

The effect of trajectory on the auditory motion aftereffect

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Abstract

The auditory motion aftereffect (aMAE) can be induced in listeners after repeated presentation of a horizontally moving sound source. Aftereffects have also been found for the individual acoustic consequences of source motion such as amplitude or frequency modulations (AM, FM). No study, however, has investigated whether combining these changes would enhance the magnitude of the aMAE, which has appeared otherwise weak relative to its visual counterpart. AM, FM and binaural changes can occur simultaneously when sources move along common translational trajectories rather than the restricted rotational paths used in previous adaptation studies. This raises the question whether the observed weakness of the aMAE is due to the improper stimulation of units responsive to the entire macrostructure induced by translational motion. The hypothesis is tested here that if integrated motion detectors exist, then including lawful amplitude and frequency changes in adapting stimuli may enhance aftereffects. Though results indicate that interaurally moving stimuli in general induce an aMAE, the acoustic macrostructure of translational motion does not appear to increase the aftereffect. A simple cross-correlation model is used to illustrate that such acoustic modulations may allow brainstem auditory centers time to recover from adaptation to translational motion.

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1. Introduction

A sound source repeatedly traversing horizontal auditory space may induce an auditory motion aftereffect (aMAE) in which sensitivity to slightly moving test stimuli shifts in the direction opposite that of adaptation (Grantham, 1989, 1998; Dong et al., 2000). Additional work has investigated aftereffects for other acoustic consequences of motion, such as level or frequency changes (Reinhardt-Rutland, 1992; Shu et al., 1993). Though these studies reveal effects of adaptation to dynamic auditory stimulation, the phenomenological experience of the aMAE remains much weaker than its visual counterpart (Grantham, 1989). Motion aftereffects are commonly attributed to the adaptation of specialized motion detectors in the perceptual pathway (Perrott et al., 1993; Niedeggen and Wist, 1998); con-

sequently, the tepid nature of the aMAE is often viewed as evidence against the existence of such analyzers in the auditory system (Middlebrooks and Green, 1991). The question remains, however, whether these weak findings are due to the absence of specialized auditory motion detectors or to the impoverished nature of the stimulation (Grantham, 1989).

1.1. The role of spectral information (HRTFs) in auditory motion processing

Stimulus impoverishment has taken many forms in early aMAE studies and was most likely caused by the computational or signal processing limitations of the time. Many early aMAE studies were conducted under headphones using spectrally limited stimuli such as pure tones, while source movement was often simulated via independent phase or level changes (Grantham and Wightman, 1979; Reinhardt-Rutland, 1992; Ehrenstein, 1994). Signal parameters were typically manipulated only to create a sense of movement under headphones and not to replicate the lawful changes in

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spatial information that a sound undergoes when moving in the real world (Jenison et al., 1998).

One important shortcoming of these early aMAE stimuli was the lack of spectral filtering that occurs when a sound reflects off an individual listener's pinnae, head and shoulders in the free-field. These filters, known as head-related transfer functions (HRTFs), are direction-dependent and may provide important information about source position. It is reasonable to ask whether hypothesized auditory motion detectors would be more responsive to, and by extension better adapted by, sources which included a listener's unique HRTFs.

This issue has been addressed in more recent studies by using sounds emanating from a speaker moving in a horizontal arc about the listener (Grantham, 1989, 1998; Dong et al., 2000). The most notable effect of adapting listeners to dynamic binaural and spectral cues in this manner was a reduction in the variability across subjects of the resulting aMAEs compared to previous headphone studies. Dong et al. (2000), using broadband stimuli played from a moving mechanical arm, reported more 'robust' motion aftereffects relative to earlier aMAE studies, though they made no direct comparison of aftereffect magnitudes. None of these studies, however, reported any phenomenological experience of an auditory 'waterfall' illusion on a par with that induced so easily in vision (Wade and Verstraten, 1998).

Though the aMAE may be more consistently measurable when using real moving stimuli, it is possible that listeners still do not rely greatly on spectral cues to determine change in source position on the horizontal plane. Evidence shows that binaural cues dominate in the perception of stationary azimuthal source positions, though spatially dependent spectral filtering appears necessary for disambiguating location along the front-back and up-down axes (Wightman and Kistler, 1997). In fact, for sources with strong low frequency components, azimuthal localization may be largely determined by interaural time differences (ITD) rather than interaural level differences (ILD) or spectral cues (Wightman and Kistler, 1992; Macpherson and Middlebrooks, 2002).

The importance of these results is that all of the aforementioned aMAE studies have used horizontal motion trajectories for their adapting stimuli. Hence, the contributions of spectral relative to binaural cues in motion perception have not been well established. One means of measuring such contributions would be to adapt listeners to vertical movement in the median plane, a trajectory where binaural cues are minimized and source position must be indicated by spectral changes (Middlebrooks and Green, 1991). To our knowledge, no aMAE has been reported for vertical auditory motion.

