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Biases of Spatial Attention in Vision and Audition

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Abstract

Neurologically normal observers misperceive the midpoint of horizontal lines as systematically *leftward* of veridical center, a phenomenon known as pseudoneglect. Pseudoneglect is attributed to a tonic asymmetry of visuospatial attention favoring left hemispace. Whereas visuospatial attention is biased toward left hemispace, some evidence suggests that audiospatial attention may possess a right hemispacial bias. If spatial attention is supramodal, then the leftward bias observed in visual line bisection should also be expressed in auditory bisection tasks. If spatial attention is modality specific then bisection errors in visual and auditory spatial judgments are potentially dissociable. Subjects performed a bisection task for spatial intervals defined by auditory stimuli, as well as a tachistoscopic visual line bisection task. Subjects showed a significant *leftward* bias in the visual line bisection task and a significant *rightward* bias in the auditory interval bisection task. Performance across both tasks was, however, significantly positively correlated. These results imply the existence of both modality specific and supramodal attentional mechanisms where visuospatial attention has a prepotent leftward vector and audiospatial attention has a prepotent rightward vector of attention. In addition, the biases of both visuospatial and audiospatial attention are correlated.

Keywords

Line Bisection; Pseudoneglect; Visuospatial Attention; Audiospatial Attention

INTRODUCTION

Hemineglect

Hemineglect refers to a deficit of attention towards stimuli located within contralesional (typically left) hemispace, defined in retinocentric, egocentric or allocentric coordinates (Bisiach, Capitani, Columbo & Spinnler, 1976; Heilman & Valenstein, 1979; Bisiach, Bulgarelli, Sterzi & Vallar, 1983; Karnath, Schenkel & Fischer, 1991; Driver, Baylis, Goodrich & Rafal, 1994; Bisiach, 1996). Left hemispacial neglect occurs most commonly after lesions to right inferior parietal or temporoparietal cortex, but may also result from lesions to frontal or cingulate cortex, or to subcortical structures (Heilman & Valenstein, 1972a; Watson, Valenstein & Heilman, 1981; Mesulam, 1981; Vallar & Perani, 1986). Line bisection tasks are commonly employed to assay asymmetries of spatial attention. Neglect patients bisect horizontal lines of moderate length significantly rightward of veridical center, as though

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ignoring the left-hand side of the stimulus or, alternatively, being hyperattentive to the right-hand side. Hemispatial neglect has also been reported to occur for auditory stimuli (Heilman & Valenstein, 1972b; Hugdahl, Wester & Asbjornsen, 1991).

Pseudoneglect

It is well established that visuospatial attention in neurologically normal subjects is asymmetrically distributed as well, resulting in a modest but systematic and significant leftward deviation of perceived line midpoint in line bisection tasks (Bradshaw, Nathan, Nettleton, Wilson & Pierson, 1987; McCourt & Olafson, 1997; McCourt & Jewell, 1999; Jewell & McCourt, 2000; McCourt, Garlinghouse & Slater, 2000; McCourt & Garlinghouse, 2000^{a,b}; McCourt, 2001; McCourt, Freeman, Tahmahkera-Stevens & Chaussee, 2001; McCourt, Garlinghouse & Butler, 2001; Foxe, McCourt & Javitt, 2003; McCourt, Garlinghouse & Reuter-Lorenz, 2005; McCourt, Shpaner, Javitt & Foxe, 2008; Leone & McCourt, 2010), a left hemifield bias in perceived luminance in the greyscales task (Nicholls, Bradshaw & Mattingley, 1999; Nicholls & Roberts, 2002), a left hemispatial bias in perceived stimulus size (Nicholls, Bradshaw & Mattingley, 1999; Charles, Sahraie & McGeorge, 2007) and numerosity (Luh, Rueckert & Levy, 1991; Nicholls, Bradshaw & Mattingley, 1999), and a left hemifield advantage in the processing of faces (Levy & Heller, 1981). This constellation of left-biased asymmetries of spatial attention is called pseudoneglect (Bowers & Heilman, 1980; Jewell & McCourt, 2000). The phenomena of neglect and pseudoneglect, as their names suggest, are theorized to be twin manifestations of a common and fundamental hemispheric asymmetry in the neural substrates of visuospatial attention (McCourt & Jewell, 1999). Supporting this idea are experiments illustrating that a variety of stimulus and task-related variables modulate the magnitude and direction of both neglect and pseudoneglect in a complimentary manner (Anderson, 1996; McCourt & Jewell, 1999).

Visual and Auditory Spatial Attention

Most research on spatial attention has focused on visual processing, but environmental space is monitored by multiple sensory modalities (Stein & Meredith, 1993), and there is a burgeoning interest in developing a comprehensive understanding of multisensory attention and perception (Calvert, Spence & Stein, 2004).

