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Adaptive Sex Differences in Auditory Motion Perception: Looming Sounds Are Special

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In 4 experiments, the authors examined sex differences in audiospatial perception of sounds that moved toward and away from the listener. Experiment 1 showed that both men and women underestimated the time-to-arrival of full-cue looming sounds. However, this perceptual bias was significantly stronger among women than among men. In Experiment 2, listeners estimated the terminal distance of sounds that approached but stopped before reaching them. Women perceived the looming sounds as closer than did men. However, in Experiment 3, with greater statistical power, the authors found no sex difference in the perceived distance of sounds that traveled away from the listener, demonstrating a sex-based specificity for auditory looming perception. Experiment 4 confirmed these results using equidistant looming and receding sounds. The findings suggest that sex differences in auditory looming perception are not due to general differences in audiospatial ability, but rather illustrate the environmental salience and evolutionary importance of perceiving looming objects.

Keywords: evolution, auditory motion perception, sex differences, looming

The ability to perceive and respond to rapidly approaching objects can have life or death consequences. Looming objects can indicate threats or opportunities that require the initiation of specific behavioral responses either to avoid, intercept, or otherwise prepare for the approaching object (Lee & Reddish, 1981). It should come as no surprise then, that significant sensory resources are allocated toward the perception of looming objects and that "looming perception" is a multimodal process that can be carried out individually by either the visual system or the auditory system, or can be concurrently conducted by both systems (Lee, Vanderweel, Hitchcock, Matejowsky, & Pettigrew, 1992).

The primary cue to perceiving looming objects in the visual domain is the optical increase in size of the retinal image that occurs as the object approaches. Auditory looming stimuli create an analogous increase in acoustic intensity as they approach, becoming increasingly louder as they draw closer to the listener. Recent investigations have begun to identify some of the specific neural mechanisms that mediate the perception of visual looming and the associated avoidant responses (Anderson & Siegel, 1999; de Jong, Shipp, Skidmore, Frackowiak, & Zeki, 1994; Gabbiani, Krapp, Koch, & Laurent, 2002; Sun & Frost, 1998). The significance of perceiving looming (vs. receding) objects is further illustrated by the finding that visual looming stimuli often cause fear or avoidance responses that are not produced by equivalent receding stimuli (Ball & Tronick, 1971; Schiff, Caviness, & Gibson, 1962) and are superior to other types of moving stimuli in attracting attention (von Muhlenen & Lleras, 2007).

Previous Work on Auditory Looming

Auditory looming has been studied relatively little when compared to its visual counterpart. Nevertheless, there is converging evidence of a perceptual bias for looming auditory motion. In other words, listeners tend to perceive a looming sound as closer than actual and judge that it has arrived when it is still some distance away. This work demonstrates a clear anisotropy in the perception of looming and receding sounds that spans human development, extends across species, and is evident in both behavioral and neurophysiological experiments. The bias for auditory looming appears to be instrumental in initiating neural and behavioral responses that aid in preparation for the arrival of the source.

Developmental studies have shown that human infants at 6 months of age can discriminate looming sounds better than receding sounds (Morrongiello, Hewitt, & Gotowiec, 1991). Infants as young as 4 months exhibit avoidance behaviors in response to looming sounds but not to equivalent receding sounds (Freiberg, Tually, & Crassini, 2001). Nonhuman primates show both behavioral and neural anisotropies consistent with a bias for looming auditory motion (Ghazanfar, Neuhoff, & Logothetis, 2002; Lu, Liang, & Wang, 2001; Maier & Ghazanfar, 2007). Furthermore, neuroimaging work in humans has identified specific neural streams that are involved in this perceptual anisotropy. Seifritz et al. (2002) showed that looming sounds but not receding sounds preferentially activate a distributed neural network involved in the perception of auditory space and motion, auditory attention, and motor planning. Bach et al. (2008) showed human amygdala activation consistent with a warning function in response to looming

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sounds. Taken together, these findings suggest that auditory looming is a salient stimulus that (a) provides unambiguous cues to source approach and (b) initiates attention, perception, and action planning specific to dealing with approaching objects.

From a psychophysical perspective, listeners both perceptually overestimate the rising intensity change and underestimate the terminal distance of a looming sound source. Neuhoff (1998) asked listeners to rate the amount of loudness change that occurred in both rising and falling intensity sounds. Rising intensity tones were found to change in loudness significantly more than falling intensity tones, despite an equal amount of intensity change in each condition. Similarly, when sound sources approach a listener and then stop a fixed distance away, they are perceived as significantly closer than sounds that recede from the listener but stop at the same fixed distance (Neuhoff, 2001). This latter study rules out any potential psychophysical confounds of terminal intensity or overall loudness because approaching and receding sounds are equidistant when they stop (and thus of equal intensity at the listener; but see Teghtsoonian, Teghtsoonian, & Canevet, 2005).

In addition, there have been several investigations of the ability of listeners to predict the arrival time of a looming sound source (Gordon & Rosenblum, 2005; Rosenblum, Carello, & Pastore, 1987; Rosenblum, Gordon, & Wuestefeld, 2000; Rosenblum, Wuestefeld, & Saldana, 1993; Schiff & Oldak, 1990). The general methodology of these studies is to present listeners with a simulated sound source that is approaching the listener. The task is to press a key when the source is perceived to have arrived. The consistent finding across these auditory time-to-arrival experiments has been that listeners underestimate arrival time and press the response key too soon.