Studies which have investigated the effect of source movement on auditory spatial perception support similar conclusions that listeners appear to make better use of dynamic binaural cues rather than dynamic spectral cues. For instance, Saberi and Perrott (1990) reported much larger minimum audible movement angles for source movement in the vertical median plane than for horizontal or even oblique trajectories. Wightman and Kistler (1999) allowed source and head movement during sound localization and found little improvement specifically in elevation judgments compared to static conditions. These results suggest that, as with static localization, auditory motion perception appears to be best for movement along the horizontal plane where binaural cues once again may dominate.

1.2. Macro-acoustic cues to auditory motion

The experiment reported here addresses another form of impoverishment common to aMAE stimuli beyond the inclusion of HRTFs. As noted earlier, sources in the previous auditory aftereffect studies have moved along a restricted rotational path in the horizontal plane. This trajectory has either been produced by rotating a speaker on a mechanical arm or been simulated under headphones via constant changes in timing or level differences (Grantham and Wightman, 1979; Reinhardt-Rutland, 1992; Ehrenstein, 1994; Grantham, 1989, 1998; Dong et al., 2000). Trajectories of many naturally moving objects, however, will rarely be purely rotational but often embody a combination of translational and rotational components (e.g., insect flight paths, vehicle trajectories). (See Fig. 1 for depictions of pure translational (A) vs. pure rotational trajectories (B).)

Translational trajectories lead to time-dependent changes in the distance and angular velocity of the source with respect to a listener (Perrott et al., 1993), and these changes can impose level (Fig. 2A), spectral (Fig. 2B) and interaural modulations (Fig. 2C) to the source vis-à-vis a stationary listener, such as an amplitude envelope and Doppler shift (Jenison, 1997). Purely rotationally moving stimuli, on the other hand, should theoretically produce none of these macro-acoustic changes (Dong et al., 2000). Unlike HRTFs, these cues may play important roles in auditory motion processing given their uniquely causal relationship to source movement (Zakarauskas and Cynader, 1991; Jenison, 1997). Several psychophysical studies have in fact shown that listeners are sensitive to and can make use of these gross amplitude and spectral changes when discriminating moving sound sources (Rosenblum et al., 1987; Lutfi and Wang, 1999; Neelon and Jenison, 2000).

This analysis raises the following questions. Is the observed weakness of the aMAE simply the diffuse

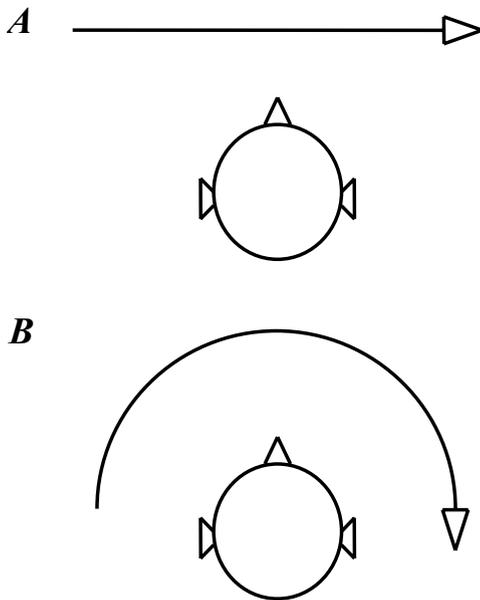


Fig. 1. Depiction of translational (A) and rotational (B) trajectories of a moving sound source.

product of disparate neuronal systems, each of which is responsive to individual acoustical attributes? Or is it due to the improper stimulation of higher-order units which are sensitive to the ensemble of changes associated with translational movement that can occur in natural environments? If such units exist, then including amplitude and frequency modulations (AM, FM) in adapting stimuli may enhance the magnitude of aMAEs.

To test this hypothesis, two types of motion stimuli were compared in Experiment 1: *translational motion* and *rotational motion* adaptors. The translational motion adaptor mimicked a sound moving along a linear trajectory, resulting in concurrent changes in spectrum, amplitude envelope and ITD. The rotational motion adaptor approximated stimuli common to auditory motion studies by using changes in ITD to model a source moving in an arc around the listener. A third, binaurally non-moving adaptor was used as a control condition. ITD was chosen as the interaural parameter to indicate motion rather than ILD since the stimuli used in the following experiments were predominantly lowpass (see below for details).

2. Methods

2.1. Stimuli

All adapting and test stimuli were synthesized from a 225 ms sample of a pre-recorded motorcycle engine, creating a stimulus rich in resonant structure. This technique was first described in detail by Jenison et al.

(1998). Basis coefficients were first extracted from the sample using Fourier analysis (see Appendix C). A series of carrier sinusoids were generated across a frequency range of 1–6000 Hz whose acoustic attributes were modified according to the experimental conditions described below. Modified sinusoids were weighted with the extracted coefficients and re-summed to produce a simulated moving vehicle. The duration of all adaptors used in the following experiment was 2s.

