The temporal growth and decay of the auditory motion aftereffect

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The present work investigated the temporal tuning of the auditory motion aftereffect (aMAE) by measuring the time course of adaptation and recovery to auditory motion exposure. On every trial, listeners were first exposed to a broadband, horizontally moving sound source for either 1 or 5 seconds, then presented moving test stimuli after delays of 0, $\frac{2}{3}$, or $1\frac{2}{3}$ seconds. All stimuli were synthesized from head related transfer functions recorded for each participant. One second of motion exposure (i.e., a single pass of the moving source) produced clearly measurable aMAEs which generally decayed monotonically after adaptation ended, while five seconds exposure produced stronger aftereffects that remained largely unattenuated across test delays. These differences may imply two components to the aMAE: a short time-constant motion illusion and a longer time-constant response bias. Finally, aftereffects were produced only by adaptor movement toward but not away from listener midline. This aftereffect asymmetry may also be a consequence of brief adaptation times and reflect initial neural response to auditory motion in primate auditory cortex. © *2004 Acoustical Society of America.* [DOI: 10.1121/1.1687834]

I. INTRODUCTION

A. Spatial and frequency tuning of the aMAE

A sound source repeatedly traversing horizontal auditory space may produce an auditory motion aftereffect (aMAE) in listeners in which sensitivity to subtly moving test stimuli shifts in the direction opposite of that presented during adaptation. Several basic attributes of the aMAE have been specified over the course of several recent experiments, most notably its tuning in the spatial and frequency domains (Grantham, 1998; Dong *et al.*, 2000). The general findings have been that the aftereffect is localized to both the spatial and spectral region of adaptation.

However, one component of the aMAE that has not been investigated in detail is its growth and decay as a function of adaptation duration. In the present work we attempt to measure these temporal aspects of the auditory motion aftereffect. Regarding the spatial tuning of the aMAE, Dong *et al.* (2000) adapted listeners for two minutes to broadband and filtered noise stimuli emanating from a speaker attached to a moving robotic arm. They found that aMAE magnitude was greatest when the test region spatially coincided with the region of adaptation and declined fairly linearly with a broad space constant as testing moved outside this region. For spatially coincident adaptation and test regions, however, the magnitude of the aMAE appeared to be largely equivalent for adaptor motion trajectories up to $\pm 35°$ around the frontal midline.

In the frequency domain, it has been known for some time that the aMAE is stronger for broadband than for pure tone adaptors (Grantham, 1989). The recent studies by Grantham (1998) and Dong *et al.* (2000) further showed that aMAEs can be created using low-, band-, and high-pass adaptors, though they often appear stronger for lowpass stimuli relative to other bandwidths. These effects of the bandwidth appear consistent with the ideas that (1) a stimulus with a broader frequency spectrum should adapt a larger area of units across tonotopic maps found at multiple physiological stages throughout the auditory system (Palmer and Summerfield, 2002); and (2) units at spatially-sensitive (and potentially motion-sensitive) stages beyond AI show a greater response to spectrally rich stimuli (Clarey *et al.*, 1992; Rauschecker *et al.*, 1995; Wessinger *et al.*, 2001). The impact of lower-frequency stimuli may further reflect the dominance of interaural time-difference cues in the horizontal motion trajectories used by these studies (Wightman and Kistler, 1992; Macpherson and Middlebrooks, 2002; Neelon and Jenison, 2003).

B. Temporal tuning of the aMAE

Judgments of visual motion can show prolonged and unexpected temporal effects to adaptation such as storage and residual effects that may last on the order of hours (Mather *et al.*, 1998). In contrast, the time course of the auditory motion aftereffect has not been well specified. Two studies have measured the duration of spatial auditory aftereffects, but only after prolonged periods of adaptation. Ehrenstein (1994) charted the recovery of adaptation to pure tones independently changing in either interaural time or level difference (ITD, ILD), and, while not finding motion aftereffects *per se*, reported a displacement aftereffect in which subjects' settings of the interaural midline had been shifted after adaptation. Plots of the mean results showed that while the displacement aftereffects initially declined in

magnitude very quickly after the adaptor ceased, some bias was still present up to 30 seconds later. Aftereffects to dynamic ILD adaptation appeared to last even longer with effects lingering up to two minutes after adaptation. This difference in recovery between motion produced by ITD and ILD cues may have some physiological support (Sanes *et al.*, 1998).