This systematic error in judging auditory time to arrival is sometimes attributed to the relatively poorer spatial resolution of the auditory system when compared to the visual system. However, Guski (1992) has suggested that the localization “error” of the auditory system should not be interpreted as error at all. In Guski’s view, rather than simply being a poor localizer, the auditory system acts as a warning system for the organism either to direct the visual system toward the object or to initiate appropriate motor responses to avoid or intercept the object. Guski’s speculation about motor planning in response to auditory looming was recently substantiated in a functional magnetic resonance imaging study by Seifritz et al. (2002), which showed preferential activation of motor planning areas by looming sounds but not receding sounds. Thus, the perceptual underestimation of arrival time and subsequent underestimation of source distance may actually provide the listener with advanced warning of the approaching source and, thus, more time than expected to prepare for its arrival.

It has been proposed that the margin of safety provided by the underestimation of arrival time may be an adaptive characteristic that has evolved because it provides a selective advantage in dealing with looming sound sources. Perceptually underestimating arrival time would have little cost and give organisms slightly more time than expected to prepare for the arrival of the sources. In this case, a slight systematic perceptual error would be more advantageous than veridical (on average) perception. In fact, the systematic underestimation of auditory time to arrival has prompted some researchers to argue that the primary function of mammalian auditory localization is not to provide an exact estimate of sound source location at all, but rather to act as a warning system and to provide input to the listener’s perceptual model of the environment (Guski, 1992; Knudsen, 2002; Popper & Fay, 1997). Thus, it seems at least plausible to hypothesize that a bias to hear looming sounds as closer than actual might have evolutionary origins.

Sex differences in the perception of looming sounds could provide support such an evolutionary hypothesis. Men and women have evolved differently to deal with sex-specific environmental challenges. If men and women differ in their perception of auditory looming, it could be an indication of sex-based differential needs in preparatory behaviors in response to looming sounds. For example, women may have benefited from a greater anticipatory bias because they were more likely to be preyed upon than males. However, in order for this line of evolutionary reasoning to be supported, we need to find evidence of sex differences in the perception of approaching sounds, but not in the perception of receding sounds, which would presumably pose a smaller threat. Sex differences in the perception of both looming and receding sounds might be explained more simply by better spatial transformation abilities typically found in males (Kimura, 1999).

Sex Differences in Auditory Looming Perception

The study of sex differences in perceptual and cognitive abilities is an inherently controversial area of investigation. However, differential performance on visuospatial tasks has been shown to be one of the most robust sex differences in cognitive processing (Kimura, 1999). Effect sizes tend to be small, but the effects themselves tend to be reliable. Spatial ability studies typically show that men perform better on tasks that require dynamic visuospatial manipulation (Collaer & Nelson, 2002; Collins & Kimura, 1997; Dabbs, Chang, Strong, & Milun, 1998) and that women perform better on tasks that require visuospatial memory (Alexander, Packard, & Peterson, 2002; Duff & Hampson, 2001; McBurney, Gaulin, Devineni, & Adams, 1997).

Curiously, almost all of the research demonstrating sex differences on spatial tasks has involved vision (Kimura, 1999; Voyer, Voyer, & Bryden, 1995). Yet, there is considerable physiological and behavioral evidence that demonstrates a strong correspondence between the perception of visual and auditory space (Auerbach & Sperling, 1974; Gutfreund, Zheng, & Knudsen, 2002; Knudsen, 2002; Stein & Meredith, 1993; Zwiers, Van Opstal, & Paige, 2003). Some work has shown sex differences in various auditory characteristics such as shorter latencies in auditory brainstem responses, and stronger click-evoked otoa-acoustic emissions in women (McFadden, 1998). Under certain conditions, men do localize sounds slightly better than women (Lewald, 2004). Perceiving the path of an approaching object and estimating its distance or time to arrival are inherently spatial tasks regardless of perceptual modality, and one previous study has specifically examined sex differences in audiovisual time-to-arrival estimates (Schiff & Oldak, 1990).

Schiff and Oldak (1990) examined the effects of perceptual modality, the trajectory of the source, and the sex of the observer on the accuracy of time-to-arrival estimates. They presented participants with films of approaching auditory objects and asked listeners in various conditions to make time-to-arrival estimates by pressing a key. In general, observers tended to underestimate time to arrival, consistent with the margin of safety hypothesis. They

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found greater accuracy rates for visual estimates than for auditory estimates of time to arrival. They also found greater accuracy for bypass trajectories than for collision trajectories.

Finally, Schiff and Oldak (1990) showed that men had more accurate estimates of time to arrival than women in both the auditory and visual modalities. However, it is important to note here that the systematic error in judging arrival time across all participants was an underestimation. Thus, phrased differently, women tended to allow for a greater margin of safety in estimating time to arrival of approaching objects.