The use of such stimuli was motivated by several reasons. First, aMAEs appear stronger for low-frequency stimuli (Grantham, 1998; Dong et al., 2000). Second, as noted earlier, if ITD is an important cue for lateral position, the strong low-frequency nature of the stimuli should help listeners better track changes in lateral position. Lastly, these stimuli were believed to further enhance for naive participants the experience of listening to a realistically passing auditory object.

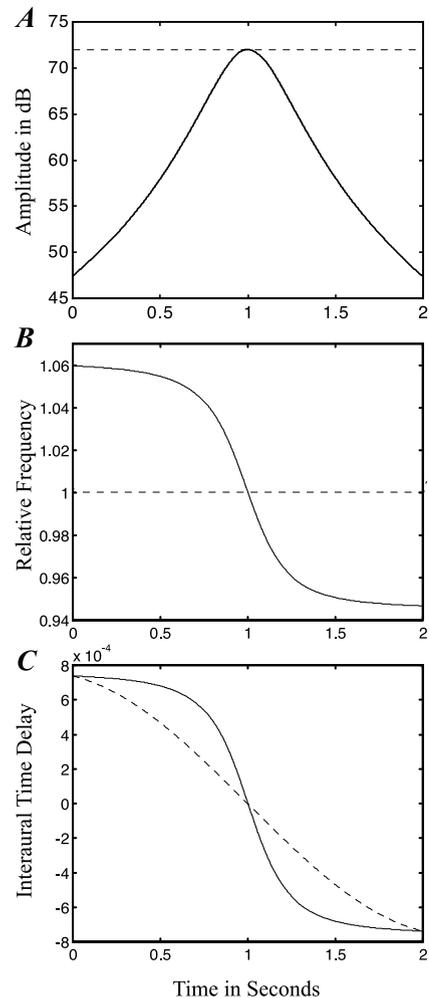


Fig. 2. Comparison of amplitudes (A), relative frequencies (due to the Doppler shift) (B) and ITD changes (C) for a sound source moving along translational (solid) versus rotational (dashed) trajectories.

2.1.1. Translational motion adaptor

Following Jenison et al. (1998), three acoustic parameters (spectrum, amplitude, ITD) of the translational motion adaptor were modulated in accord with the kinematics of physical acoustics to model a linearly passing vehicle (Morse and Ingard, 1968). These parameters were selected based upon previous work which showed they are sufficient to uniquely characterize moving sound sources (Rosenblum et al., 1987; Jenison, 1997; Lutfi and Wang, 1999). Specifically, each left and right sinusoid in the vehicle decomposition was amplitude-modulated following an inverse square law of distance, and Doppler and interaurally phase-shifted as a function of angular velocity, all with respect to a source traveling at a virtual velocity of 20 m/s, and passing a listener at 5 m at the closest point of approach (see Appendix for details). Interaural movement was created through interaural phase modulation only (see Appendix B). This process modeled the waveform of a vehicle passing in front of the listener along a projected linear path spanning approximately $+76^\circ$ (right) to -76° (left). (Maximal excursions of $\pm 90^\circ$ would require a theoretically infinite linear travel distance.)

2.1.2. Rotational motion adaptor

The trajectory of the rotational motion adaptor was created by modulating ITD to mimic a constant change in incident horizontal angle spanning $+76^\circ$ to -76° . This dynamic ITD was applied to the vehicle stimulus described above without spectrum or amplitude modulations, resulting in an engine-like stimulus moving in a virtual arc around the listener at a constant angular speed of $76^\circ/\text{s}$. It is important to note that the linear trajectory of the translational adaptor produces a non-linear change in angular velocity (Fig. 2C). This makes its speed in constant angular deg/s position-dependent unlike that of the rotational adaptor. Fig. 3 presents spectrograms of the translational (A) and rotational (B) adaptors. Leftward moving stimuli ap-

peared to start on the listener's right side ($+76^\circ$) and then pass to the left (-76°), and vice versa for rightward stimuli.

2.1.3. Control adaptor

To measure a comparison baseline performance, a third condition presented a diotic version of the translational motion adaptor: a stimulus undergoing frequency and amplitude modulations as a result of a linear trajectory, but with no changes in ITD. This gave the appearance of a vehicle passing the listener from front to back, but unchanging across azimuth.

2.1.4. Test stimuli

Thirteen stimuli were used to test for a motion after-effect after adaptation. All test stimuli began with zero ITD and appeared centered at azimuthal midline. ITD was then modulated to trace an arc in the manner of the rotational motion adaptor, with excursions ranging from $+18^\circ$ (right) to -18° (left) in steps of 3° . Duration of test stimuli was 750 ms, resulting in angular speeds from approximately $+24^\circ/\text{s}$ to $-24^\circ/\text{s}$ in steps of $4^\circ/\text{s}$. The center stimulus in this sequence did not move ($0^\circ/\text{s}$). This range of excursions was chosen to provide sufficiently detectable endpoints ($\pm 18^\circ$), along with midpoints that fell within minimum audible movement angles of $2\text{--}5^\circ$ (Grantham, 1997). Test stimuli included no amplitude or frequency modulations, such that they were variants of the rotational motion class.