Pseudoneglect arises due to a prepotent vector of visuospatial attention deployed into left hemispace by the dominant right cerebral hemisphere. There is some evidence for a rightward asymmetry in the deployment of spatial attention within the auditory modality (Cusak, Carlyon & Robertson, 2001; Dufour, Touzalin & Candas, 2007; Corral & Escera, 2008; see however: Bisiach, Cornacchia, Sterzi & Vallar, 1984; Vallar, Guariglia, Nico & Bisiach, 1995; Kerkhoff, Artinger & Ziegler, 1999). If the leftward bias observed in visuospatial attention arises from asymmetry in a supramodal attentional system, then both visual and auditory spatial attention should be similarly biased. If, however, a bias in auditory spatial attention is found which differs from that for visuospatial attention, then this implies that auditory and visual spatial attention are governed by modality-specific processes. Using a within-subjects design we investigate the relationship between biases in visual and auditory spatial attention using visual line bisection and auditory interval bisection tasks.

METHODS

Subjects

Subjects were 33 dextral students (18 male, mean age = 22.9 years; 15 female, mean age = 23.7 years). Handedness laterality quotients were assessed using a standard instrument (Oldfield, 1971) on which a composite score of -100 denotes exclusive left-handedness, and +100 denotes exclusive right-handedness. Mean handedness laterality quotients for males and

females were +77.2 and +78.0, respectively. There was no significant difference in mean age or handedness laterality score between male and female subjects [$F_{1,31} = 0.15$, $p = 0.70$, and $F_{1,31} = 0.02$, $p = 0.90$, respectively]. Subsequent inferential statistical tests were therefore conducted on data collapsed across subject sex.

The study was conducted in accordance with The Code of Ethics of the World Medical Association (Declaration of Helsinki) for experiments involving human subjects. Prior to their participation in the study all subjects provided written informed consent, and all procedures were approved by the Institutional Review Board of North Dakota State University.

Stimuli

Auditory Interval Bisection (AB)—Figure 1 illustrates a schematic of the horizontal array of 27 speakers used to deliver the auditory stimuli. At a distance of 110 cm the inter-speaker separation was 1.02° of spatial angle. The spatial interval to be bisected was defined by two speakers with a spatial separation of 26.6° . This spatial interval was defined on each trial by the delivery of two complex tones (200 Hz and 400 Hz squarewaves; 65 dB SPL) of 300 msec duration. The target consisted of a complex tone (300 Hz squarewave; 65 dB SPL) which was also 300 msec in duration. On a given trial the target tone could appear at one of 13 spatial locations ranging from $\pm 10.2^\circ$ with respect to veridical interval midpoint. Ambient noise level was 45 dB SPL. Auditory calibration was performed using a sound level meter (Extech, model 407764).

Visual Line Bisection (VB)—Figure 2 illustrates the stimuli used in the visual line bisection task. Horizontal lines of 100% Michelson contrast were tachistoscopically presented for 150 ms. At a viewing distance of 70 cm the lines subtended $19.06^\circ \times 0.33^\circ$ of visual angle. Lines were pre-transected at 29 locations ranging from $\pm 1.66^\circ$ with respect to veridical line midpoint. Mean display luminance was 67 cd/m^2 . Display resolution was 640×480 pixels ($26.52^\circ \times 19.89^\circ$), and the screen refresh rate was 60 Hz. Luminance and contrast calibration were performed using a spot photometer (Konica Minolta LS110).

Procedure

Both AB and VB experiments were conducted in a single session. The order of presentation of the two tasks was counterbalanced across subjects. Subjects were seated in straight-backed chairs with their midsagittal plane aligned with the midpoint of the speaker array and the visual display. All subjects had normal or corrected-to-normal vision. Audiometric tests confirmed that all subjects had normal auditory thresholds. Subjects performed the AB task with eyes closed. In both the visual and auditory bisection tasks a programmed microcomputer sensed and collected subject responses (Presentation: Neurobehavioral Systems, Inc.).

Auditory Interval Bisection (AB)—Figure 1 illustrates the stimulus arrangement and experimental procedure used in the auditory interval bisection task. Subjects faced the array. Three tones were presented sequentially. The first two tones (t_1 and t_2) served to define the 26.6° spatial interval to be bisected. Following the presentation of the third (target) tone (t_3), subjects judged whether the spatial location of the target tone was to the left or right of the midpoint of the spatial interval defined by the two fiducial tones. The sequence of fiducial tones was presented with an interstimulus interval (ISI) of 100 msec. The target tone was presented 300 msec after the second fiducial tone. Subsequent trials began 400 msec after subject response.