Here we examined sex differences in predicting the arrival time of looming sounds and in estimating the terminal distance of both looming and receding sounds. In Experiment 1, we presented listeners with realistic three-dimensional looming sounds and asked them to judge when the source arrived. We wanted to examine time-to-arrival estimates under full acoustic cue conditions. Thus, unlike the previous work of Schiff and Oldak (1990), we did not occlude the final approach portion of the sound. Participants simply listened to approaching sounds and pressed a key when they judged that the source had arrived. This provided a more ecologically valid example of a real-world looming sound source. In Experiment 2, we presented listeners with looming sounds that came to a stop at fixed distances before reaching them. We then asked for an estimate of how far away the sound was when it stopped. In Experiment 3, listeners provided a similar distance estimate for sounds that receded from the listener and then stopped at a fixed distance. In Experiment 4, we asked listeners to make terminal distance estimates of both looming and receding sounds.

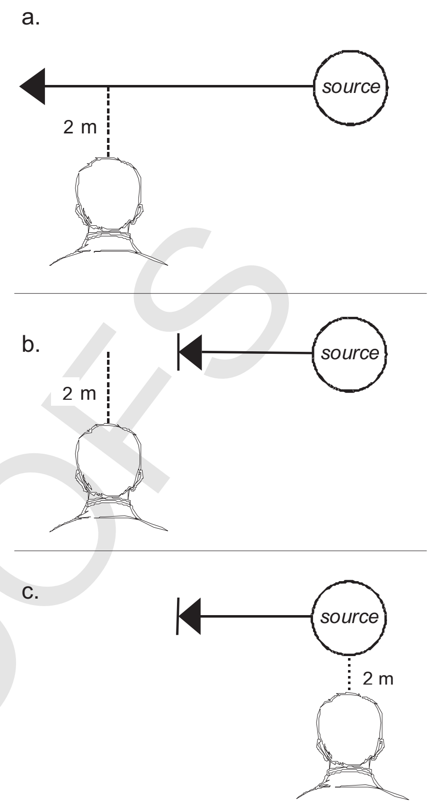

Figure 1. Schematic diagram of stimulus conditions for Experiments 1–3. (a) In Experiment 1, the sound approached and then passed the listener at 15, 20, or 25 m/s. Listeners pressed a key to estimate time to arrival. (b) In Experiment 2, the sound approached the listener and then stopped either 22.5 or 37.5 m from the listener. Listeners estimated the distance from listening point to the terminal point of the sound's path. (c) In Experiment 3, the sound receded from the listener and then stopped 15, 30, or 45 m away. Listeners estimated the distance from listening point to the terminal point of the sound's path.

Experiment 1

Method

Participants. All 50 participants were college students between 18 and 21 years of age. All reported normal hearing, were enrolled in psychology courses, and received course credit for participation. Twenty-five of the participants were men, and 25 were women. None was aware of the hypothesis being tested.

Apparatus and stimuli. Stimuli consisted of a moving virtual sound source that began 60 m from the listener and approached at 15, 20, or 25 m/s (and arrived at the listener in 4, 3, and 2.4 s, respectively). The sound source was a square wave with a fundamental frequency of 700 Hz, a source intensity of 88-dB sound pressure level, and a sampling rate of 44.1 kHz. The listening point was situated 2 m from the straight-line trajectory of the source, with the listener facing perpendicular to the source's path such that the interaural axis was parallel with it (see Figure 1). The source height was 0.5 m and it approached the listener from the side, passed in front of the listener, and then continued on. Half of the participants in each group heard the sound approach from the left, and half heard it approach from the right. The simulation provided a strikingly realistic three-dimensional sound source approach that included absolute delay (to account for the speed of sound and the changing distance between the listener and the source), Doppler shift, atmospheric filtering, gain attenuation due to atmospheric spreading, ground reflection attenuation, and head-related transfer function (HRTF) from the MIT KEMAR data set (Gardner & Martin, 1995; see the Appendix for simulation details). We used a bypass trajectory in order to maximize interaural cues to the source's approach and provide a conservative test of our hypothesis. The sounds were saved as wav files on a personal computer and presented via Sony MDRv-600 headphones. The same personal computer also recorded the participant responses.

Design and procedure. Prior to the experimental trials, each listener heard three introductory trials where the source approached and passed the listener at each of the three different velocities. No response was required for introductory trials. Next, each listener was presented with four trials at each approach velocity for a total of 12 trials. All trials were presented in random order. Listeners were instructed to imagine that they were standing on the side of a road, facing it perpendicularly. They were told that they would hear a sound source approach and that their task was to press a key when they heard the source directly in front of them, at its point of closest approach. The sound source continued moving until a keypress terminated the trial. After a brief pause, the next trial began. In this and all of the following experiments, participants were instructed to remain still and to refrain from moving their head while the sounds were playing.

Results and Discussion

We averaged responses in each condition to yield one data point for each participant in each condition. The means for each condition are shown in Figure 2. We conducted a 2 × 3 analysis of variance (ANOVA), with sex as a between-subjects variable and velocity as a within-subjects variable (see Table 1). We found that both men, $t(24) = 3.4$, $p < .01$, and women, $t(24) = 4.6$, $p < .01$, underestimated time to arrival. However, the time-to-arrival estimates of women showed significantly greater underestimation than the estimates of men. In other words, women showed a significantly greater anticipatory bias for the looming stimuli than men did. These results are consistent with the pattern of findings by Schiff and Oldak (1990). We calculated effect size using Cortina and Nouri's (2000) conservative correction for repeated measures designs and found an effect size for sex of $d = 0.76$.