Note that no ILDs or HRTFs were added to any of the stimuli used in the experiments reported here. Again, published evidence shows that judgments of azimuthal position for stimuli with strong low-frequency components are predominantly determined by ITD (Wightman and Kistler, 1992; Macpherson and Middlebrooks, 2002). Due to the lowpass nature of the engine source sound, the power spectrum for the stimuli used in this experiment is maximal between 200 and 500 Hz and steadily declines over 40 dB by 1 kHz (Fig. 4).

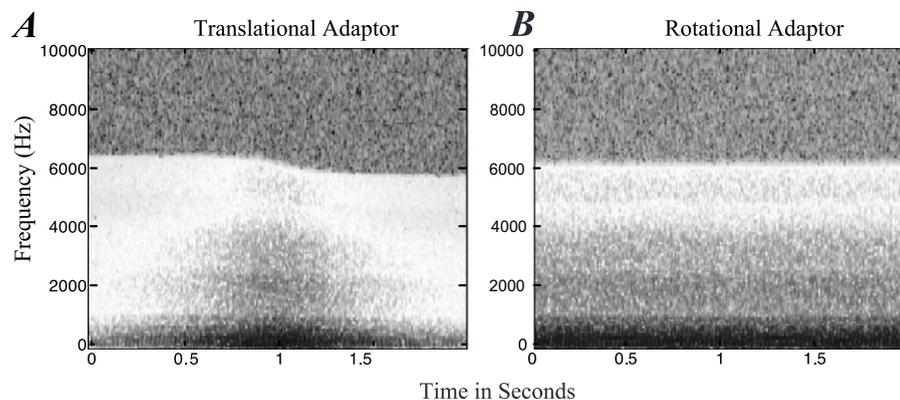


Fig. 3. Comparison of spectrograms for a sound source moving along translational (A) versus rotational (B) trajectories. Note the amplitude and spectral changes resulting from the translational trajectory.

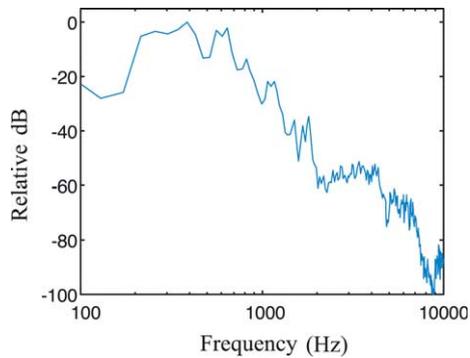


Fig. 4. Power spectral density profile of the stimuli used in this experiment.

It is assumed that given this spectral profile the inclusion of ILD or HRTFs would add little to the successful lateral tracking of these stimuli, although this remains to be tested.

2.2. Procedure

The results reported below were from seven introductory psychology students who participated in four 1 h experimental sessions for extra credit. All reported normal hearing and none had participated in psychoacoustic experiments prior to this one. Subjects first took part in a 15 min pilot session which presented only the control condition to familiarize them with the procedure. In each experimental session, subjects were tested in all three adaptor conditions (translational, rotational, and control), lasting approximately 20 min each. All adaptors moved in the same direction within each single session, and testing on different directions occurred on separate days. Presentation order of adaptor conditions and directions was counterbalanced across subjects and sessions. Subjects took part in two sessions for each motion direction and results were combined in the following analyses. The use of human subjects and the experimental methods were approved by the Human Subjects Committee of the UW-Madison Office of Research Services. All subjects participating in this research provided written informed consent prior to beginning the study.

In each adaptor condition, subjects first listened to the adapting stimulus for 1 min. One of the 13 test stimuli was then played at random immediately following the end of this initial adaptation period, and subjects were asked to respond with a mouseclick whether this sound was moving to the left or right. Upon responding, the adapting stimulus was played again for 8 s (equal to four passes of the virtual stimulus) to ‘refresh’ listener adaptation, followed by another test stimulus. This process continued until all 13 test stimuli were presented eight times. See Fig. 5 for a depiction of stimulus presentation.

Stimuli were anti-alias-filtered (9.6 kHz corner frequency) and presented over headphones (Sennheiser HD 540 Reference II) using a 16 bit digital-to-analog converter (Tucker-Davis Technologies PD1). Peak sound pressure level (SPL) from each phone was equated at approximately 72 dB for all adaptors and test stimuli. Presentation of the stimuli was controlled by computer, which recorded subject responses.