Subjects performed two blocks of trials. In one block the left fiducial tone preceded the right fiducial tone in a left-to-right sequence ($AB_{L \rightarrow R}$); the second block employed a right-to-left tone sequence ($AB_{R \rightarrow L}$). The order of presentation of the two sequences was counterbalanced

across subjects. Within a block of trials the target tone (t_3) could appear randomly at one of 13 different speaker locations. Subjects made fifteen bisection judgments in conjunction with each of the 13 target tone locations, such that the determination of perceived auditory interval midpoint was based on a total of 195 (13 target tone locations \times 15 judgments per location) forced-choice trials. Subjects indicated decisions using the right hand to depress a left or right mouse button, as appropriate.

Visual Line Bisection (VB)—Lines were tachistoscopically presented for 150 ms; intertrial interval varied randomly, with a boxcar distribution, between 500-1000 ms following subject response. Lines of each contrast polarity appeared with equal frequency and the order of appearance of lines with different transector locations was randomized within blocks of trials. Subjects made ten bisection judgments at each of the 29 transector locations, such that the determination of perceived line midpoint was based on a total of 290 (29 transector locations \times 10 judgments per location) forced-choice trials. Subjects indicated decisions using the right hand to depress a left or right mouse button, as appropriate.

Data Analysis

For both VB and AB tasks the dependent measure was the proportion of trials on which subjects judged that the visual line transector or auditory target was located to the left of the midpoint of the line (VB task) or spatial interval (AB task). Psychometric functions were derived using the method of constant stimuli. Multidimensional unconstrained nonlinear optimization (Nelder & Mead, 1965) was used to fit logistic functions to the psychometric data using maximum likelihood optimization. The logistic function is described by the equation

$$p(x) = \frac{1}{1 + \exp\left(-\frac{x-\mu}{\sigma}\right)}$$

where x refers to the spatial location of the visual line transector or the auditory target, μ is the point of subjective equality (PSE), corresponding to the inflection point of the sigmoidal function, and σ is the standard deviation whose value is inversely proportional to discrimination precision. Line transector and auditory target locations corresponding to a 50% probability of “left” responses (μ), and corresponding standard deviations (σ) were estimated for each subject in each condition. Subsequent inferential statistical tests, including one-sample and paired sample t-tests, were conducted on these optimized values of PSE and standard deviation. The t-statistics were used to calculate estimates of effect size using the formula, $d = 2t / \sqrt{df}$ (Cohen, 1988). By convention, an effect size of ± 0.2 is considered to be small, a value of ± 0.5 is moderate and a value of ± 0.8 or greater is considered a large effect (Cohen, 1992).

RESULTS

Auditory Interval Bisection (AB) Accuracy (Bias)

The leftmost bars of Figure 3 plot mean PSE (± 1 sem) in the $AB_{L \rightarrow R}$ and $AB_{R \rightarrow L}$ conditions. Mean PSE was 0.195° (0.73% interval length) in the $AB_{L \rightarrow R}$ condition and 1.627° (6.12% interval length) in the $AB_{R \rightarrow L}$ condition. A paired-samples t-test reveals that mean PSE in the $AB_{R \rightarrow L}$ condition is significantly rightward of the mean PSE in the $AB_{L \rightarrow R}$ condition [$t_{32} = 4.50$, $p < .001$, $d = 1.59$], indicating a highly significant effect of directional attentional scanning. Single-sample t-tests reveal that mean bisection error was significantly rightward of veridical in the $AB_{R \rightarrow L}$ condition [$t_{32} = 5.04$, $p < .001$, $d = 1.78$] but not in the $AB_{L \rightarrow R}$ condition [$t_{32} = 0.57$, $p = .573$, $d = 0.20$]. The third bar in Fig. 3 plots the average bisection error in the AB condition collapsed across the two fiducial tone direction conditions (AB_{AVE}). A single-

sample t-test confirms that the average auditory bisection error (0.911°) deviates significantly rightward of veridical interval midpoint (3.42% interval length) [$t_{32} = 3.12, p = .004, d = 1.10$].

Visual Line Bisection (VB) Accuracy (Bias)

The rightmost bar of Fig. 3 plots mean bisection error in the VB task which was -0.117° (0.61% line length). A single-sample t-test shows that visual bisection error is significantly leftward of veridical line midpoint [$t_{32} = -3.51, p = .001, d = -1.24$].

Auditory Interval versus Visual Line Bisection

Figure 4 plots VB versus AB_{AVE} PSE for the entire sample of 33 subjects. Despite the significant difference in the direction of visual and auditory hemispatial bias, there is a significant positive correlation between bisection errors across the two sensory modalities [$r_{32} = 0.38, p = .029$].

