hemispaces for the midline standard is also likely due to this range effect. As with the overall shape of the reaction time profile, the right standard condition had a different result. In this case the attentional gradient overlapped for the narrow and wide conditions, suggesting a reference frame centered on absolute space rather than the expected range of sound locations. In a previous study, we found most brain sources coded for space relative to an attended location, except for a left parietal region that first coded for absolute space before switching to a relative space representation (Mock et al., 2015). Note that the range manipulations also implicitly examine stimulus probability, with p = 0 for locations outside the range. A role for short-term memory is also embedded in the range experiment because the determination of range requires some experience over trials to define and maintain knowledge of the current range.

4.3. Broader considerations

The quadratic reaction time profile strongly suggests that at least two factors are needed to explain the current reaction time results. One is an attention gradient centered on the standard location that diminishes in strength with distance, and concept that is well-supported by prior findings (Cave, 2013). The reaction time benefits of responding to stimuli at the standard location indicates a top-down influence due to task instructions and experience with it being the most probable stimulus location. However, a diminishing gradient centered on the standard location cannot explain why reaction times speed-up at far shift locations. Some form of bottom-up orienting may be needed to explain the quadratic profile. We considered the orienting response, and although it was not falsified, the idea that the quadratic function was due to a classic orienting response that would habituate at faster rates was not supported by the current results.

Other possibilities are inspired by the ecologically-based idea that spatial hearing acts as an early warning system (Schafer, 1977; Scharf, 1998), which may have a different spatial tuning than the voluntary, top-down attention gradient. Note that factors and mechanisms discussed above reflect the algorithmic level of cognitive description, and are compatible with broader ecological considerations (Marr, 1982). Within this scheme, one possibility is to have a bottom-up orienting process biased for locations away from the top down focus. This arrangement was proposed in the context of visual search, where large attentional shifts away from the currently attended location may

encourage efficient sampling (Bahcall & Kowler, 1999), and has been explored by our lab via computational modeling (Golob, Venable et al., 2017). The second possibility is a bottom-up attentional bias with comparable sensitivity in all directions. It is worth noting that unlike the visual system there is no auditory equivalent of the limited visual field of the fovea: audition has panoramic sensitivity at all times. In this scenario the top-down function would have a region of facilitation flanked by inhibition, which returns to a baseline level of attentional bias for the remaining locations. The finding that reaction times were comparable for standards and the farthest shift location is problematic for this account because there would be little attentional facilitation at the standard location. Lastly, it is worth noting that a wide, but nonetheless restricted, range of locations was tested (180°). The above possibilities for bottom-up orienting may depend on the spatial range of the sounds, with "edge effects" in a restricted range but panoramic orienting with a full 360° azimuth range of sound locations.

Generally speaking, we suggest that a stability-flexibility dilemma (Liljenström, 2003) (also termed the "shielding–shifting dilemma" (Goschke & Bolte, 2014)) is inherent to focusing attention at one location while diffusely monitoring others. This may be an instance of a functional incompatibility, similar in kind to what is studied in memory systems (Sherry & Schacter, 1987). Researchers have historically distinguished voluntary and involuntary attention, and neuroscientific methods are revealing the neural basis of complementary and interactive attention systems dedicated to goal-directed and stimulus driven processing (Corbetta, Patel, & Shulman, 2008). We speculate that the main finding of quadratic-shaped auditory attention gradients may be the net result of interplay among these two attentional systems.

Differences among standard locations fell into two categories: far left and midline standards vs. far right standards. The right side standard condition differed by having smaller reaction time increases when the stimulus location shifted (Experiments 1 and 2), and did not scale with the range of locations (Experiment 3). Previous auditory studies using a cue-target paradigm did not note any asymmetries (Mondor & Zatorre, 1995; Rorden & Driver, 2001). Perhaps the most prominent auditory asymmetry is the "right ear advantage", which is evident with sustained attention during dichotic listening (Hugdahl, 2003; Kimura, 1967; Yurgil & Golob, 2010). When different stimuli with similar basic perceptual features, such as two consonant-vowels, are simultaneously presented to the left and right ears via headphones participants are usually more likely to perceive and remember information delivered to the right ear, particularly for verbal material. The bias towards the right ear is readily manipulated by instructions on where to attend (Bryden, Munhall, & Allard, 1983; Hugdahl, Carlsson, & Eichele, 2001). One intriguing possibility is that the "right ear advantage" is a spatial, rather than an ear, bias (Morais, 1974; Morais & Bertelson, 1975). Future work is needed to test this possibility, as we do not currently have a good explanation for the substantial performance asymmetries evident when the standard location was at the far left vs. far right locations.

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