3. Results

Fig. 6 plots results for the three adaptor motion conditions for leftward (A) and rightward (B) directions in terms of percent right responses averaged across all subjects for the 13 test stimulus levels. In theory, aftereffects should be seen as an increase (decrease) in percent right responses after exposure to leftward (rightward) moving adaptors (Grantham, 1998). For clarification, Fig. 7 presents logistic functions fitted to these data. Aftereffect shifts in psychometric functions are seen as shifts relative to the control for the two moving adaptor conditions for both directions, and supported by a significant three-way interaction ($F(24,144) = 1.70$; $P < 0.05$) in the omnibus three-factor, repeated-measures ANOVA.

Following Dong et al. (2000), 50% points for each listener were estimated from the logistic functions and used as a summary measure of the aftereffect magnitude. These values represent the test stimulus which should appear stationary after adaptation; in principle, adaptation to leftward motion should produce negative aMAE magnitudes (that is, a slightly leftward moving test stimulus should appear stationary) and vice versa for rightward adaptors. To view the overall effects of translational versus rotational motion, control aMAE magnitudes were first subtracted from the motion condition magnitudes for both directions. The resulting values were then averaged for each listener across direction by reversing the sign of the leftward motion aMAE magnitudes. This process removed any potential biases of listeners to respond rightward or leftward more often in general, but also preserved individual differences in degree and sign of the motion aMAE magnitudes. The final, combined aMAE magnitudes across listeners and directions are presented in Fig. 8.

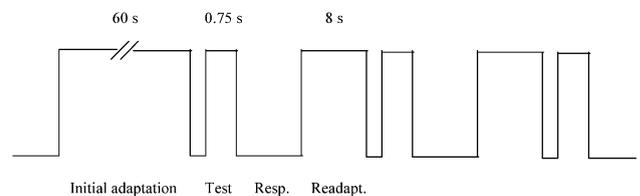


Fig. 5. Duration and order sequence of the stimuli in the adaptation procedure.

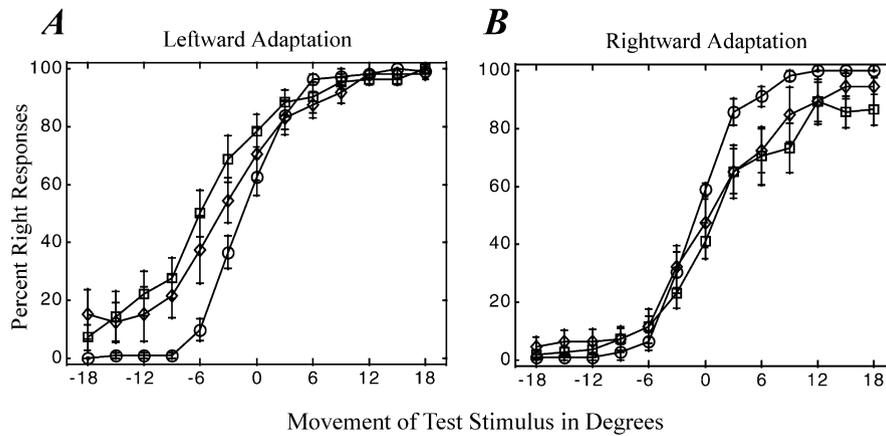


Fig. 6. Results of adapting to leftward (A) and rightward (B) motion as a function of test stimulus excursion. Percent right responses averaged across listeners are plotted for translational (diamond), rotational (square) and control (circle) adaptor conditions.

A one-factor, repeated-measures ANOVA on these data revealed a significant difference in aMAE magnitude between the two motion adaptors ($F(1,6)=9.78$; $P<0.05$). Contrary to the hypothesis motivating this experiment, it appears that translational motion produces a smaller aftereffect compared to rotational motion. This result should be interpreted with caution, however, as the summarizing effect of estimating aMAE magnitudes ignores the similarities in the tail regions of the psychometric functions of the two adaptors seen in Figs. 6 and 7. It appears from these figures that any differences between the two adaptors occur most notably for slightly moving test stimuli which is exactly where aMAE magnitudes will be estimated from the process described above (i.e., near zero). Grantham (1989) has in fact argued that the aftereffect reflected in stationary test stimuli may be due in part to a response bias rather than a true sensory effect, while the sensory aftereffect dominates for moving test stimuli. If so, then the difference in aMAE magnitudes seen here may not reflect the overall similarity in aftereffect strength of the two adaptors.

It is worth noting that the average aMAE magnitude for the rotational adaptor is almost twice as large as the largest reported by Dong et al. (2000) (5.76 deg/s versus approximately 3 deg/s, respectively). This is most likely due to the fact that the angular velocity of the rotational adaptor was roughly four times that of their fastest adaptor (20 deg/s). In fact, this negatively increasing aMAE magnitude as a function of adaptor velocity fits quite well with the trend of their results. The result that aftereffects created from varying stimulus ITDs under headphones can be as strong as from sound sources moving in the free field parallels the finding that ITD dominates stationary azimuthal sound perception for sources rich in low-frequency energy (Wightman and Kistler, 1992; Macpherson and Middlebrooks, 2002). This similarity suggests that HRTF spectral cues may likewise be discounted relative to binaural cues in the perception of lateral auditory motion. It is important to note, however, that the aMAE magnitudes produced here appear to be more variable across listeners than those reported by Dong et al. (2000) (standard deviation of combined rotational

