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AUDITORY MOTION AND LOCALIZATION

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By almost any measure, determining the spatial location and path of movement of objects in the environment is a primary task of most perceptual systems. The ability to localize acoustic sources is considered by many to be the most important task of the vertebrate auditory system (Popper & Fay, 1997). Accurate estimates of spatial location facilitate proper navigation through the environment and precise interaction with objects and organisms. In the visual system there is a relatively isomorphic correspondence between spatial positions in the environment and equivalent points on the retina. This correspondence is well preserved through cellular organization throughout much of the physiology of the visual pathway. There is a tonotopic organization in the auditory system that corresponds to an ordered *frequency* scale, and some early work was suggestive of place coding in the auditory cortex for spatial position (Coleman, 1959). However, the correspondence between spatial position and neuronal representation is not nearly as detailed as that of the visual system.

Instead, spatial position is calculated using a number of different sources of information, including differences in the characteristics of a sound as it arrives at each ear. These differences are both temporal and spectral and are created by the spatial separation of the two ears and the influence of the head, torso, and pinnae. Rather than neurons tuned to a single spatial position or region, there is evidence to suggest that single neurons in the auditory cortex are panoramic and respond to source locations through 360° of azimuth. Spatial position appears to be represented in these cells by the pattern rather than the rate of neuronal firing (Fitzpatrick, Batra, Stanford, & Kuwada, 1997; Middlebrooks, Clock, Xu, & Green, 1994; Middlebrooks, Xu, Clock, & Green, 1998).

Perhaps as a result of the different means of coding spatial information in the auditory and visual systems, the spatial resolution of the visual system is much better than that of the auditory system and the temporal resolution of the auditory system generally exceeds that of the visual system. Thus, the two systems complement each other as well as one might expect given the millions of years that that evolutionary processes have had to shape the respective systems. Some of the deficits of the visual system, for example, not being able to perceive 360° of azimuth at a time or to sense around corners, are compensated for by the auditory system, which accomplishes both of these tasks nicely. From an evolutionary perspective, it is perhaps no accident that the perceptual systems have evolved to take advantage of these particular characteristics of the environment. For example, the wavelength of visible light makes it such that very good spatial resolution is physically possible. The characteristics of sound waves are such that they are less susceptible than light to the influence of obstacles, corners, or shadows (Griffin, 1959). Thus, the respective sensory systems have evolved to take advantage of the available information in the physical environment.

Yet, it is interesting to note that much of the research on auditory localization has been conducted with stationary static sounds. Often listeners in the laboratory are asked to choose the source location of a presented sound from an array of several loudspeakers. However, the number and position of the loudspeakers, and thus the number of possible response choices, are typically quite restricted. This setup differs from listening in a natural environment in several ways. First, in the laboratory, there is usually an equal probability of a sound coming from any given speaker in the array, regardless of whether the source is in front, behind, or even above or below the listener. This is often not the case in a natural listening environment, particularly when the space directly above the head is investigated. Sounds more often emanate from somewhere on or near the horizontal plane than from above or below the listener. Unlike those in the laboratory setup, on the other hand, the *potential* locations in a natural environment from which a sound could emanate are unlimited. The importance of the number and placement of available responses was manifest in a study by Perrett and Noble (1995) that showed that the available response choices in a localization task can influence localization performance significantly. Thus, investigations with highly constrained response choices are somewhat limited in their ability to inform us about localization in a more natural listening environment (Middlebrooks & Green, 1990). Furthermore, identifying the location of static sound sources from a fixed listening location is a condition that probably occurs less often than more dynamic examples of localization tasks. In addition to presenting static stimuli in anechoic environments, investigators sometimes even limit head movements of the listeners by either immobilization or instruction (Blauert, 1997).

To be fair, however, the primary goal of such investigations is usually to test hypotheses about particular mechanisms and processes that allow listeners to localize sound sources, not to develop ecological theories of how listeners use acoustic information under more natural listening conditions. Furthermore, the

experimental control and internal validity afforded by these types of investigations are of great value in determining the particular cues with which listeners can identify source location as well as in defining the limitations of localization abilities under any conditions. Such studies continue to provide important information about how listeners localize and have also laid the groundwork for more recent investigations with dynamic stimuli. Even so, much of the work on dynamic localization has not used actual sound sources in motion. More often, studies employ auditory "apparent motion." For example, a typical experimental setup might include a linear array of loudspeakers. If a signal is sent to each speaker in succession with the appropriate interstimulus interval, listeners report the perception of auditory motion. Still other work has employed headphone presentation of stimuli to produce auditory apparent motion, usually varying only one cue to localization at a time such as monaural intensity change or interaural level difference. In evaluating these various approaches, it is clear that many of the findings with stationary static stimuli do not predict well the results of experiments with dynamic stimuli (see later). The difference between studies that use apparent motion and actual motion appears to be smaller. However, the number of experiments that use real auditory motion is probably to small to evaluate this comparison properly.

There are several advantages to using apparent motion to investigate localization and motion perception. First, any mechanism that produces real motion also generates some sound itself that may interfere with the target signal. Second, using apparent motion, especially in headphones, allows the researcher to present different auditory motion cues selectively and examine the relative contribution of each while factoring out the effects of the others.

STATIONARY LOCALIZATION

There are a considerable number of studies that examine the ability of listeners to localize sounds in the horizontal plane (roughly defined as the plane that passes through the head at ear level). There is less work that investigates localization in the median (or sagittal) plane and still less on the ability of listeners to determine the distance of a sound's source (Scharf & Houtsma, 1986). It is likely that the preponderance of work done in the horizontal plane is due to the fact that this plane can be easily simulated in headphones. Although there are clearly differences between horizontal localization of external sounds and what has been called "lateralization" of sounds in headphones, the two methodologies have provided a reasonably clear picture of the physical cues that are used to localize sounds in the horizontal plane.