We also found a significant main effect for velocity. Although listeners underestimated time to arrival in all three velocity conditions, the amount of underestimation decreased as source velocity increased ($d = 0.90$). Finally, the interaction between sex and velocity was significant. Pairwise comparisons showed that male and female estimates were significantly different at each velocity, but as velocity increased the difference in arrival time estimation between men and women decreased.

Table 1
Analysis of Variance for Time-to-Arrival Estimates in Experiment 1

Source	*df*	*MS*	*F*	*p*
Within subjects				
Velocity	2	1,895,884.51	**43.16**	<.0001
Velocity × Sex	2	191,532.60	**4.36**	.015
Error	96	43,930.98		
Between subjects				
Sex	1	2,692,730.0	**6.55**	.014
Error	48	410,984.2		

Note. Boldface denotes statistically significant values.

Experiment 2

Experiment 1 showed that women underestimate the arrival time of a looming sound source more than do men. In Experiment 2, we tested the hypothesis that the difference in the arrival time estimates of men and women stems from differences in perceiving the distance of looming sounds. We presented listeners with sounds that approached and then stopped at fixed distances from the listener. We then asked for an estimate of how far away the sound was when it stopped. Based on the difference in time-to-arrival estimates in Experiment 1, we hypothesized that terminal distance judgments made by women would be significantly closer than those made by men.

Method

Participants. Twenty male and 20 female listeners participated in Experiment 2. All were college students between the ages of 18 and 22 years. All participants reported normal hearing and received course credit for participation. None was aware of the hypothesis being tested, and none had participated in Experiment 1.

Apparatus and stimuli. Stimuli consisted of a moving virtual sound with the same source and trajectory characteristics as those used in Experiment 1. However, in Experiment 2, all sounds approached the listener at 15 m/s for a duration of 1.5 s. Half of the sounds began 60 m from the listener, and the other half began 45 m

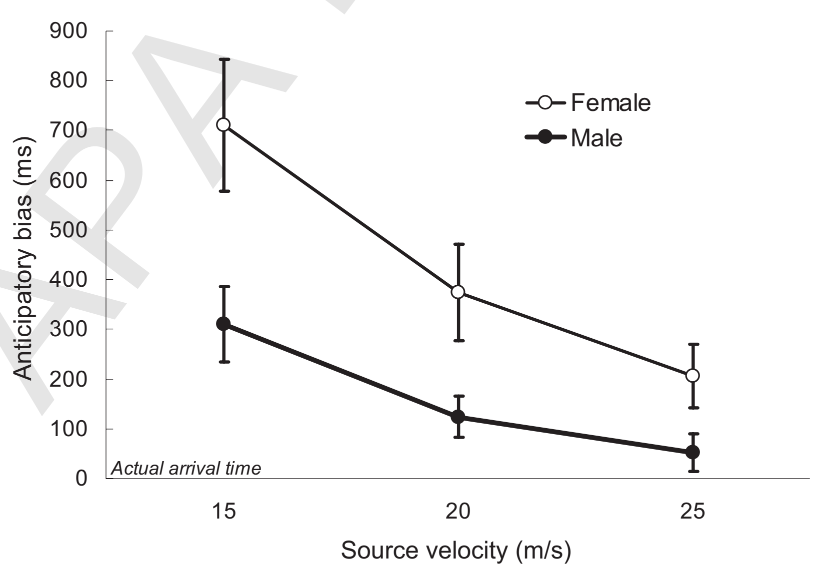

Figure 2. Mean time-to-arrival estimates by sex in each velocity condition (with error bars denoting standard error). The main effects of sex and velocity as well as the interaction are statistically significant. Women perceive looming sounds as arriving significantly sooner than do men.

from the listener. Thus, sounds moving toward the listener from 60 m at 15 m/s for 1.5 s traveled 22.5 m from their origin and ended 37.5 m from the listener. Sounds starting at 45 m from the listener also traveled 22.5 m from their origin but ended closer to the listener, at a distance of 22.5 m (see Figure 1b). Half of the participants in each group heard the sound approach from the left, and half heard it approach from the right.

Design and procedure. Prior to the experimental trials, each listener heard four introductory trials where the source approached from each of the two starting distances twice. No response was required for introductory trials. Next, each listener was presented with six experimental trials at each starting distance for a total of 12 trials. All trials were presented in random order. Listeners were instructed to imagine that they were standing on the side of a road, facing it perpendicularly. They were told that they would hear a sound source approach and then stop some distance from them. After each stimulus was presented, a 100-mm computerized visual analog scale appeared on the computer screen. The left end of the scale was labeled *very near* and the right end was labeled *very far*. Listeners were instructed to use the computer mouse to move a cursor to a spot on the scale that best described the location of the approaching sound when it stopped. We avoided using verbal estimates of distance because there are well-documented sex differences in the use of Euclidian metrics to describe distance (Dabbs et al., 1998; Galea & Kimura, 1993; MacFadden, Elias, & Saucier, 2003; Miller & Santoni, 1986; Ward, Newcombe, & Overton, 1986). Thus, we chose a nonmetric visual analog scale response in order to avoid any sex differences in verbal distance estimates or understanding of units of measure. Previous work has used this metric to examine sex differences in perception (Platek, Burch, & Gallup, 2001; Savic, Berglund, Gulyas, & Roland, 2001).