Auditory Interval Bisection (AB) and Visual Line Bisection (VB) Precision

Figure 5 plots mean standard deviation (precision) values for the AB and VB tasks. There was no significant difference in mean precision between the $AB_{L \rightarrow R}$ (1.87°) and $AB_{R \rightarrow L}$ conditions (2.06°) [$t_{32} = -1.60, p = .120, d = 0.57$]. Average precision in the auditory interval bisection task (1.97°) is significantly poorer than in the visual line bisection task (0.25°) [$t_{32} = 15.11, p < .001, d = 5.34$].

DISCUSSION

Visual versus Auditory Spatial Processing

Whereas the neural basis for visual spatial localization is well understood, the neural mechanisms for sound source localization are still a subject of considerable debate (Zatorre, Bouffard, Ahad & Belin, 2002). The visual system is organized for spatial localization; it possesses numerous spatiotopically mapped low-level cortical areas (e.g., V1, V2, V3) in which the spatial location of stimuli is mapped explicitly. By contrast, auditory cortex is tonotopically mapped; sound localization depends primarily on interaural time and intensity differences, with some contribution from monaural spectral cues (Blauert, 1996). It is not known with certainty how these cues are processed by the auditory system to achieve sound localization (Richter, Schroger & Rubsamen, 2009). In addition, central auditory projections have a large ipsilateral component that is absent in the visual system, and whereas the neural networks subserving visuospatial attention are largely housed in the right hemisphere (Nobre, Sebestyen, Gitelman, Mesulam, Frackowiak & Frith, 1997; Kastner & Ungerleider, 2000), there is substantial evidence for both right and left hemisphere involvement in sound localization and audiospatial attention (Bellmann, Meuli & Clarke, 2001; Clarke et al., 2000; 2002; Zatorre, Bouffard, Ahad & Belin, 2002; Richter, Schroger & Rubsamen, 2009).

Visuospatial Attention

Our results for the visual line bisection task contribute to the growing consensus that visuospatial attention in neurologically normal subjects exhibits a small, but significant and consistent leftward bias, i.e., pseudoneglect (Bowers & Heilman, 1980; McCourt & Olafson, 1997; Nicholls, Bradshaw & Mattingley, 1999; McCourt & Jewell, 1999; Jewell & McCourt, 2000; McCourt, 2001; McCourt et al., 2005; 2008; Leone & McCourt, 2010; Dickinson & Intraub, 2009). The leftward bias of normal subjects and the profound rightward bias of neglect patients are twin manifestations of the specialization of neural networks in the right hemisphere for the deployment of visuospatial attention (Heilman & Valenstein, 1979; Mesulam, 2000; Kinsbourne, 1970; 1977; 1993; Nobre, Sebestyen, Gitelman, Mesulam, Frackowiak & Frith, 1997; Kastner & Ungerleider, 2000). The emerging consensus is that the (normally) dominant

right hemisphere projects a prepotent vector of visuospatial attention into contralateral (left) hemisphere, differentially increasing the salience of left hemisphere in general (in egocentric coordinates), and the left-hand portions of visual stimuli such as lines (in allocentric coordinates), thereby biasing perceived midpoint leftwards (Anderson, 1996; McCourt & Jewell, 1999).

Audiospatial Attention

Our results for the auditory interval bisection task indicate that audiospatial attention in neurologically normal subjects exhibits a significant rightward bias. This finding is consistent with several previous reports. Cusak, Carlyon & Robertson (2001) manipulated the interaural time delay (ITD) of headphone-delivered noise bursts and found that six of seven control subjects perceived sounds with positive ITDs (consistent with a physical sound source located in right hemisphere) as located on the midsagittal plane. Dufour, Touzalin & Candas (2007) delivered noise bursts from two speakers situated at $\pm 30^\circ$ with respect to the midsagittal plane. Subjects judged the location of the binaurally fused stimuli to be aligned with the auditory midline when the left speaker possessed a greater physical intensity, and stimuli with an interaural intensity difference of zero were perceived to be located rightward of the midsagittal plane. Corral & Escera (2008) embedded novel sounds (distracters) in a repetitive stream of auditory stimuli and presented these at various azimuthal locations relative to gaze direction while subjects were engaged in a demanding visual discrimination task. They found a significant effect of distracting sounds on visual task performance only for distracters delivered in right hemisphere. Sosa, Clarke & McCourt (2009) used a tachistoscopic visual line bisection paradigm to assess whether exogenous lateral auditory cues can bias PSE and to characterize the manner in which auditory (A) and visual (V) cues combine to jointly influence PSE. They found a significant hemifield asymmetry in the weights assigned to A and V cues, where V cues were more heavily weighted in left hemisphere and A cues were more heavily weighted in right hemisphere.