In a more recent study, Dong *et al.* (1999) explored the duration of the aMAE after 10 minutes of adaptation to a 1-octave lowpass noise source emanating from a speaker attached to a horizontally moving robotic arm. Their results also show that the aMAE is largest immediately after adaptation, and declines exponentially to near zero after approximately 10 minutes. Ehrenstein's data must be interpreted with caution since, as noted above, motion aftereffects are more reliably produced with free-field, wideband stimuli rather than pure tones (Grantham, 1998; Dong *et al.*, 2000), possibly making his findings of a qualitatively different nature. Despite the results of both of these studies, Grantham (Grantham and Wightman, 1979; Grantham, 1989; 1998) has stated that the lifespan of auditory motion aftereffects is very brief, perhaps only lasting for a few seconds after adaptation ends. Given that aftereffects produced by different types of visual motion may show different time courses (Mather *et al.*, 1998), it is possible that these conflicting statements are a result of measuring aMAEs with different stimuli and procedures which may have produced adaptation effects on different time scales (Malone *et al.*, 2002). Grantham has further suggested there are in fact two components to the aMAE: a short time-constant motion illusion (i.e., a true motion aftereffect), and a longer time-constant motion desensitization in the direction of adaptation (i.e., response bias). It is possible that the recovery from motion adaptation charted by Ehrenstein and Dong, *et al.* mostly reflects the latter effects.

C. Contrast explanations of aftereffects

Exploring these temporal issues may help determine whether the aMAE truly arises from the adaptation of auditory motion selective cells, or is instead related to the briefer contrast effect a moving stimulus may have on a neuron's subsequent response properties. The latter result would argue against the necessity of dedicated motion detectors to explain phenomena like the aMAE. McAlpine and his colleagues have in fact proposed such a contrast model to explain apparent motion selectivity in the guinea pig inferior colliculus (IC) (McAlpine *et al.*, 2000; Ingham *et al.*, 2001). Several physiological studies have claimed that auditory cells in the mammalian brainstem and cortex can exhibit motion direction selectivity (Ahissar *et al.*, 1992; Spitzer and Semple, 1993; Jiang *et al.*, 2000; Jenison *et al.*, 2001; Malone *et al.*, 2002). This conclusion is often based on the finding that the receptive fields of many cells are skewed by auditory motion such that they exhibit greater responsiveness to a sound source passing through the field in one but not the opposite direction (Spitzer and Semple, 1998; Wilson and O'Neill, 1998; Malone *et al.*, 2002). Though these latter studies found virtually no neurons that are only responsive to moving

sources rather than stationary sources, such skewed responses might be viewed as a neural basis for signaling direction of sound source movement.

McAlpine and colleagues (McAlpine *et al.*, 2000; Ingham *et al.*, 2001) have argued that this change in the receptive field shape may be due to the history of source movement through the response area rather than a specialized reaction to a particular motion vector. The authors exposed IC cells to dichotic pure tones whose interaural phase differences (IPD) were oscillated to simulate back-and-forth interaural movement. They found that the change in the receptive field shape was caused by a cell's adaptation to the interaural locus of the dynamic stimulus passing through its IPD receptive field. Direction selectivity appeared because the cell responded strongly to the initial movement of the phase into its receptive field and more weakly when the phase change suddenly reversed direction and exited the receptive field. Adaptation to the initial stimulation was reported to have time constants no greater than 500 ms for the majority of the recorded cells. This implied that the skewed response should disappear if enough time was allowed to pass before the reversal of the stimulus movement (e.g., $>$500 ms). Indeed, the authors showed that this skewed response, and as a consequence the apparent motion selectivity, could be attenuated when the cell was given such time to recover from its initial response to the dynamic IPD stimulus. A biologically-inspired computational model of binaural processing has also made use of a similar time constant to properly reproduce the neural response to dynamic IPD stimuli (Cai *et al.*, 1998).