Results and Discussion

We averaged responses in each condition to obtain one data point for each participant in each terminal distance condition. The
F3 mean responses for each condition are shown in Figure 3. We conducted 2 × 2 mixed ANOVA, with sex as a between-subjects
T2 variable and distance as a within-subjects variable (see Table 2). We found a main effect for distance indicating that sounds ending 22.5 m from the listener were perceived as significantly closer than those ending 37.5 m from the listener ($d = 0.33$). We also found a main effect for sex indicating that across both distances, women perceived the sounds to terminate significantly closer to them than did men. The effect size for this sex difference was $d = 0.78$.

What then might account for the sex difference in processing looming sounds? One explanation might be that like visuospatial transformations, men simply demonstrate more accurate performance than women on tasks that require audiospatial transformation. The greater accuracy of men on the time-to-arrival task might simply be the result of better audiospatial processing. We examined this hypothesis in Experiment 3.

Experiment 3

If sex differences in auditory time-to-arrival estimates are simply due to better audiospatial abilities of men, then we should expect sex differences in auditory motion and distance perception,

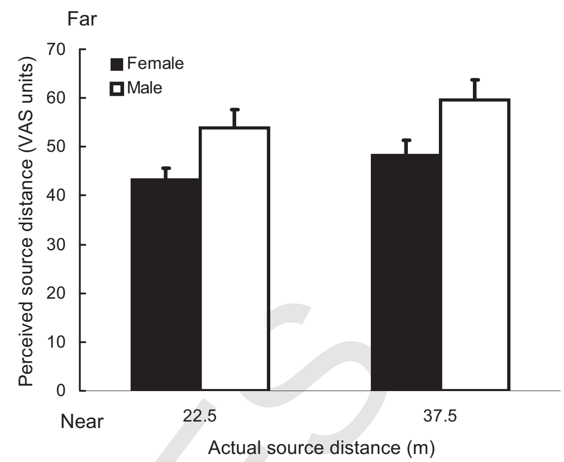

Figure 3. Mean estimates of terminal distance on a visual analog scale (VAS) for 15 m/s looming sounds in each condition in Experiment 2 (with error bars denoting standard error). The main effect of source distance is statistically significant, and women perceive looming sounds as significantly closer than do men. (For all VAS measures, the maximum scale value was 100, but the values were not visible to the participants.)

like those found in Experiment 2, regardless of the trajectory of the sound source. Sex differences in the perception of sound sources that are moving away from the listeners would be difficult to attribute to an evolutionary explanation and could be explained by the many studies that have shown that men perform better on spatial transformation tasks (for a review, see Kimura, 1999). On the other hand, if the demonstrated sex differences in perceiving looming sounds do not occur with receding sounds, then a stronger case can be made for the looming bias as a sexually differentiated evolutionary adaptation. In Experiment 3, we presented sounds that traveled away from the listener and then stopped. We then asked listeners to make a distance estimate of the terminal position of the sounds as was done in Experiment 2.

Method

Participants. Thirty male and 30 female listeners participated in Experiment 3. All were college students between the ages of 18 and 21 years. All participants reported normal hearing and received course credit for participation. None was aware of the hypothesis being tested, and none had participated in the previous experiments.

Apparatus and stimuli. Stimuli consisted of a moving virtual sound source with the same source characteristics as those used in Experiment 1. However, in Experiment 3, all sounds began 2 m directly in front of the listener and receded along a path parallel to the interaural axis (perpendicular to the facing direction) at 15 m/s for a duration of 1, 2, or 3 s. Thus, the terminal distance of the sounds was 15, 30, or 45 m from the source origin (see Figure 1c). Half of the participants in each group heard the sound depart to the left, and half heard it depart to the right.

Design and procedure. Prior to the experimental trials, each listener heard six introductory trials where the source receded to each of the three terminal distances twice. No response was required for introductory trials. Next, each listener was presented

Table 2
Analysis of Variance for Approaching Distance Estimates in Experiment 2

Source	*df*	*MS*	*F*	*p*
Within subjects				
Distance	1	587.58	**18.58**	<.001
Distance × Sex	1	2.87	.091	.765
Error	38	31.63		
Between subjects				
Sex	1	2,378.27	**6.13**	.018
Error	38	388.11		

Note. Boldface denotes statistically significant values.

with six experimental trials in each terminal distance condition for a total of 18 trials. All trials were presented in random order. Listeners were instructed to imagine that they were standing on the side of a road, facing it perpendicularly. They were told that they would hear a sound source travel away from them and then stop some distance from them. After each stimulus was presented, the same 100-mm computerized visual analog scale used in Experiment 2 appeared on the computer screen. Once again, we used this nonmetric scale to avoid the confound of sex differences in the use of Euclidian metrics in describing distance. Listeners were instructed to use the computer mouse to move a cursor to a spot on the scale that best described the location of the receding sound when it stopped.