Attentional Scanning—Our results from the auditory interval bisection task show significantly greater rightward error in the $AB_{R \rightarrow L}$ versus $AB_{L \rightarrow R}$ condition. This result is consistent with previous findings. In their review and meta-analytic treatment of the visual pseudoneglect literature Jewell & McCourt (2000) noted that directional scanning, as executed either overtly (e.g., oculomotor or limb scanning) or covertly (absent eye or limb movements), exerted a significant modulatory influence on perceived line midpoint such that left-to-right scanning was associated with significantly larger leftward bisection errors than right-to-left scanning (Chokron, Bartolomeo, Perenin, Helft & Imbert, 1998; Chokron & Imbert, 1993a;b; Halligan, Manning & Marshall, 1991; Brodie & Pettigrew, 1996), which can sometime lead to rightward bisection errors. The asymmetrical effect of directional scanning on perceptual asymmetries has been studied behaviorally (McCourt & Jewell, 1999; McCourt, Garlinghouse & Slater, 2000; Nicholls & Roberts, 2002) but the neural basis for this effect is still poorly understood, particularly since covert shifts of spatial attention leftward or rightward from fixation are generally associated with increased activation of contralateral extrastriate and parietal cortical areas (Yamaguchi, Tsuchiya & Kobayashi, 1995; Kelley, Serences, Giesbrecht & Yantis, 2008). Thus, according to activation-orientation theory (Kinsbourne, 1970; 1977; 1993) the increased left hemisphere activation which accompanies a left-to-right attentional shift would predict smaller leftward bisection errors, whereas the opposite finding is observed. It is nonetheless interesting and potentially significant that directional scanning has a similar profound influence on interval midpoint estimation in both visual and auditory modalities.

Supramodal Spatial Attention

Based on findings that the severity and direction of inattention for visual and auditory stimuli is positively correlated in neglect patients (Pavani, Husain, Ladavas & Driver, 2004), and on neuroimaging studies of normal subjects which show largely coextensive regions of increased BOLD signal for shifts of spatial attention to visual and auditory cues, it has been suggested that spatial attention is supramodal (Krumbholz, Nobis, Weatheritt & Fink, 2009). To the extent that we likewise find a significant positive correlation between normal attentional biases in visual and auditory interval bisection tasks our results are consistent with this hypothesis. However, the quite different distributions of visual and auditory spatial attention are more difficult to reconcile with a supramodal mechanism.

Left Hemisphere Control of Audiospatial Attention: A Hypothesis

Five experimental/clinical findings that a model of visual and auditory spatial attention must explain in an integrated fashion are: 1) the leftward bias of normal visuospatial attention, i.e., pseudoneglect; 2) the rightward bias of normal audiospatial attention; 3) the positive correlation of these biases in normal observers; 4) the rightward bias of both visuospatial and audiospatial attention following right hemisphere damage, i.e., hemineglect; and 5) the positive correlation between errors of visuospatial and audiospatial attention in patients with hemineglect.

There is strong evidence for a lateralized neural network for visuospatial attention where the right hemisphere deploys attention into both contralateral (left) and ipsilateral (right) hemispace and the left hemisphere attends primarily to contralateral (right) hemispace (Mesulam, 1981; Anderson, 1996; Gitelman, Nobre, Parrish, LaBar, Kim, Meyer & Mesulam, 1999). Based on our present findings, as well as on cognate results from other laboratories (Cusak et al., 2001; Dufour et al., 2007; Corral & Escera, 2008), we postulate the existence of a left hemisphere based network governing audiospatial attention. Just as the right hemisphere is attentive to visual events in both contralateral and ipsilateral hemispace, there is converging evidence that sounds confined to left hemispace activate only the contralateral (right) hemisphere, whereas sounds located in right hemispace cause bihemispheric activation (Deouell, Bentin & Giard, 1998; Kaiser, Lutzenberger, Preissl, Ackermann & Birbaumer, 2000; Krumbholz, Schonwiesner, von Cramon, Rubsamen, Shah, Ziles & Fink, 2005; Krumbholz, Hewson-Stoate & Schonwiesner, 2007; Petit, Simon, Joliot, Andersson, Bertin, Zago, Mellet & Tzourio-Mazoyer, 2007; Schonwiesner, Krumbholz, Rubsamen, Fink & von Cramon, 2007; Hine & Debener, 2007). Further, just as the right hemisphere's specialization for visuospatial attention increases the salience of visual stimuli in left hemispace and leads to tonic leftward error in tasks like visual line bisection, so the left hemisphere's specialization for audiospatial attention causes a tonic rightward bias in auditory midline and interval judgments. If, as suggested by the activation-orientation theory (Kinsbourne, 1970; 1977; 1993) the left and right cerebral hemispheres compete for control of various functions (such as speech production or the deployment of spatial attention) via a process of mutual inhibition, then any phasic stimulation of the right hemisphere will up-regulate activity in visuospatial networks and so exacerbate the normal tonic leftward error in line bisection. Due to mutual interhemispheric inhibition the phasic stimulation of the right hemisphere will also result in the down-regulation of activity in the audiospatial attention networks of the left hemisphere. Since the strongest vector of audiospatial attention from the left hemisphere is directed towards right hemispace, the weakening of this vector will cause a leftward shift of PSE in auditory interval bisection tasks. The complimentary pattern of altered attentional biases will result from phasic stimulation of the left hemisphere (i.e., a rightward shift of both visual line bisection and auditory interval bisection). Thus, despite the different directions of the prepotent vectors of visuospatial and audiospatial attention, interhemispheric inhibition explains the correlated nature of these biases. While phasic changes of relative hemispheric activity serve to illustrate this point, it should be noted that any static imbalances in right versus left hemispheric