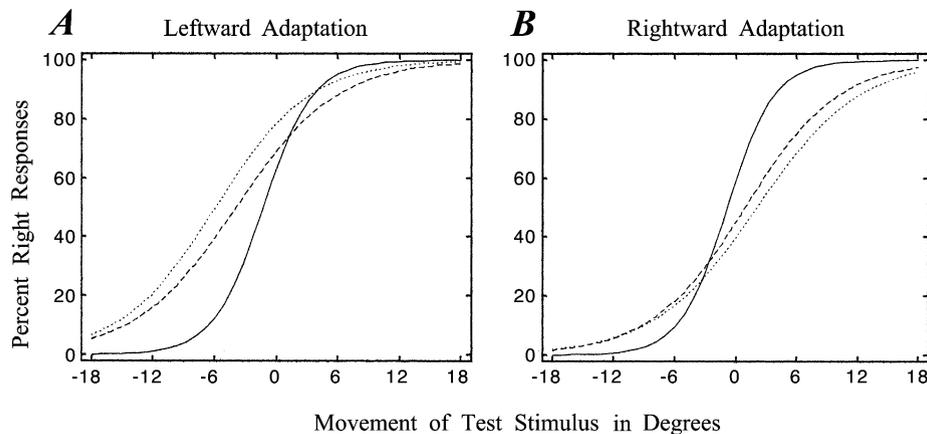


Fig. 7. Logistic functions fitted to the translational (dashed), rotational (dotted) and control (solid) adaptor data from Fig. 6 for leftward (A) and rightward (B) adaptation.

adaptor aMAE magnitudes = 6.4 deg/s). Hence, the inclusion of individualized HRTFs in moving sources may still lead to a more consistent perceptual experience of auditory motion.

4. Discussion

The experiment reported here investigated whether the rotational trajectory exclusively used in previous aMAE studies may have contributed to the phenomenological weakness of the reported findings (Grantham, 1989). In contrast, hypothesized auditory motion detectors may be better stimulated by the ensemble of acoustic attributes arising from translational sound source movement (e.g., AM, FM) over the uniform interaural changes of rotational motion. There is ample evidence that auditory units are responsive to the individual hallmarks of translationally moving sounds: directional frequency sweeps, amplitude modulations, and interaural differences (see Clarey et al., 1992, for a review). If units exist which show special sensitivity to stimuli embodying all three attributes simultaneously, as moving sound sources often do in the real world, then translationally moving signals might provide greater stimulation, leading to stronger aftereffects.

The results reveal that interaurally moving auditory stimuli generally increase judging subsequent sounds to be traveling in directions opposite that of adaptation. These results are viewed as an aMAE. However, there is insufficient evidence to support the hypothesis that added acoustical macrostructure of translational motion enhances the aMAE over changes in ITD alone (i.e., rotational motion). On the contrary, there appears to be a significant decline in the aftereffect magnitude for the translational adaptor compared to the rotational adaptor, though the two moving adaptors generally appear similar over the wider range of test velocities actually used.

The simplest explanation for the lack of aMAE enhancement by the translational adaptor is that ‘complex’ auditory motion cells stimulated by the combined acoustic correlates of translational movement do not exist. There are several alternative explanations that should be considered, however. First, and perhaps most importantly, the uniform level of the rotational adaptor may have more consistently stimulated motion-sensitive units than the varying amplitude of the translational adaptor. Though all adapting stimuli were equated for peak SPL, translational and rotational adaptors differed in root mean square SPL due to the effect of the former’s amplitude envelope (approx. 65 vs. 72 dB, respectively). This difference in energy between the two adaptors, seen clearly in Fig. 2A, may have affected the amount of neural adaptation and led

to a difference in aftereffect strength. Similarly, the Doppler shift varied to some extent the translational adaptor’s spectrum along the frequency tuning response of units in the auditory pathway, possibly leading to only partial adaptation of these units.

As noted earlier, linear spatial trajectories produce non-linear ITD, frequency and amplitude modulations that include periods of shallow change (Fig. 2). These relatively static regions may have further given units time to recover from adaptation to these cues in the translational condition. Though the time constant of adaptation to auditory motion is still not well specified, the aMAE is believed to decay on the order of seconds after adaptor offset (Grantham, 1989; Ehrenstein, 1994). It appears from the profiles in Fig. 2 that the frequency and ITD modulations of the translational adaptor begin to asymptote toward their minima by roughly 1.5s after onset, while the amplitude declines by almost 15 dB. During the initial adaptation period, the ending and beginning 0.5s of two sequential translational adaptors thus provide up to 1s of little FM and ITD change, both at a reduced level, which may be enough to weaken the aMAE magnitude in that condition. This would suggest a very short time constant for recovery from auditory motion adaptation.