Results

We averaged the six responses in each condition to obtain one data point for each participant in each terminal distance condition.
F4 The mean responses for each condition are shown in Figure 4. We conducted 2 × 3 mixed ANOVA, with sex as a between-subjects
T3 variable and distance as a within-subjects variable (see Table 3). We found a main effect for distance indicating that listeners could accurately discriminate between the three terminal distances (d = 3.9). However, contrary to Experiment 2 and despite a more powerful experimental design, we failed to find a sex difference in distance estimates for sounds that receded from the listener.

The lack of a sex difference in estimating the terminal distance of receding sounds suggests that sex differences in auditory looming perception are not simply due to general differences in audiospatial processing. If it were, we would expect to see such differences regardless of the direction that the sound traveled. Rather, the specific conditions under which sex differences in auditory motion perception occur suggest that looming sounds are salient environmental stimuli that require preparation for action that may be differentiated by the sex of the listener. We explore this idea further in the General Discussion.

Experiment 4

Experiments 1–3 demonstrate a directionally specific sex difference in the perception of egocentric auditory motion. Looming sounds are perceived as closer by women than by men. There were no analogous sex differences for receding sounds. Our goal in Experiments 1–3 was to examine how listeners might react to novel looming and receding sounds without a lot of practice. This would most closely approximate what might occur under more natural conditions. However, compared to typical perception experiments, each experiment used a limited number of trials. In Experiment 4, we examined the generality of this finding by giving listeners more practice and exposure to looming and receding stimuli and asked them to make terminal distance estimates of both looming and receding stimuli. Also, although the distances used in Experiment 3 encompass those used in Experiment 2, we used the same terminal distance for approaching and receding sounds in Experiment 4 to rule out sex differences that might be based on the different specific distances used between Experiments 2 and 3.

Method

Participants. Twenty-eight male and 28 female listeners participated in Experiment 4. All were college students between the ages of 18 and 22 years. All participants reported normal hearing and received course credit for participation. None was aware of the hypothesis being tested, and none had participated in the previous experiments.

Apparatus and stimuli. Stimuli consisted of approaching and receding virtual sound sources traveling at 15 m/s with the same source characteristics as those used in Experiment 1. All sounds traveled along a linear virtual path 2 m directly in front of the listener that was perpendicular to the interaural axis. Approaching sounds started 60 m from the listener and stopped 15 m from the listener's position next to the path. On receding trials, the sound source first approached the listener from a starting distance of 30 m and then passed, receding on the other side of the listener to a distance 15 m. For both approaching and receding trials, the stimulus duration was always 3 s, total distance traveled was always 45 m, and the terminal distance was always 15 m from the listener's position perpendicular to the path. Half of the sounds started on the left of the listener, and the other half started on the right.

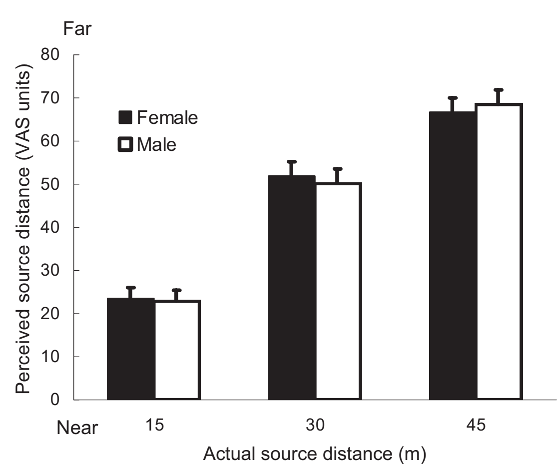

Figure 4. Mean estimates of terminal distance on a visual analog scale (VAS) for 15 m/s receding sounds in each condition in Experiment 3 (with error bars denoting standard error). The main effect of source distance was statistically significant. However, there was no significant difference between the distance estimates of men and women.

Table 3
Analysis of Variance for Receding Distance Estimates in Experiment 3

Source	*df*	*MS*	*F*	*p*
Within-subjects source				
Distance	2	30,256.17	**183.38**	<.0001
Distance × Sex	2	46.20	.280	.756
Error	116	164.99		
Between-subjects source				
Sex	1	58.37	.113	.738
Error	58	517.97		

Note. Boldface denotes statistically significant value.

Design and procedure. Prior to the experimental trials, each listener made terminal distance judgments on 20 practice trials where the source approached and receded 10 times each. The listener's task was to indicate the terminal distance of the source on each trial using the same method employed in Experiments 2 and 3. After practice, each listener was presented with 30 experimental trials each for both approaching and receding stimuli for a total of 60 trials. All trials were presented in random order. Listeners were instructed to imagine that they were standing on the side of a road, facing it perpendicularly. They were told that some sounds would approach them and stop before reaching them (approaching trials) and that others would not stop until after they had passed them (receding trials). After each stimulus was presented, listeners made distance estimates using the same computerized visual analog scale used in Experiment 2 and 3.