A comparable debate between contrast effects and the selective adaptation of specialized feature detectors also appeared in the speech perception literature in the 1970s. At the time, speech perception was thought to be mediated by specialized detectors which could be experimentally adapted by the repeated presentation of their corresponding phonemic features. Diehl *et al.* (1985), however, showed that many of these effects could be created after a single presentation of the "adapting" phoneme and thus argued that it was the contrastive context of the adaptor and test pairing that created the shift rather than the fatiguing of dedicated phonemic feature detectors. In an interesting parallel to McAlpine and colleagues' study, Diehl, *et al.* also showed that inserting pauses between each repetition of the stimulus during the adaptation period altered the resulting judgments of the subsequent test stimuli. The relevance to the current work is that the aMAE has always been considered analogous in nature to the vMAE and hence assumed to arise from the adaptation of direction-selective cells by prolonged, continuous motion exposure. Both the early behavioral results of Diehl, *et al.*, and the recent neurophysiological findings of McAlpine, *et al.*, question whether the aMAE must be created in this manner and call for a more detailed psychophysical investigation into the growth of and recovery from auditory motion adaptation.

D. Time course of aMAE may specify physiological sources

The brief duration of the adaptation used by McAlpine and colleagues to explain apparent motion direction selectiv-

ity in the IC implies short-lived aMAEs. However, a more recent physiological investigation (Malone *et al.*, 2002) provides evidence that the adaptation of cortical cells to auditory motion may operate on multiple time scales, from tens of milliseconds to several seconds. Also using pure tones varying in IPD, Malone *et al.* found many units in primary auditory cortex of awake rhesus monkeys that appeared to be direction selective for simulated azimuthal motion within ecological ranges. This sensitivity manifested itself in two ways: as greater responses to moving versus stationary stimuli across the same IPDs, and as dramatic shifts in azimuthal tuning toward the origin of motion (see also Wilson and O'Neill, 1998). In the majority of these units, the receptive field shift resulted in greater activation for a single direction of motion (within ecologically plausible IPDs), suggesting a basis for encoding auditory motion direction.

However, these shifts diminished after even a few seconds of exposure to the moving stimulus, and azimuthal receptive field shapes approached those of the cells' responses to static IPD stimuli. That is, brief exposure to auditory motion may have reduced the potential ability of such cells to code for motion direction. This change due to adaptation could provide a physiological foundation for the desensitization component of the auditory motion aftereffect (Grantham, 1998). These researchers also reported that unadapted units showed post-inhibitory rebound when movement ended and the stimulus remained in a static position (see Sanes *et al.*, 1998, for a similar effect in IC). Such a rebound in activity could also be taken as a signal for the presence of motion in the opposite direction and has been cited as another potential basis of the motion aftereffect in vision (Niedeggen and Wist, 1998). These results provide important evidence that the effects of adaptation to auditory motion may evolve over several seconds time, rather than milliseconds, and have multiple physiological loci, including primary auditory cortex.

E. The present experiment

The preceding discussion has established that many details remain unknown regarding the time course of the auditory motion aftereffect. Further, two possible physiological locations in the brainstem and cortex (e.g., inferior colliculus vs auditory cortices) have been identified as potential sources for the aMAE; however, their adaptation to auditory motion may exhibit different temporal responses. In order to better characterize the time course of the auditory motion aftereffect and hence its possible physiological contributors, several combinations of timing parameters are explored in the following experiment. The typical aMAE paradigm initially presents a moving sound repeatedly for an extended period of adaptation, followed by a series of brief test probes and shorter re-adaptation periods. In the current experiment, the initial prolonged adaptation period is skipped and listeners instead hear sequences of either one or five seconds of initial motion adaptation, followed by probe stimuli presented after different time delays. Regarding the chosen adaptor durations, it is possible that the aMAE may emerge after one second of motion adaptation (e.g., a single pass of a one second duration moving adaptor), as was discovered by Diehl *et al.* (1985). In this case, the aMAE for one second of adaptation should be as strong as for five seconds; alternatively, the longer adaptation period may create a significantly larger bias in judgments of subsequent moving test stimuli, suggesting a more linear growth of the aftereffect with the amount of motion exposure. Finally, it is possible both 1 and 5 seconds of adaptation may not be enough to fully realize the motion aftereffect. These exposure durations are chosen mainly to ease general listener fatigue by limiting experimental sessions to reasonable durations. Results will determine whether these adaptation durations are reasonable.