One of the earliest studies to examine localization in the horizontal plane and the physical cues that listeners use to localize was conducted by Stevens and Newman (1936). Listeners were seated in a tall chair on a rooftop to avoid reflected sound and were asked to identify the angular position of a loudspeaker

that could circle the listener on the end of a boom. Stevens and Newman are credited as being the first to provide empirical evidence for the "duality theory" of localization, an idea that had been proposed by Rayleigh as early as 1907. By the time Stevens and Newman presented their data, duality theory was generally accepted on logical grounds alone (Scharf & Houtsma, 1986). Duality theory proposes that listeners use both interaural intensity differences (IIDs) and interaural phase differences (IPDs) to localize sound sources in the horizontal plane. Using pure tone stimuli that ranged in frequency from about 400 to 10,000 Hz, they found that listeners used IPDs to localize sounds below about 1500 Hz and IIDs to localize sounds above about 4000 Hz. As one might expect, localization performance was worst between 1500 and 4000 Hz.

Whereas Stevens and Newman primarily examined localization *accuracy*, Mills (1958) employed a different methodology to examine localization *precision*. Essentially, Mills was interested in the smallest amount of source displacement that could be reliably detected. He seated listeners in an anechoic chamber and played sounds from a loudspeaker mounted on the end of a boom. The initial sound was followed by a second sound that was played after the boom had been moved to the left or right. The task of the listener was to determine the direction in which the sound source had been moved. The angle at which listeners achieved an accuracy rate of 75% was termed the minimum audible angle (MAA). Mills found that the MAA was dependent upon both frequency and azimuth. Performance was best at 0° azimuth (directly in front of the listener) and deteriorated as azimuth was increased to 75°. At 0° azimuth the MAA was less than 4° for all frequencies tested between 200 and 4000 Hz.

Perrott and his colleagues have conducted extensive work on MAAs and how they differ from minimum audible movement angles (MAMAs). For example, Mills (1958) showed that a 500-Hz stationary tone can be localized to within plus or minus 1° of azimuth. Thus, we might predict that the listeners would be able to detect the motion of a sound source once it has traveled at least 2°. Nonetheless, a sound source in motion can travel up to 10 times this distance before the motion can be detected, and the velocity of the source influences the distance required for detection (Harris & Sergeant, 1971; Perrott & Musicant, 1981). Other work has examined how MAAs interact with the precedence effect (Perrott, Marlborough, Merrill, & Strybel, 1989; Saberi & Perrott, 1990) and differences between MAAs in horizon and azimuth (Perrott & Saberi, 1990).

The MAA paradigm has also been used to examine the ability of listeners to determine the "facing angle" of a directional sound source. An audible facing angle is formally defined by a line between a source and a listener and a ray in the direction in which the source is radiating (see Fig. 1). Under certain conditions, listeners can discriminate between facing angles that differ by as little as 9° (Neuhoff, Rodstrom, & Vaidya, 2001). In this study, a burst of broadband noise was played in an anechoic room through a small loudspeaker that directly faced the listener. After the stimulus was presented, the loudspeaker silently rotated on
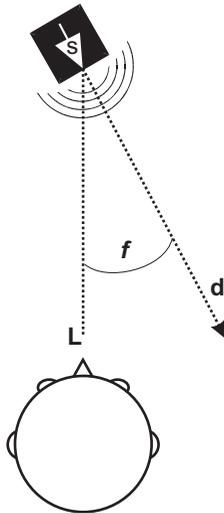
FIGURE 1   The audible facing angle *f* is defined by a line between the source *s* and listener *L* and the ray *d* in the direction in which the source is radiating.

its axis to either the left or the right. The same burst of noise was then played again. The task of the blindfolded listener was to determine the direction of rotation. The minimum audible facing angle (MAFA) was found to be dependent on the distance between the source and the listener and also on the directivity (or pattern of acoustic dispersion) of the source. The closer the listener was to the source and the narrower the pattern of directivity, the better listeners could discern differences between facing angles.

From an ecological perspective, localizing filtered pure tones in one plane on a reflectionless rooftop or detecting source displacement in an anechoic chamber leaves much to be desired. However, Stevens and Newman also found that if presented with broader spectrum sounds, for example, unfiltered pure tones that produced an audible click, or broadband noise, listeners could localize with less error. Presumably, for sounds with sufficient bandwidth, listeners could use both IPD and IID information in addition to interaural time differences (ITDs). Mills found an effect of source frequency that showed that localization precision was best for frequencies between about 200 and 1000 Hz. More recently, researchers have shown that auditory localization for some listeners is comparable in real environments and virtual auditory environments in which interaural differences in the signal are synthesized to simulate virtual auditory sources in space (Loomis, Hebert, & Cicinelli, 1990). These findings are particularly encouraging to those involved in developing devices to provide navigation information to the visually impaired.

HORIZON AND AZIMUTH

In several studies, researchers have asked listeners to locate sounds in the near space around the head. In these studies the location of the stimulus varied freely in elevation and azimuth, although distance from the listener was held constant. Makous and Middlebrooks (1990) used a head-pointing technique to examine the ability to localize sounds in both the vertical and horizontal planes. Listeners were seated in the center of a coordinate sphere with a radius of 1.2 m, and the stimuli were presented in 340° of azimuth and 100° of elevation in 10° increments. The task was simply to orient toward or face the perceived location of the sound source. After extensive training with feedback, listeners typically showed errors of less than 5° in both the horizontal and vertical dimensions directly in front of the listener. Accuracy diminished as sounds were presented from more peripheral locations.

Oldfield and Parker (1984) conducted a similar study in which listeners indicated the perceived location of a sound source on a coordinate sphere whose radius was 0.92 m. Perceived location was specified by using a special pointing "gun." The results were largely concordant with those of Makous and Middlebrooks (1990). Listeners showed better performance in front of the head than behind. Both Makous and Middlebrooks (1990) and Oldfield & Parker (1984) have argued that the use of pointing or orienting responses may be superior to other methods for indicating spatial position. For example, Makous and Middlebrooks cited better performance for listeners using the head-pointing technique over a similar study by Wightman and Kistler (1989) that used a verbal response technique, despite the fact that the characteristics of the stimuli used by Wightman and Kistler should have made localization easier.