Results

We averaged responses to obtain one data point for each participant in each direction condition. The mean response in
F5 each condition are shown in Figure 5. We conducted a 2 × 2 mixed ANOVA, with sex as a between-subjects variable and direction of travel as a within-subjects variable. We found a main effect for direction indicating looming sounds were perceived as significantly closer than equidistant receding sounds, $F(1, 54) = 81.91$, $p < .01$ ($d = 0.22$). There was no main effect for sex, $F(1, 54) = 0.69$, *ns*. However, there was a critical significant interaction between sex and direction of travel that confirmed the results of Experiments 3 and 4, $F(1, 54) = 5.43$, $p < .05$. For looming sounds, judgments of terminal distance made by women were significantly closer than those made by men, $t(54) = 2.98$, $p < .01$. However, for receding sounds there was no significant difference in distance estimates between men and women, $t(54) = 0.77$, *ns*.

General Discussion

Our results demonstrate sex differences in the perception of looming sounds and suggest that these differences are not due to general performance differences between men and women on spatial transformation tasks. We propose that the specific stimulus conditions under which sex differences in auditory motion perception occur underscore the environmental salience and evolutionary importance of perceiving looming sounds. In Experiment 1, we found that although both sexes underestimated the arrival time of looming sounds, women showed significantly greater underestimation than men. In Experiment 2, we confirmed that women perceive looming sounds as closer than do men. We found significant sex differences in estimating the perceived terminal distance of looming sounds that stopped before reaching the listener, with women showing significantly closer distance estimates than men. In tracking the approach of looming sounds in Experiments 1 and 2, listeners had to continually update the spatial position of the source in order to estimate either time to arrival or terminal distance. Many studies have shown that males tend to outperform females on tasks that require such spatial transformation (Kimura, 1999). However, if the sex difference in perceiving looming sounds was simply another example of more accurate male performance on a spatial transformation task, then we would expect that terminal distance estimates for sound sources traveling away from the listener would show similar sex differences. Contrary to this hypothesis, in Experiments 3 and 4 we failed to find any significant difference in the terminal distance estimates of men and women for sounds that traveled away from the listener.

An Evolutionary Hypothesis

What then might account for the directional specificity of sex differences in processing moving sounds? We speculate that there may be an evolutionary explanation. Sex differences aside, the general perceptual bias to hear looming sounds as closer than actual may be an adaptation that provides a selective advantage (Neuhoff, 1998, 2001). Perceiving a looming sound

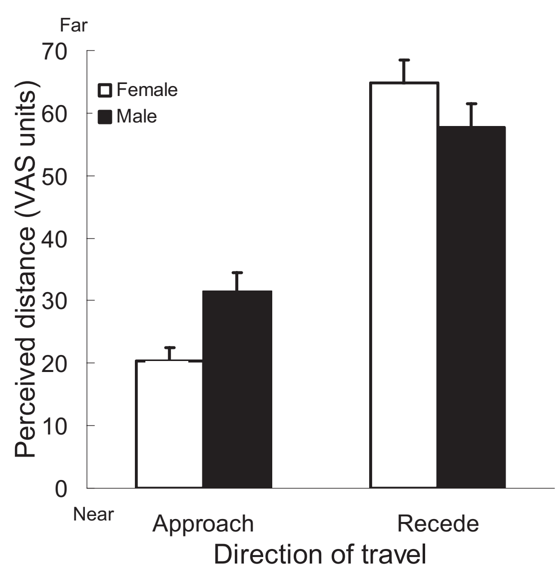

Figure 5. Mean estimates of terminal distance on a visual analog scale (VAS) for 15 m/s approaching and receding sounds in Experiment 4 (with error bars denoting standard error). The main effect of direction was statistically significant. There was also a significant interaction between sex and direction of travel. Women perceive looming sounds as closer than do men. However, there was no sex difference for receding sounds.

tapraid5/zfn-xhp/zfn-xhp/zfn00608/zfn2286d08z | xppws | S=1 | 8/6/08 | 13:31 | Art: 2006-0429

as closer than actual yields more time than expected to engage in preparatory behaviors prior to its arrival. Although such a perceptual bias is technically an error in perception, the cost of a false positive (making preparatory actions too early) is far less than the cost of a false negative (making preparatory actions too late; Haselton & Nettle, 2006). Thus, the bias to respond early to looming sources could have been shaped by natural selection.

To the extent that men and women have faced different evolutionary challenges, they have evolved different physiological and psychological mechanisms to deal with those challenges (Buss, 2003). It may be that the current data are exemplary of exactly this type of differentiation. In particular, some of the most robust physical differences between men and women are in strength, running speed, and stature (McDowell, Fryar, Hirsch, & Ogden, 2005; Nicolay & Walker, 2005; Whipp & Ward, 1992). The distributions clearly overlap, but on average, men tend to be bigger, stronger, and faster than women. If the bias for auditory looming is an adaptive behavioral characteristic that facilitates survival by allowing more time for preparatory behaviors, then researchers might expect sex differences in the form of a greater looming bias in women who, given the physical differences outlined above, would be more susceptible than men to predation or assault. However, most receding sounds do not require preparatory behaviors. Thus, according to the adaptive hypothesis, male and female performance on localizing sounds that travel away from the listener should be relatively equal.