At the same time, the experiment also varies how quickly the test stimulus is presented after adaptor cessation, using delays of 0, $\frac{2}{3}$, or $1\frac{2}{3}$ seconds. This range spans the different adaptation time courses reported in McAlpine *et al.* (2000) and Malone *et al.* (2002). Finally, test stimuli are also pseudo-randomly presented over the course of a single experimental block (see below) such that an equal number of test stimulus parameters are presented across each third of the block. This allows for measuring the possible growth of the aMAE over the course of multiple re-adaptation periods which occur during testing blocks.

II. METHODS

A. Subjects

5 females and 3 males (age range: 21–30 yrs.) served as subjects. All 8 were experienced in auditory motion aftereffect experiments but were naïve to the purposes of this particular study. Five of the subjects had also participated in a pilot version of this experiment. All had clinically normal hearing as assessed by an audiogram and were paid for their participation.

B. Stimuli

1. Synthesis of auditory motion

The pinnae, head and shoulders impose spectral and timing changes on an incident sound at the two ears which can be characterized by a pair of filters known as head-related transfer functions (HRTFs). Different source positions result in different filter pairs, and thus HRTFs carry information about spatial location. One method for synthesizing auditory motion under headphones is to interpolate across HRTFs recorded for an individual listener at particular spatial locations (Wightman and Kistler, 1999; Jacobsen *et al.*, 2001; Carlile and Best, 2002). This process mimics the change at a listener's ears that occurs when a real sound source changes spatial position in the environment. The headphone presentation of a stimulus convolved with these interpolated filters should then result in the perceptual experience of an externalized sound moving smoothly across space.

In an anechoic chamber, HRTFs for both ears were recorded for each listener using Sennheiser capsule microphones (KE4-211-2) in blocked meatus placement (Møller *et al.*, 1995). Filters were measured with a roughly 75 dB SPL, 100 k sampled wideband periodic chirp stimulus presented from loudspeakers at 541 source positions (10-degree azimuth intervals from 180 to −170 degrees and 10-degree

elevation intervals from 90 to −60 degrees relative to the horizontal plane). The effects of the presentation headphones (Beyer Dynamic DT 990) were also measured at the listener's ears at this time in order to compensate for their effect on stimulus presentation during experimentation. Following measurement, all HRTFs were downsampled to 50 k.

Minimum-phase versions of the time domain counterpart to the recorded HRTFs, the head-related impulse responses (HRIRs), were used in the interpolation process (Kistler and Wightman, 1992). This process removed the phase component while retaining the amplitude spectrum of the HRIR, thus allowing for an accurate spatial interpolation of the impulse responses across time samples while easing independent parametrization of ITD. For each listener and each ear, left and right minimum-phase HRIRs were piecewise cubic Hermite interpolated across the range of motion for each moving stimulus at a resolution fine enough to produce smooth apparent movement (see below for details). Interaural time delays were estimated from the peak of the cross-correlation between the left and right HRIRs for each recorded spatial location. An equal resolution was also interpolated for the timing delays between the two ears, which were then applied to the two signal channels. Recombining the interpolated delays and minimum-phase HRIRs resulted in two signals which mimicked the natural changes in spatial cues (ITD, ILD, monaural spectral cues) that occur at the two ears to a sound source when it moves around a listener. These signals were then convolved with inverse filters of the presentation headphones to cancel out their nonspatial filtering effects during stimulus delivery.