4.1. A physiological model of the effects of auditory motion

Many of the issues raised above can be visualized using a simple, widely accepted cross-correlation model of binaural perception (Stern and Trahiotis, 1995). In this view, left and right signals are first passed through a model of the auditory periphery. The peak of their cross-correlation profile summed across frequency channels can be then taken to estimate subjective lateral position. This process models the output of a coincidence-detection network such as may exist in the medial superior olive (MSO) (Joris et al., 1998).

Here, the physiological effect of auditory motion will be viewed as the change in the cross-correlation (delay) activity profile over time. Inasmuch as adaptation is proportional to neural activity (Kashino and Nishida, 1998; Niedeggen and Wist, 1998), the magnitude and shape of this running cross-correlation profile will be taken as a predictor of the strength of the resulting aftereffect. To simulate the effects of the auditory periphery, left and right signals of the translational and rotational adaptors were first bandpass filtered using a bank of 28 frequency channels equally spaced from 50 to 2000 Hz along an ERB-rate scale (Moore and Glasberg, 1986), half-wave rectified and then lowpass filtered (Stern and Trahiotis, 1995). Next, the running cross-correlation between left and right signals averaged across frequency was computed, weighted by a function

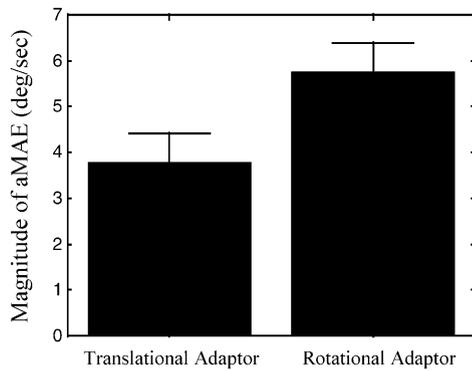


Fig. 8. Magnitudes and estimated standard errors of the aMAE for translational motion (left) and rotational motion (right) adaptors averaged across all listeners and both directions (see text for details).

approximating the distribution of coincidence units across interaural delay. A Gaussian function centered over zero ITD was chosen to model this distribution, which emphasized the hypothesized greater number of units tuned to smaller internal delays (Stern and Trahiotis, 1995). Though more recent coincidence models make this distribution a function of frequency to better extract ITD for envelopes of high-frequency stimuli (Stern and Shear, 1996), a simple Gaussian approximation was adopted here since the moving sounds in this experiment exhibit maximal energy at frequencies below 1000 Hz. Finally, lateralization estimates were calculated as the maximum of coincidence unit activity across delay.

Fig. 9 presents the resulting interaural delay over time for the translational (A) and rotational (B) adaptors, where contour brightness corresponds to cross-correlation magnitude in log scale. For visual clarity, the running delay profile was smoothed with a Gaussian kernel to simulate spatio-temporal integration (Stern and Trahiotis, 1995). Overlaid on the plots are thick lines depicting the maxima of the running profiles, which are taken as point estimates of the interaural delay of the signals.

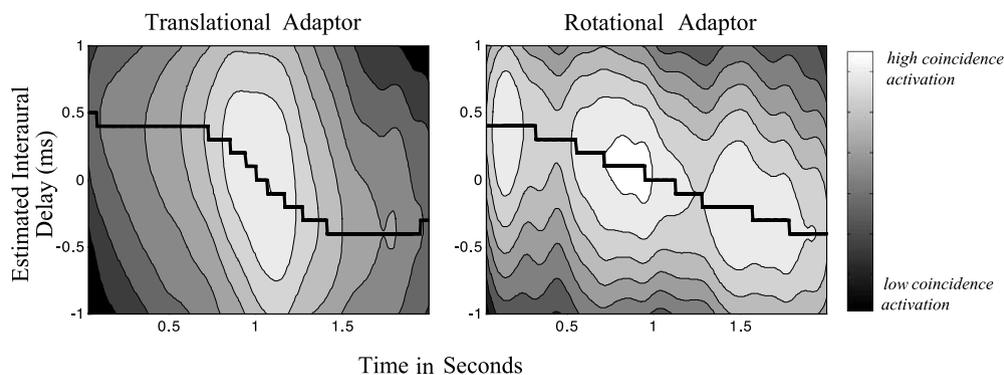


Fig. 9. Output over time of a cross-correlation model of binaural perception to the translational (A) and rotational (B) adaptors used in this experiment. Contour brightness (color bar) corresponds to estimated interaural delay magnitude in log scale.

It is clear from these plots that the rotational adaptor (Fig. 9B) has a much longer period of relatively constant activation across delay than the translational adaptor. The greater slope of the translational adaptor's peak delay near its strongest amplitude (~ 0 s) also implies less time available to activate units tuned to these delays (Joris et al., 1998). (Possible adaptation due to the relatively constant activation at the beginning and end of the signal is presumably offset by the substantially diminished envelope at these points.) If the running delay profile is assumed to be proportional to the resulting adaptation (Kashino and Nishida, 1998), then a smaller aMAE magnitude would clearly be predicted for the translational adaptor.