activation (due to individual differences) will also result in correlated bisection errors across the visual and auditory modality.

In hemineglect following right hemisphere lesions the normal leftward vector of visuospatial attention from the right hemisphere is greatly weakened; the distribution of visuospatial attention which remains is dominated by the left hemisphere and is strongly right-biased (Anderson, 1996). In addition, according to activation-orientation theory, right hemisphere lesions will allow the left hemisphere to be released from inhibition. Such disinhibition increases the normally right-biased distribution of audiospatial attention. Thus, here too a correlated pattern of increased rightward errors is produced in both visual and auditory tasks. Finally, this theory makes a testable prediction: if audiospatial attention depends on left hemisphere neural networks, then lesions to the left hemisphere should cause leftward shifts in audiospatial attention, and a pattern of greater left bias in auditory bisection tasks.

CONCLUSIONS

In contrast to the significant leftward bias of visuospatial attention, a significant rightward attentional bias characterizes midpoint judgments of spatial intervals defined via the auditory modality. This dissociation implies that the neural architectures which underpin spatial attention are modality specific, and that distinct networks govern the deployment of visuospatial and audiospatial attention. This dissociation is moderated by a significant positive correlation between bisection errors across the visual and auditory modalities which is consistent with the activation-orientation theory of mutual interhemispheric inhibition.

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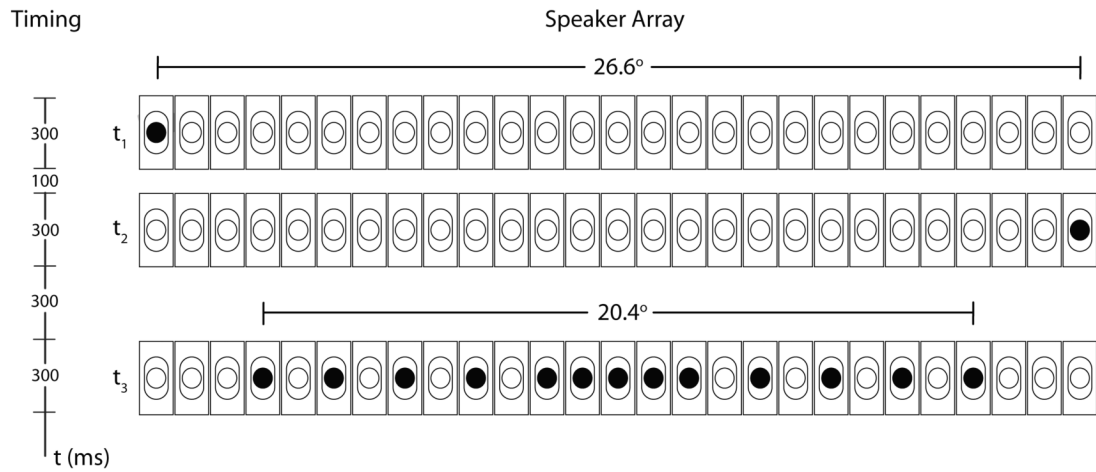


Figure 1.

A schematic diagram of the horizontal array of 27 speakers used to deliver the auditory stimuli. At a distance of 110 cm the inter-speaker separation was 1.02° of spatial angle. The spatial interval to be bisected was defined by two speakers with a spatial separation of 26.6° . On a given trial the target tone could appear at one of 13 spatial locations ranging from $\pm 10.2^\circ$ with respect to veridical interval midpoint.