2. Moving adaptors

Adaptors were 1-second Gaussian noise samples convolved with interpolated HRIRs as described above for each listener to simulate leftward and rightward motion between 0 and ±30 degrees azimuth (0 degrees elevation). Adaptors were thus simulated to move in both directions in both frontal hemifields, where negative/positive signs indicate azimuths left/right of listener midline, respectively. Given the predominant responsiveness of IC and cortical neurons to contralaterally located sound stimuli (Ahissar *et al.*, 1992; Brugge *et al.*, 1996; Clarey *et al.*, 1992; Spizter and Semple, 1998; McAlpine *et al.*, 2000; Malone *et al.*, 2002; Middlebrooks *et al.*, 2002), stimuli did not cross midline in order to limit the recovery of such physiological structures from adaptation, which could occur if sounds were allowed to move through ipsilateral space. Figure 1 provides a depiction of the adaptor trajectories. 1200 filters were interpolated for the 30-degree trajectories which resulted in spatial motion resolution of approximately 0.025 degrees. This resolution was fine enough to create smooth apparent motion according to both previous studies using auditory motion synthesized in a similar manner (Wightman and Kistler, 1999; Carlile and Best, 2002) and listeners' comments in this experiment. At the end of generation, all stimuli (adaptors and test probes) were down-sampled from 50 k to 40 k Hz in order to conserve computer memory space, normalized to an approximately 66
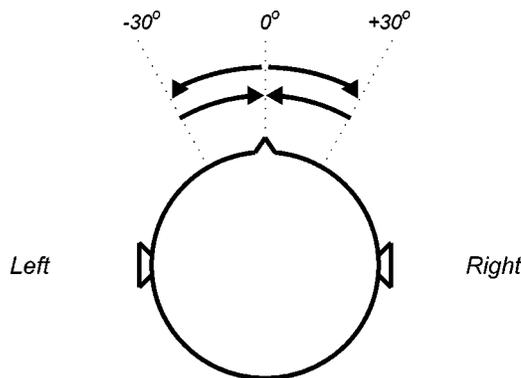

FIG. 1. Depiction of adaptor motion trajectories used in the present experiment.

dB(A) sound pressure level (SPL), and then 10 ms cosine-windowed to eliminate onset/offset transients

3. Test stimuli (probes)

Test stimuli were also 1-second Gaussian noise samples convolved with interpolated individualized HRIRs to simulate auditory motion as described earlier. Test stimuli began at either ±20 degrees (sign indicates hemifield) and moved ±10, ±6 or ±2 degrees from the starting point, where the negative/positive sign here indicates movement leftward/rightward of the starting position, respectively. This range of test stimuli motion was chosen to encompass endpoints spanning reported minimum audible movement angles of approximately 3 degrees (Grantham, 1995), and has been successfully used before in auditory motion aftereffect studies (Grantham, 1998; Dong *et al.*, 1999). Spatial resolution of interpolated HRIRs was the same as used for the moving adaptors.

4. Experimental stimuli combined with delays

To ensure the proper timing of experimental stimuli, each trial presented a single auditory stimulus formed from the desired number of adaptors (i.e., adaptation duration), the desired test stimulus, and the desired experimental delay inserted between them. This was achieved by adding to either a single or 5 concatenated adaptors one of the 6 possible test stimuli (±10, ±6, ±2 degrees) from the same hemifield, with zero-padded buffers inserted in between to create silent delays of 0, $\frac{2}{3}$ and $1\frac{2}{3}$ seconds. No delays were inserted between repetitions of the moving adaptor in the 5-second condition beyond the 10ms rise/fall cosine windows. Nine replications of each combination of adaptor, delay, and test movement level were created off-line and presented to the listener during a single experimental block, totaling 162 stimuli. Listeners' "left/right" responses to these nine test exemplars formed the basis of the psychometric functions used to asses the effects of auditory motion adaptation.