One common element among all three of these studies is the extensive practice that participants engaged in prior to the actual recording localization performance. Oldfield and Parker's listeners were given at least 2 hours of training prior to data collection. Makous and Middlebrooks' (1990) listeners engaged in 10 to 20 training sessions. The authors of both studies provided extensive feedback during these practice sessions. Typically, training and feedback are provided in order to acquaint participants with the apparatus and to reduce the variability of responses. From the standpoint of traditional psychoacoustics, this practice makes sense because it better informs us of the limits of localization abilities by reducing variation. However, from an ecological perspective this practice is perhaps questionable because, although it may give us some insight into the limits of localization abilities, it tells us little of how listeners localize sounds under more novel conditions.

ELEVATION

The localization of sound sources in the vertical midline cannot be accomplished by analysis of any interaural differences in the arriving signal because a

source in the median plane is equidistant from the two ears (excluding any differences caused by head asymmetry or facing angle). However, listeners are reasonably good at localizing sounds in the median plane provided that the sounds have a relatively broad spectrum. In fact, it appears that spectral information is critical to accurate localization in the median plane. Blauert (1969) found that when narrowband stimuli are presented in the median plane, judgments of location (either front, back, or above) are almost entirely dependent upon frequency, rather than amplitude or actual location (see also Pratt, 1930; Roffler & Butler, 1968a, 1968b; Trimble, 1934). Blauert has termed the frequency ranges that produce this effect "directional bands." Other work has shown that median plane localization suffers when pinnae cues are eliminated by occlusion (Roffler & Butler, 1968a). The experiments of Blauert and others were typically conducted in an anechoic environment, and listeners were restrained so that head movements were eliminated. Thus, in a natural environment the errors in localization reported are unlikely to occur for several reasons. First, many naturally occurring sounds contain broader spectra, thereby eliminating spatial ambiguity. Second, head movements can create interaural differences that would help resolve spatial position. Still, this finding is important in that it gives some insight into the physical cues that the auditory system uses to localize sounds in the median plane.

These findings also provided a framework for more recent work that attempts to tie these psychophysical results to specific physiological structures in the auditory system that are implicated in the localization of median plane sound sources. For example, using single-cell and cluster recordings, Xu, Furukawa, and Middlebrooks (1999) have identified cortical neurons in cats that accurately identify the median plane location of broadband signals. These are signals that both cats and humans can localize reasonably well. Furthermore, when narrowband stimuli were used, the output of the cortical responding specified incorrect spatial locations, much like those found in the psychophysical studies such as those conducted by Blauert (1969).

DISTANCE

Much as with the perception of visual distance, there are several sources of information that listeners can use to determine the distance of sound sources. Two of the most informative cues are intensity change and reverberation (Bronkhorst & Houtgast, 1999; Zahorik, 2002). Others have to do with source familiarity and the increased atmospheric damping of high frequencies as source distance increases (Little, Mershon, & Cox, 1992). Mershon and colleagues (Mershon, Ballenger, Little, McMurtry *et al*., 1989; Mershon & Bowers, 1979; Mershon & King, 1975) have shown that differences in intensity do not necessarily serve as an absolute cue to auditory distance. However, such differences do provide strong cues to changes in source distance, and greater reverberation is typically associated with more distant sources. Source familiarity can influence distance

perception, with some work showing that more errors occur when listeners are asked to judge the distance of familiar "real-world" sounds such as those created by vehicles than when asked to judge the distance of white noise (Barnecutt & Pfeffer, 1998).

Much of the work on auditory distance perception has focused primarily on the perception of sources that are greater than 1 m from the listener. However, more recent work has highlighted special acoustic circumstances that occur when sources are close to the listener (Shinn-Cunningham, Santarelli, & Kopco, 2000). One might even argue that sources closer to the listener have greater importance from an evolutionary and ecological perspective. There is some work that shows that listeners are particularly sensitive to auditory distance for near sources. In a set of experiments on "auditory reachability," blindfolded listeners heard a rattle that was shaken by a mechanical device at various distances from the listener (Rosenblum, Wuestefeld, & Anderson, 1996). Rosenblum and his colleagues found that listeners could readily discriminate between source locations that were within their reach and those that were not. They also found that listeners were sensitive to the advantage provided by bending at the hip when reaching versus simply extending an arm. Furthermore, when estimates of reachability were scaled to account for differences in reach between individuals due to arm and torso length, differences in reachability estimates between individuals disappeared. Thus, the auditory perception of what is within one's reach appears to be scaled to one's body dimensions.

There does appear to be some corroborating physiological evidence to support the claim the listeners can discriminate between sources that are reachable and those that are not. Graziano, Reiss, and Gross (1999) examined ventral premotor cortex neurons in the frontal lobe of macaque monkeys. They identified cells that had spatial receptive fields extending only a limited distance outward from the head. In addition to auditory stimuli, these cells responded to tactile and visual stimul. Graziano *et al*. examined distance limitations in auditory receptive fields by manipulating the distance between a loudspeaker and the head. They found that the ventral premotor cortex neurons would respond to sounds presented 10 cm from the head but not to sounds presented 30 or 50 cm away, even though stimuli at all distances covered the same range of amplitudes. Visual representation in PMv is primarily limited to the space within reaching distance. Thus, these "trimodal" cells appear to process auditory spatial information only at distances that are within the reach of the listener.

DEVELOPMENT

A limited ability to localize sounds is present at birth. However, it appears that the ability becomes worse before it becomes better. Muir, Clifton, and Clarkson (1989) demonstrated a U-shaped function in localization performance for infants who ranged in age from 3 days to 7 months. The pattern of development is probably due to a maturational shift in locus of control from subcortical to cortical

structures (Muir *et al.*, 1989). Morrongiello, Fenwick, Hillier, and Chance (1994) found that newborns could could differentiate between hemifields in localizing sources and showed some ability to localize within hemifields. Infants made head-turning adjustments to ongoing sounds that moved within a hemifield, suggesting that the infants used more than simple onset differences to determine the hemifield of the source. Ashmead, Clifton, and Perris (1987) examined localization precision in infants 26 to 30 weeks old and found minimum audible angles of about 19°, performance considerably poorer that that of adults, whose MAAs are generally 1 to 2°. These results suggest developmental trends in localization that subsequent work has investigated.