Direct experimental tests of evolutionary hypotheses about behavioral adaptations in humans are not possible, and our data do not readily differentiate between evolutionary and experiential explanations for the phenomenon. Nonetheless, in this case, an adaptive hypothesis would seem to be much more parsimonious than an experiential one. For example, an experiential explanation might propose that men may have more experience with sounding objects in motion than do women and, thus, show greater accuracy on an auditory time-to-arrival task. Yet, in order for an experiential hypothesis to explain all of the current data, men would have to have more experience than women with looming sounds but the same amount of experience as women with receding sounds. We suggest that the adaptive hypothesis is more compelling.

In addition, other work provides converging evidence for the more fundamental adaptive hypothesis that the bias for auditory looming has been shaped by natural selection. Nonhuman primate species have been shown to exhibit the very same perceptual bias, and concomitant physiological mechanisms implicated in processing the phenomenon have been identified (Ghazanfar et al., 2002; Lu, Liang, & Wang, 2001; Maier & Ghazanfar, 2007; Maier, Neuhoff, Logothetis, & Ghazanfar, 2004). Human neuroimaging studies have shown that looming tones act as a warning cue that preferentially activate a neural network responsible for attention allocation, motor planning, and the translation of sensory input into ecologically appropriate action (Bach et al., 2008; Seifritz et al., 2002). Together these findings illustrate strong neural and behavioral responses across species that initiate perception and preparation for action in response to looming sounds. These responses far outweigh any analogous neural or behavioral responses to equivalent receding sounds.

Conclusions

Our data demonstrate a characteristic of auditory motion perception that may provide a selective advantage in processing looming sound sources. The environmental salience of auditory looming appears to be reflected in its increased perceptual salience as indicated by an anticipatory bias in time-to-arrival tasks and compressed auditory distance estimates of looming versus receding sounds. The demonstration of sex differences in this anisotropic perceptual bias provides converging evidence for the evolutionary origins of the phenomenon and suggests that the well-documented sex differences in visuospatial transformation abilities are accompanied by corresponding, but directionally specific, sex differences in audiospatial processing.

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Appendix

Stimulus Simulation Parameters

The listener in the simulation is 2 m from the ground and 2 m from the path. The source is 0.5 m from the ground. The source signal is processed by the following components in this order:

Absolute delay

Atmospheric filter

Spreading roll-off gain

Ground reflection attenuation

Head-related transfer function (HRTF) filter

Absolute Delay

Absolute delay is implemented using a continuously variable delay line. The length of the delay (in samples) is given by

$$\text{Delay}(t) = \frac{\text{EmDist}(t)}{c}$$

Where EmDist(t) is the distance (in samples) between the listener and the emission position of the source and c is the speed of sound. The speed of sound used in this simulation is

$$c = 344.26 \cdot \frac{m}{s}$$

The emission position is the location the source was Delay(t) samples ago.

$$\overrightarrow{\text{EmPos}(t)} = \overrightarrow{\text{SrcPos}(t-\text{Delay}(t))}$$

Therefore the emission distance is

$$\text{EmDist}(t) = \left| \overrightarrow{\text{SrcPos}(t-\text{Delay}(t))} - \overrightarrow{\text{HeadPos}(t)} \right|$$

The Doppler pitch shift is caused by the change in the delay line lengths as the emission distance changes. The resulting pitch shift factor is

$$\text{Doppler}(v_S) = \frac{1}{1 - \frac{v_s}{c}}$$

Where v_s is the velocity of the source projected onto the vector between the source and the listener.

Atmospheric Filter

The atmospheric filter is a two-pole infinite impulse response filter. The two poles are both located at $1 - \alpha$. This gives the transfer function:

$$H(z) = \left(\frac{1-\alpha}{1-\alpha \cdot z^{-1}}\right)^2, \; 0 \le \alpha \le 1$$

Alpha is calculated as follows:

$$\alpha(t) = \frac{\text{EmDist}(t)}{\text{EmDist}(t) + \text{AbDist}}$$

Where AbDist is a predefined absorption distance, which sets the distance at which $\alpha = 0.5$. For this simulation AbDist = 50 m.

Spreading Roll-Off Gain

The gain attenuation due to atmospheric spreading loss is calculated by

$$\text{Gain}(t) = \left(\frac{\text{Zero\_dBDist}}{\text{EmDist}(t)}\right)^{\mu\sigma}$$

Where Zero_dBDist is the distance at which the gain will be 0 dB, μ is the medium roll-off exponential, and σ is the source roll-off exponential. For this simulation Zero_dBDist = 2 m, and $\mu = \sigma = 1$.

Ground Reflection Attenuation

For this simulation the ground reflection is given a constant –3 dB attenuation compared with the direct source. This is a reasonable amount of attenuation for a hard surface like asphalt.

HRTF Filtering

The Kemar HRTF data set from MIT was used to provide Head Related Transfer Function filtering. Note that the position used for filtering is the emission position: EmPos(t).

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