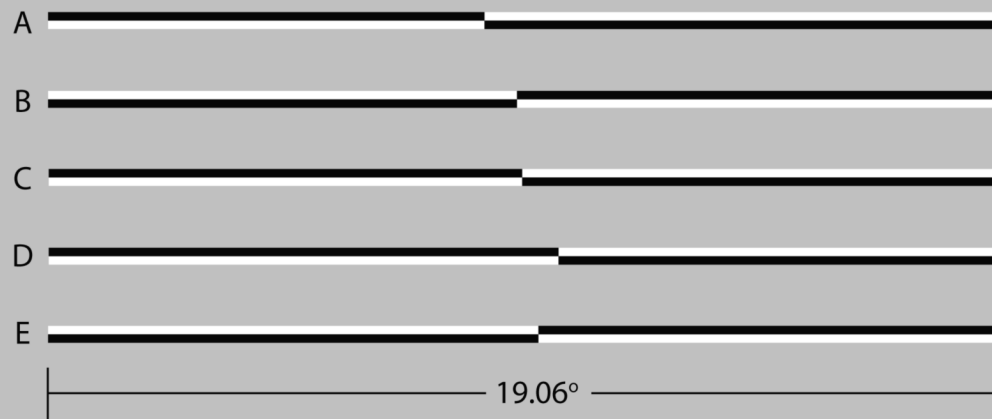


Figure 2.

Examples of line stimuli used in the experiments. The members of the upper pair (A, B) are transected to the left of veridical line midpoint (by -0.75° and -0.08° , respectively). The members of the lower pair (D, E) are transected to the right of veridical center (by $+0.70^\circ$ and $+0.33^\circ$, respectively). Line C is veridically transected. The members of line pairs (A, B) and (D, E) differ in contrast polarity. Lines of opposite polarity appeared with equal frequency and were counterbalanced within and across blocks of trials.

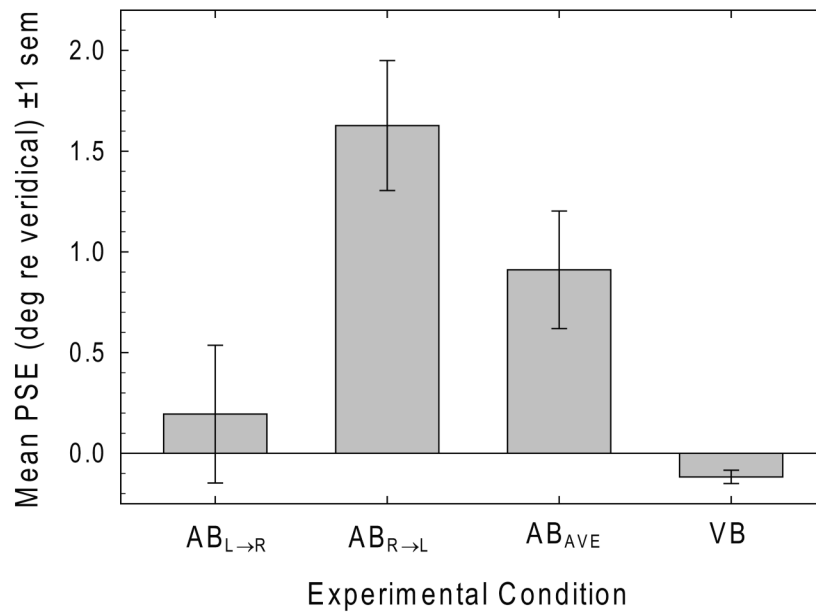


Figure 3. Leftmost bars plot mean PSE in the AB_{L→R} and AB_{R→L} conditions. Mean PSE in the AB_{R→L} condition is significantly rightward of the mean PSE in the AB_{L→R} condition, indicating a significant effect of directional attentional scanning. Mean bisection error was significantly rightward of veridical in the AB_{R→L} condition, but not in the AB_{L→R} condition. The third bar plots the average bisection error in the AB condition. Average auditory bisection error deviates significantly rightward of veridical interval midpoint. The rightmost bar plots mean bisection error in the VB task, which deviates significantly leftward of veridical line midpoint.