Morrongiello (1988) found a steady increase in localization precision as infants increased in age from 6 to 18 months. Performance increased almost linearly from MAAs of about 12° at 6 months to those of about 4° at 18 months. Between 6 and 18 months, infants (like adults) also showed better localization precision in the horizontal plane than the vertical plane. Morrongiello suggested that localization improvement with age may be the result of anatomical and neurological development, particularly in the auditory cortex, where development lags lower structures in the human auditory system (Clifton, Morrongiello, Kulig, & Dowd, 1981; Hecox, 1975).

In addition to developmental investigations of directional hearing, some work has examined the development of auditory distance perception. Typically, this methodology involves the infant making a distinction between sounds that are reachable and those that are not. Work has shown that infants as young as 6 months can use auditory information alone to make accurate judgments about the reachability of sources of sound (Clifton, Rochat, Litovsky, & Perris, 1991; Clifton, Rochat, Robin, & Bertheir, 1994). However, their strategy for determining auditory distance appears to be somewhat different from that of adults. Infants tend to weight cues to distance more equally, whereas adults in the same task rely more heavily on sound pressure level (Litovsky & Clifton, 1992). A comprehensive discussion of development and ecological psychoacoustics by Werner and Liebold can be found in Chap. 8.

MOTION PERCEPTION

The specific mechanisms that allow human listeners to process auditory motion are a matter of considerable debate. There are two general competing theories about how auditory motion is processed. The first theory suggests that listeners perceive auditory motion by simply comparing static "snapshots" of an auditory source in time and space (Grantham, 1985). Thus, according to snapshot theory, the mechanism behind the processing and of detection and processing of auditory motion is the same that is used to detect sources that are not in motion. The auditory system simply samples the auditory source at different points in time and makes a comparison of the samples in order to detect motion.

Velocity information could be obtained by comparing the distance traveled and the time elapsed during the motion.

Alternatively, the auditory system may respond directly to the motion of acoustic sources. Evidence for this position comes from both psychophysical studies that show that listeners are sensitive to motion information between the starting and ending points of auditory motion and physiological studies that show cellular responding to specific types of auditory motion. Perrott, Costantino, and Ball (1993) showed that listeners could discriminate between accelerating and decelerating auditory motion that traversed the same distance in the same elapsed time. The snapshot theory of motion detection runs into difficulty in accounting for these results. Acceleration discrimination could not be accomplished by simply comparing the endpoints of the path of motion and using the time between the two to determine acceleration because these factors were held constant in both conditions.

Grantham (1997) has suggested that both snapshot theory and direct perception of auditory motion may be at work in perceiving moving sounds. Grantham presented listeners with both dynamic and stationary sound sources. The task was to say whether sources in the dynamic condition were moving or stationary and whether the sounds in the static condition came from the same or different spatial locations. Essentially, the experiments investigated whether the middle of a source's trajectory provided any advantage to listeners in processing auditory motion. Snapshot theory would predict that listeners need only the endpoints of travel (such as those provided in the stationary condition) to make accurate estimates of sources motion. However, improved performance in the dynamic condition could not be accounted for by snapshot theory alone. The results suggested that for slow moving targets (20°/s) in the horizontal plane, the dynamic portion of a sound source's travel provides improved performance in processing auditory motion. The advantage provided by dynamic information was slight. Nonetheless, it cannot be accounted for by snapshot theory alone. At higher velocities (60°/s) the advantage afforded by dynamic cues disappeared. Thus, if the auditory system does use dynamic information in processing auditory motion, it may only do so within a restricted range of velocities. In examining thresholds for velocity discrimination, Carlile and Best (2002) have suggested that listeners may use both true motion perception and displacement detection simultaneously when both cues are available. Their listeners could discriminate well between auditory stimuli at different velocities. However, the highest thresholds for discrimination occurred when the duration of the motion was varied randomly. Thus, velocity discrimination was best if aided by displacement cues.

The study of the neural basis of auditory motion perception has seen great advances with the advent of brain imaging techniques that can investigate auditory perception. Specific neural mechanisms that process auditory motion have been identified (Baumgart, Gaschler-Markefski, Woldorff, Heinze, & Scheich, 1999; Griffiths, Bench, & Frackowiak, 1994; Griffiths, Green, Rees, & Rees, 2000; Warren, Zielinski, Green, Rauschecker, & Griffiths, 2002). These areas of

activation often include premotor cortices, indication a preparation for action in response to the moving source. Moreover, brain imaging in combination with virtual spatial displays has identified a common cortical substrate composed of the planum temporale, superior parietal cortex, and premotor cortex that appears to process auditory motion in both vertical and horizontal directions (Pavani, Macaluso, Warren, Driver, & Griffiths, 2002).

AUDITORY LOOMING

A host of acoustic variables support the perception of sound sources in motion (see Jenison, 1997, for an excellent review). Jennison has shown that the motion of sound sources structures that acoustic array such that higher order variables such as interaural delay, Doppler shift, and average sound intensity specify the kinematics of the source. There is some evidence that suggests that listeners may rely more heavily on some of these cues than others. Rosenblum, Carello, and Pastore (1987) examined the relative contribution of each of these cues in estimating time to contact with a simulated approaching source. They found that when interaural differences, monaural loudness change, and the Doppler effect are manipulated so that they specify different arrival times within the same stimulus, listeners rely most heavily on loudness change, followed by interaural time differences and, to a lesser extent, the Doppler effect.