At first blush, the visible differences in the delay profiles between the two adaptors appear to explain the difference in aMAE magnitude seen in the experimental results (Fig. 8): the more extensive and prolonged activation of the coincidence units by the rotational adaptor should lead to their greater adaptation, and by extension a larger aMAE, than would be the case for the translational adaptor. This activation difference would then manifest itself as a difference in aMAE magnitude similar to the one seen in Fig. 8. Coupled with the fact that the cross-correlation model of lateralization is often viewed as a model of the MSO (Joris et al., 1998), these results imply that the site of adaptation to at least lateral auditory motion and its resulting aftereffect may in fact be sub-cortical. However, it is notable that although the output of the model reveals significant differences, the overall strength of the aftereffect between the two adaptors is surprisingly similar (Figs. 6 and 7). This suggests that physiological areas beyond the MSO may still be contributing to the aMAE.

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Appendix. Synthesis methods

A. Modulation of frequency (FM) and amplitude (AM)

When a moving sound source has a component of its relative velocity along a line connecting it to a receiver, the frequency at which the receiver encounters radiated waves from the source depends upon the direction of the relative movements (i.e., toward or away from each other). This observation is referred to as the Doppler effect (Morse and Ingard, 1968). The scaling of the frequency measured at the source to that measured at the receiver (listener) can be approximated by the function

$$g(t) = 1 - \frac{\dot{x}x(t) + \dot{y}y(t)}{cr(t)} \quad (1)$$

where

$$r(t) = \sqrt{x(t)^2 + y(t)^2}, \quad (2)$$

\dot{x} and \dot{y} are the vector elements of the sound source velocity with respect to listener, $x(t)$ and $y(t)$ are the positions of the sound source with respect to the listener, and c is speed of sound in air. The Doppler effect measured at the receiver can be viewed as an instantaneous frequency modulation imposed on each frequency component of the sound source, such that $f_i^R(t) = f_i^S(t)g(t)$, for the i th frequency component of the signal. We can define a general time-dependent signal

$$s_i(t) = A_i \cos(\theta_i(t)) \quad (3)$$

where $\theta_i(t)$ is the instantaneous phase. The instantaneous frequency at the receiver can be defined in terms of the instantaneous phase as

$$f_i^R(t) = \frac{1}{2\pi} \frac{d\theta_i(t)}{dt} \quad (4)$$

and can be obtained by integration

$$\theta_i(t) = 2\pi f_i^S \int_0^t g(\lambda) d\lambda \quad (5)$$

Substituting Eq. 1 into Eq. 5 and evaluating the integral yields a remarkably simple instantaneous phase generation function for Doppler (after removal of a constant phase term)

$$\theta_i(t) = 2\pi f_i^S \left(t - \frac{r(t)}{c} \right) \quad (6)$$

where $r(t)$ is the time-varying range.

In an anechoic environment the measured sound intensity follows an inverse square law, where the intensity varies inversely as the square of the range $r(t)$ between the receiver and source. Pressure, therefore, varies as the inverse of $r(t)$, such that

$$\alpha(t) = \frac{\eta}{r(t)} \quad (7)$$

where η is a constant related to intrinsic power.

B. Modulation of interaural phase

ITD is the difference between the time of arrival of a sound at each ear caused by the reflection and diffraction of the head. In general, ITD depends on both frequency and the angle of incidence, although there are several approximations that simplify these dependences (Kuhn, 1977). In the present simulations, the ITD is defined by

$$\delta(t) = \frac{2a}{c} \frac{x(t)}{r(t)} \quad (8)$$

where a is the radius of the average head (8.75 cm), $x(t)$ is the coordinate on the x -axis, and $r(t)$ is again the time-varying range from the receiver to the source. Frequency-dependent interaural phase can then be defined as

$$\phi_i(t) = 2\pi f_i^S g(t) \delta(t) \quad (9)$$

C. Static sound source analysis and motion synthesis

There are several possible transforms that could be used to decompose a static sound source into sinusoidal bases. The obvious choice is the Fourier transform. A window of a sampled static sound of size N is selected and the Fourier coefficients are extracted. Fourier summation is then used to synthesize each of the binaural signals

$$S_L(t) = \alpha(t) \sum_{i=1}^N \left[A_i \cos\left(\theta_i(t) - \frac{\phi_i(t)}{2}\right) + B_i \sin\left(\theta_i(t) - \frac{\phi_i(t)}{2}\right) \right] \quad (10)$$

and

$$S_R(t) = \alpha(t) \sum_{i=1}^N \left[A_i \cos\left(\theta_i(t) + \frac{\phi_i(t)}{2}\right) + B_i \sin\left(\theta_i(t) + \frac{\phi_i(t)}{2}\right) \right] \quad (11)$$

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