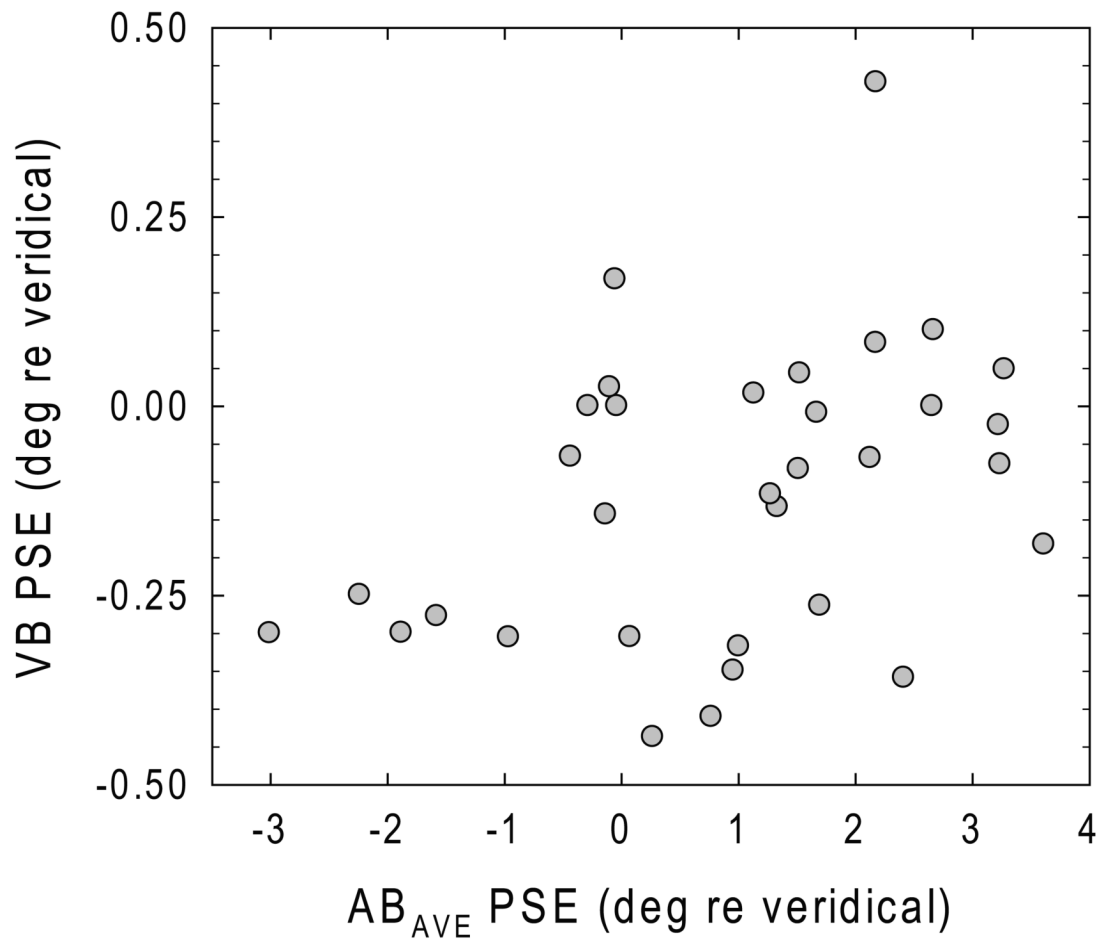


Figure 4. VB PSE plotted against AB_{AVE} PSE for the entire sample of 33 subjects. Bisection error in the two tasks is significantly correlated.

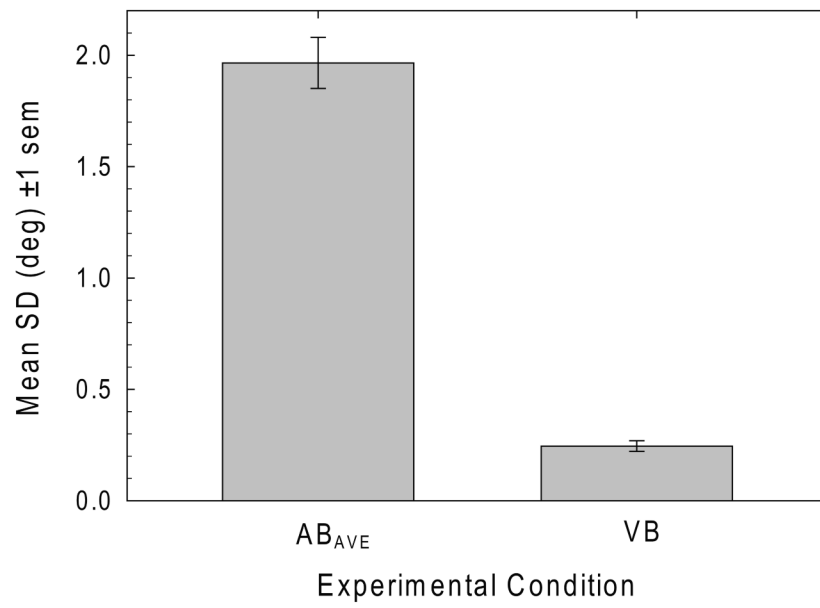


Figure 5. Mean standard deviations of the logistic function fits to the psychometric data AB and VB tasks. Average bisection precision in the AB task is significantly poorer than in the VB task.