Given the relative salience of a clear physical cue to the time of closest approach in both interaural time difference and monaural intensity change, perhaps the findings of Rosenblum *et al*. (1987) are not surprising. Both interaural time differences and monaural intensity change have salient physical characteristics that mark the point of closest passage for a sound source. Assuming that the listener is facing the straight-line path of the source perpendicularly (see Fig. 2), interaural differences shrink to zero when the source is at its closest point, and monaural intensity change is at its peak. The Doppler shift has no such salient characteristic. The change in frequency produced by the Doppler follows the formula

$$f_{obs} = f_{src}\left(\frac{v_{snd}}{v_{snd} - v_{src} \cos\theta} \right)$$

where f_{obs} = frequency observed, f_{src} = frequency of source, v_{src} = velocity of source, v_{snd} = velocity of sound, and θ = approach angle of source. For a constant-frequency approaching source, the frequency that arrives at the observation point is initially higher than the frequency that is emitted by the source. The observed frequency remains essentially constant at first, falls at a successively increasing rate as the source approaches, drops rapidly as the source passes, and finally drops at a successively decreasing rate as the source recedes (Fig. 2). The rate of the frequency drop depends on the distance from the observer to the path of the source. The magnitude of the frequency drop depends on the speed of the source.
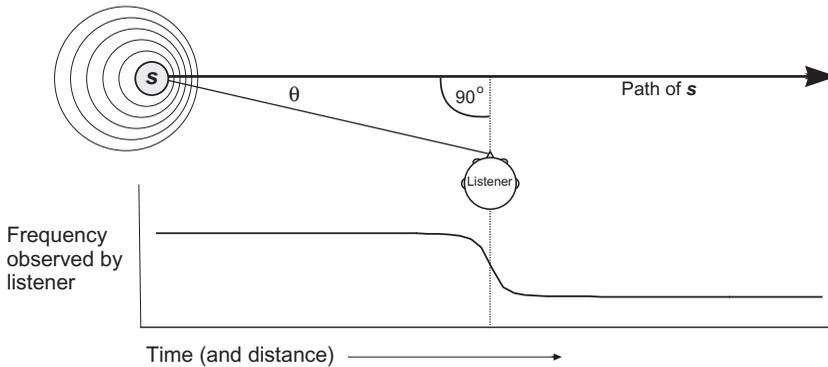
FIGURE 2   For a listener whose interaural axis is parallel to the path of a moving sound source, interaural differences shrink to zero when the source is at its closest point, and monaural intensity change is at its peak. The frequency at the listening point remains essentially constant at first, falls at a successively increasing rate as the source approaches, drops rapidly as the source passes, and finally drops at a successively decreasing rate as the source recedes.

At the point of closest passage, the frequency of the source is in the midst of a dramatic drop.

However, despite the drop in frequency, listeners tend to report hearing a rise in pitch as acoustic sources approach. The apparent paradox between falling frequency and the perception of rising pitch on approach has been termed the "Doppler illusion" (Neuhoff & McBeath, 1996). The effect is so pervasive that it has even worked itself into the physics literature. Many texts erroneously imply that approaching sources produce a rise in frequency on approach (McBeath & Neuhoff, 2002; Neuhoff & McBeath, 1996).

The pattern of rising intensity produced by an approaching source is particularly salient information on source approach. Shaw, McGowan, and Turvey (1991) have termed this pattern of change "acoustic tau," after the visual variable tau that specifies time to contact by the pattern of optical expansion produced by visual approaching objects. The derivation of acoustic tau by Shaw *et al*. shows that the acoustic change in intensity produced by a sound source moving rectilinearly toward a listener at a constant velocity specifies the time to contact with the listener.

However, whether listeners actually use this information to predict arrival time accurately is an issue of some debate. When asked to predict arrival time on the basis of auditory cues, listeners often err on the side of safety, expecting contact before the source actually arrives (Rosenblum, Wuestefeld, & Saldana, 1993; Schiff & Oldak, 1990). Alternatively, listeners have also been asked to estimate time to contact with a sound source while using intensity change to guide their locomotion toward a stationary source. Performance is slightly more accurate in this condition (Ashmead, Davis, & Northington, 1995; Rosenblum, Gordon, & Jarquin, 2000). However, the tendency to err on the side of safety is still apparent, with listeners stopping well short of the stationary target location.

Guski (1992) has suggested that perhaps this type of "error" should not be interpreted as such. He proposed that when a sound source and a listener are coming closer together, the primary role of the auditory system in localizing the source is that of warning, either to direct the visual system toward the object if time allows or to initiate appropriate behaviors to avoid the object. In this view, precise judgments about time to contact are not as important as a categorical decision about whether the listener has time to turn to look or must simply jump out of the way. This idea is echoed by Popper and Fay (1997), who suggested that the primary function of auditory localization may not be to provide exact estimates of source location but rather to provide input to the listener's perceptual model of the environment. Thus, under some circumstances distortions, errors, or biases in auditory localization may prove to be adaptive.

The relationship between monaural loudness change and auditory approach has received some attention. However, there is some debate about whether loudness change per se (for example, rising and falling intensity tones presented in headphones) can be equated with localizing approaching and receding sources. In one set of experiments, listeners reliably overestimated the change in intensity of rising loudness tones relative to equivalent falling intensity tones (Neuhoff, 1998). Listeners were presented with equivalent rising and falling intensity signals and asked to rate the amount of loudness change that occurred in each case. Despite an identical amount of loudness change (falling intensity signals were simply rising intensity signals played backward), listeners judged rising intensity tones to change more than falling tones. In a natural environment in the context of approaching and receding sources, this overestimation could provide a selective advantage because rising intensity can signal movement of the source toward a listener. The bias was found to be stronger at higher levels, suggesting that rising loudness is even more critical when a sound source is either close or loud. The bias was also specific to tones and did not occur with broadband noise. Tonal sounds are produced by a wide variety of single sound sources and in a natural environment are produced almost exclusively by biological organisms. Thus, anticipating such a source's approach is an important environmental event. However, tonal sounds are almost never produced by simultaneously sounding dispersed sources. Multiple sounding sources in a natural environment often result in the production of broadband noise. Thus, tonality can act as a reliable marker for single-source identity and can help listeners distinguish important signals from background noise. These results suggested a privileged status of dynamic rising loudness for harmonic tones and an asymmetry in the neural coding of harmonic dynamic intensity change that provides a selective advantage.

However, Canevet and colleagues have challenged the evolutionary implications of these findings. Simple loudness change in headphones is vastly different from the kind of acoustic change produced by an approaching source in a natural environment (Canévet, Scharf, Schlauch, Teghtsoonian, & Teghtsoonian, 1999). First, the intensity change produced by an approaching source follows the

inverse-square law, whereby changes in intensity occur at a faster and faster rate as the source draws closer to the listener. The rate of intensity change used by Neuhoff (1998) was linear, thus specifying decelerating approaching sources and accelerating receding sources. Second, the sounds were heard through headphones, but the inferences made concerned free-field auditory motion. Consistent differences have been shown between both loudness and localization estimates with sounds heard in headphones and those heard in a free-field setting (e.g., (Hartley & Carpenter, 1974; Stream & Dirks, 1974; Wightman & Kistler, 1989)). Finally, listeners were asked simply to make estimates of loudness change. Although it is likely that monaural loudness change is a primary cue that listeners use to judge auditory source approach (Rosenblum, Carello, & Pastore, 1987), it is possible that the estimates of loudness change do not correspond well to estimates of distance change in a natural listening environment (but see Warren, 1958, 1963, for an alternative view).

To address these concerns, Neuhoff (2001) conducted three subsequent experiments. If listeners have indeed evolved to be more sensitive to approaching sounds than receding sounds based on intensity change, several predictions could be made. First, given equal change in intensity, rising intensity sounds should be perceived to change in loudness more than falling intensity sounds. Similarly, given equal stopping points in a natural environment, approaching sounds should be perceived as being closer than receding sounds. This would provide a margin of safety on approach that could provide a selective advantage. Second, at higher intensity levels, the disparity between rising and falling loudness change should be greater. A bias for rising intensity would be more advantageous for loud (close) sounds than for soft (distant) sounds. Finally, the bias for source approach should be greater for tones than for noise.

In the subsequent experiments, listeners heard approaching and receding sounds in an open field and indicated the perceived starting and stopping points of the auditory motion (see Fig. 3). Results showed that approaching sounds were perceived as starting and stopping closer than receding sounds despite the fact that all sounds had equal starting and stopping points (see Fig. 4). The effect was greater for tones than for noise. The evidence suggests that an asymmetry in the neural coding of approaching and receding auditory motion is an evolutionary adaptation that provides advanced warning of approaching acoustic sources. However, theories regarding the evolution of a perceptual characteristic must be evaluated carefully. It is, to say the least, difficult to do experiments that directly test evolutionary hypotheses in humans. Thus, converging evidence from different methods and perspectives is required.

Currently, there is psychophysical, physiological, and phylogenetic converging evidence that supports the role of the auditory system as a warning mechanism in processing approaching sources and the adaptive characteristics of the rising intensity bias. First, Schiff and Oldak (1990) examined accuracy in judging time to arrival in both the auditory and visual modalities. They specifically examined the effects of gender and source trajectory in each modality. In one
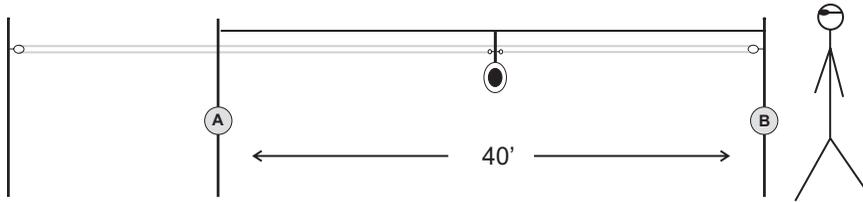
FIGURE 3   In Neuhoff (2001), blindfolded listeners heard approaching and receding sounds that had a common terminus. Approaching sounds began 40 feet from the listener (point A) and stopped at a distance of 20 feet. Receding sounds started at the listener (point B) and moved away 20 feet.
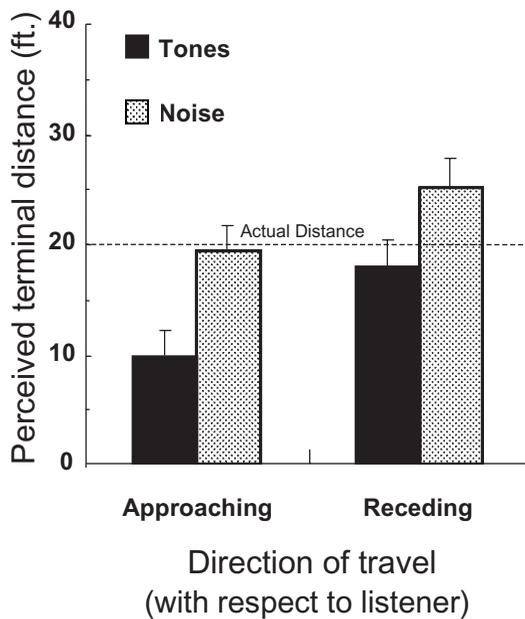

FIGURE 4   Despite equidistant points of termination, approaching sounds were perceived to stop significantly closer than receding sounds. Harmonic tones were perceived as stopping significantly closer than broadband noise.

condition the source was on a collision course with the listener. In another the source traveled a path that would bypass the listener at a safe distance. From an evolutionary perspective one would predict greater underestimation of time to contact when the source is on a collision course. Indeed, this is exactly what Schiff and Oldak found. Listeners underestimated arrival time across all conditions. However, the underestimation was greater when the source was on a collision course with the observer. Furthermore, the further the angle of approach was from a collision course, the more accurate time-to-arrival estimates were (Schiff & Oldak, 1990). Schiff and Oldak also found that females tended to under-

estimate arrival time more than males. It is unclear whether this underestimation is due to greater risk-taking behavior by males than females or better spatiotemporal skills. However, it should be noted that these results are consistent with hunter–gatherer theories of sex-specific spatial ability (Eals & Silverman, 1994; Silverman & Eals, 1992; Silverman & Phillips, 1998). In either case, the authors suggested that such cautious estimates of arrival time would provide survival benefits, particularly in situations in which judgment errors are likely.

Ashmead *et al*. (1995) investigated the case in which a listener is in motion toward a stationary sound source. They asked listeners to make auditory distance judgments as they listened to the source while walking toward it or while standing still. The information provided by the relative motion between the source and observer yielded better estimates of source location. However, walking to the source yielded estimates of source location that were closer to the listener than estimates made while listening in place. Ashmead *et al*. also manipulated the level of the source in order to make it appear nearer or farther from the listener. For example, as the listener approached, the intensity level of the source was either increased to make it sound nearer or decreased to make it sound farther. They found that increases in intensity produced appropriate undershooting of the target but that decreases did not produce the expected overshooting. This robust resistance to overshooting auditory targets supports the idea that the auditory system in localizing sources errs on the side of safety and acts as a warning system.

At the physiological level, there is evidence that cells in the auditory system are selective in processing directional motion and that neural firing rates in response to auditory motion can vary asymmetrically based on direction of travel (Doan & Saunders, 1999; Kautz & Wagner, 1998; Rauschecker & Harris, 1989; Wagner, Kautz, & Poganiatz, 1997; Wagner & Takahashi, 1992; Wilson & O'Neill, 1998). Evidence also comes from electrophysiological recordings, which show that a greater proportion of primary auditory cortical neurons are selective for rising intensity than for falling intensity (Lu, Liang, & Wang, 2001). Furthermore, the human brain mechanisms that process this perceptual bias have also been identified. Functional magnetic resonance imaging has demonstrated that specific motion-sensitive neural streams show anisotropic responses to rising versus falling intensity tones (Seifritz *et al*., 2002). Rising intensity tones preferentially activate a neural network responsible for attention allocation, motor planning, and the translation of sensory input into ecologically appropriate action. All of these processes suggest preparation for the arrival of a looming acoustic source (see Fig. 5).

Finally, if the bias for rising intensity is truly a product of evolution, we would expect to see the same phenomenon in a closely related species. To test this hypothesis, rhesus monkeys were presented with equivalent rising and falling intensity tones and noise from a hidden loudspeaker (Ghazanfar, Neuhoff, & Logothetis, 2002). The duration of an orienting response (a head turn toward the loudspeaker) was measured after each stimulus presentation. The results showed that nonhuman primates exhibit a strikingly similar spectrum-specific bias for
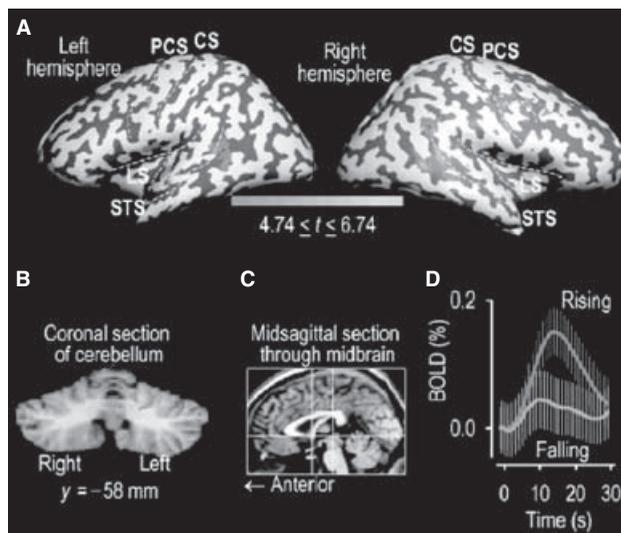
FIGURE 5   Cortical activation by "looming" compared with "receding" tones. (A) The general linear contrast "rising versus falling" intensity tones yielded a neural network comprising bilaterally the superior temporal sulci and the middle temporal gyri, the right temporoparietal junction encompassing the inferior portion of the angular gyrus, the right motor and lateral premotor cortices mainly on the right hemisphere, the left frontal operculum and discrete areas (B) in the left superior posterior cerebellar cortex and (C) in the midbrain (possibly representing the reticular formation). (D) Condition specific averaged (and standard errors; linear interpolation to one sample per second) blood oxygen level–dependent (BOLD) signal responses in all areas shown in (A)–(C). CS, central sulcus; LS, lateral sulcus; PCS, precentral sulcus; STS, superior temporal sulcus. The results indicate a preferential treatment of looming sounds and preparation for actions in response to auditory looming. (From Seifritz *et al*., 2002.)

rising intensity. Subjects oriented over twice as long to rising intensity tones than to falling intensity tones (see Fig. 6). However, analogous to the human data, there was no difference in the duration of orienting to rising and falling intensity noise.

ECHOLOCATION

The human ability to use the auditory system to localize objects in the environment is perhaps most acute (and probably has the greatest ecological validity) in the case of blind listeners who use echolocation. In the strict sense of the term, echolocation is determining the location of objects in the environment on the basis of how they reflect sounds produced by the listener. However, some researchers have used the term to include the use of ambient reflected sound that is not produced by the listener (Ashmead & Wall, 1999; Ashmead *et al*., 1998). Bats are perhaps the most proficient echolocating species, listening to reflected vocalizations for navigational guidance in three-dimensional flight as well as the
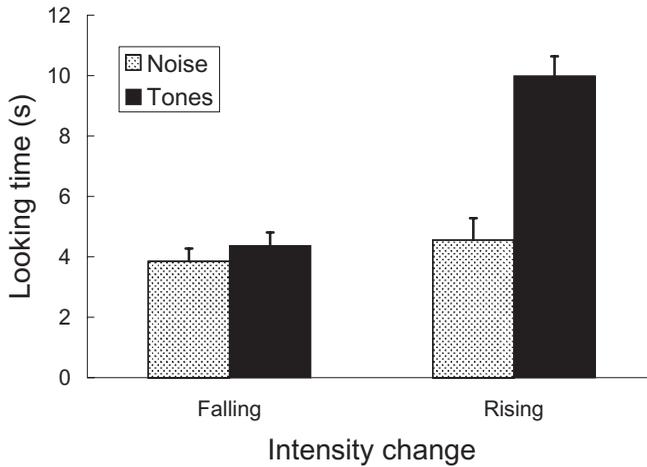
FIGURE 6   Duration of an orienting response in rhesus monkeys in response to rising versus falling intensity tones and noise. The results mirror the pattern of auditory looming results in humans. Rising intensity tones are given priority over falling intensity tones. However, there is no difference between rising and falling intensity noise (Ghazanfar, Neuhoff, & Logothetis, 2002).

tracking and capture of prey (Griffin, 1958). Humans rely predominantly on vision for localization, tracking, and navigation. Yet, despite the dominance of the visual system, humans have also been show to be able to use echolocation (for a review see Stoffregen & Pittenger, 1995).

Much of the work on human echolocation has involved blind participants. Early investigations examined what had been termed "facial vision," wherein blind participants could detect objects and obstacles that were at close range (Dallenbach, 1941; Supa, Cotzin, & Dallenbach, 1944). Prior to this work, there was some question about the modality that was actually used to detect obstacles. Many blind participants in earlier less systematic work insisted that they "felt" the presences of obstacles in their path. Many hypothesized that the ability of the blind to avoid obstacles was based on a tactile sense, perhaps based on changes in air pressure detected by the face (thus, the term facial vision).

However, Dallenbach and his colleagues (Dallenbach, 1941; Supa *et al*., 1944) showed unequivocally that the key to successful navigation around obstacles for the blind was echolocation. Several of these studies examined the ability of blind and blindfolded sighted listeners to detect a large obstacle as they approached it. The experiment was conducted indoors, and it was found that, in general, blind listeners could perform the task better than sighted listeners. Furthermore, performance was better when the motion of the listener produced sound. For example, performance was better when listeners made estimates while wearing shoes on a hardwood floor than when in stocking feet on carpet. The unequivocal evidence for acoustic rather than tactile cues was provided when a microphone was mechanically moved toward the obstacle, the output of which was fed

through headphones to a listener in another room. Performance was equal to that which occurred when the listener approached the obstacle personally. Covering the skin and otherwise interfering with tactile senses decreased performance only slightly (presumably because the ears were also covered). However, preventing acoustic input by plugging the listener's ears resulted in an absolute failure to sense the obstacle on all trials. These main findings were replicated outdoors under conditions of higher ambient noise (Ammons, Worchel, & Dallenbach, 1953).

One case study examined the ability of a blind 11-year-old boy to ride a bicycle while avoiding obstacles (McCarty & Worchel, 1954). The boy rode a bicycle over a course in which two obstacles had been placed. He detected the obstacles by making a clicking sound with his mouth and listening for a difference in the pitch of the echo. After 40 trials without a collision, the boy was instructed to ride as swiftly as possible through the course. A similar level of performance was maintained at increased rates of speed. This particular ability has also been documented anecdotally elsewhere (Griffin, 1959). Other studies have shown that some listeners can use echolocation with remarkable accuracy to estimate object size and distance and as a general tool for mobility (Boehm, 1986; Rice & Feinstein, 1965a, 1965b; Rice, Feinstein, & Schusterman, 1965; Taylor, 1966).

With some exceptions, blind listeners have generally been shown to echolocate better than sighted listeners. In an effort to examine the psychoacoustic underpinnings of this finding, Arias and colleagues (1993) compared the peripheral and central auditory functioning of blind listeners who were good obstacle detectors with that of sighted listeners. Audiological tests and brainstem evoked responses showed that blind listeners were faster than sighted listeners in auditory processing. In addition, it was found that echolocating signals were processed more slowly than standard stimuli and that they may be processed in the superior olivary complex of the midbrain. Blind listeners have also been show to have improved spatial tuning in the auditory periphery when compared with sighted listeners (Roeder, Teder-Saelejaervi, Sterr, Hillyard, & Neville, 1999). Electrophysiological recordings suggest that this behavioral advantage stems from compensatory reorganization of brain areas.

Initially, it was thought that there was a relationship between high-frequency hearing and echolocation abilities. However, several investigations have brought this idea into question. Carlson-Smith and Weiner (1996) developed a battery of audiometric tests to examine what particular auditory skills are correlated with good echolocation abilities. In their examination of nine echolocators there was no relationship between high-frequency hearing and the ability to echolocate. Furthermore, Ashmead and colleagues (1998) found that blind children used primarily ambient low-frequency sounds to navigate successfully through artificially constructed hallways and walking paths.

It does appear that motion cues produced by movement of the echolocator improve localization estimates. Rosenblum *et al*. (2000) had listeners estimate the location of a wall by echolocating in a stationary condition or while walking.

There was a slight advantage in the walking condition, suggesting that listeners may use echoic time-to-contact information. Reflected sound can also be used to some extent to determine whether there is sufficient room between a sound source and a wall to permit unimpeded passage for the listener (Russell, 1997). Other work has shown that listeners can detect the presence of occluding objects between a sound source and the listener (Ader, 1935; Russell, 1997). However, in some cases occluding objects can make the source sound as though it is simply farther away.

It should be noted that echolocation is probably not a task that is used exclusively by the blind. Stoffregen and Pittenger (1995) have presented a detailed exposition of the types of information that are available to listeners via echolocation. In addition to distance and azimuth information about objects in the environment, there is within a reflected signal information that can specify characteristics of shape, material, size, motion, and time to contact. Stoffregen and Pittenger (1995) suggested that echolocation is used far more often than one might suppose and that a research focus on echolocating bats coupled with the dominance of the human visual system may obscure the often used but perhaps unnoticed echolocation skills of sighted listeners. Work showing that listeners can indeed discern shape, length, and material characteristics from objects that generate sound provides indirect support for this proposition (Carello, Anderson, & Kunkler-Peck, 1998; Kunkler-Peck & Turvey, 2000; Lakatos, McAdams, & Causse, 1997; Lutfi, 2001).

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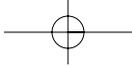
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