C. Procedure

Subjects sat in front of a computer which controlled all instruction and stimulus presentation and recorded all re-
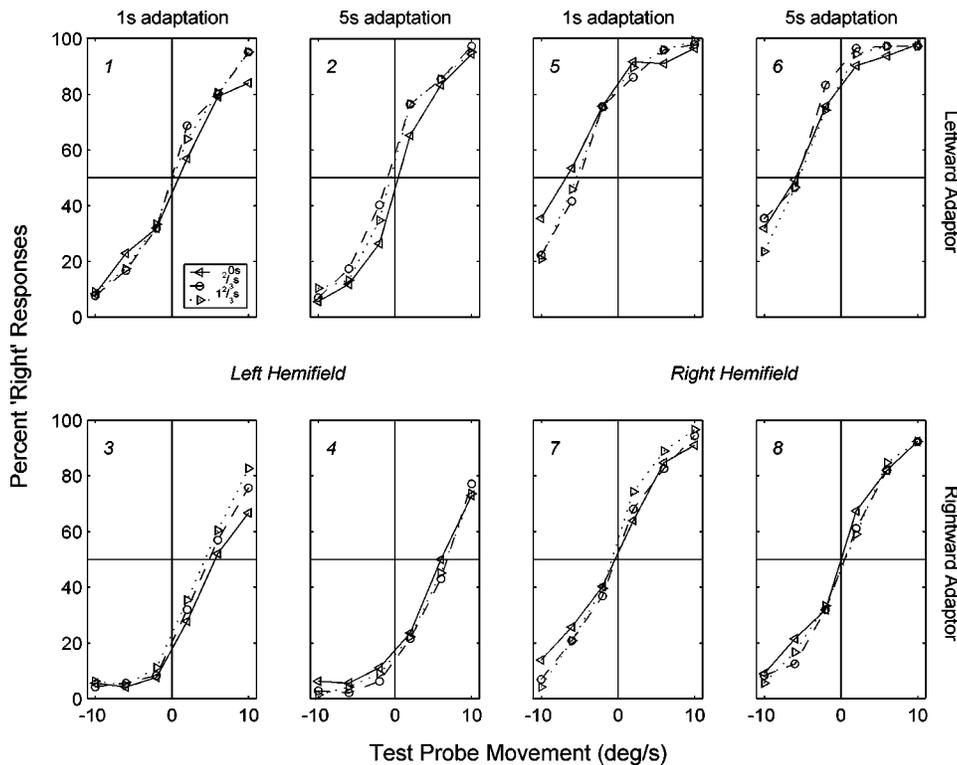
FIG. 2. Results averaged across 8 subjects for each hemifield (*left* = subplots *1–4*; *right* = subplots *5–8*), adaptor duration (*columns*), adaptor direction (*rows*), and test delay (*solid left arrows* = 0 s; *dashed circles* = $\frac{2}{3}$ s; *dotted right arrows* = $1\frac{2}{3}$ s) in terms of percent "right" responses as a function of the test probe movement.

sponses via the keyboard. On a single trial, subjects were presented with 1 s or 5 s of motion adaptation (i.e., exposed to 1 or 5 adaptors in a row), a delay of either 0, $\frac{2}{3}$ and $1\frac{2}{3}$ seconds, and then a 1 s test stimulus. After this combined stimulus had finished, two boxes, each 14×12 cm, appeared side-by-side in the middle of the screen bearing the labels *rightward* ("*p*") and *leftward* ("*q*"). Subjects were required to respond whether the test stimulus had moved rightward or leftward by pressing a "*p*" or "*q*," respectively, on the keyboard. To cue listeners as to which part of the combined stimulus they should respond, the two response boxes were not displayed during stimulus presentation while instead a 4×25 cm box was shown in the upper part of the screen. The color of this box was red during the adaptation and delay period of each stimulus presentation, indicating the subject was only to listen during this time; at the end of the delay period, the box color changed to green to indicate the start of the target test stimulus to which the subject had to respond. At least one second passed after a response and before the next trial began, though the actual delay of the next stimulus could be greater depending upon the speed of response. No feedback was provided for responses to the test stimuli.

Subjects performed in 2 repetitions of the 8 possible experimental blocks representing each combination of the two hemifields (left, right), two adaptor durations (1 s, 5 s), and two adaptor motion directions (leftward, rightward). A single block presented sounds for only one hemifield, one adaptor duration, and one adaptor motion direction, in order to properly create a well-localized aftereffect (i.e., presenting opposite adaptor directions during the same block should theoretically cancel out adaptation effects and thus fail to produce an aftereffect). Individual blocks lasted either ap-

proximately 10–12 or 21–23 minutes, depending on adaptor duration.

After completing a block, subjects were required to wait at least 5 minutes before beginning the next block, to allow them time to recover from the previous adaptation effects. Stimuli in the same hemifield were never presented in two successive blocks; otherwise, the presentation order of adaptor duration and direction was random. Subjects normally did not complete more than 3 blocks per session (i.e., per day) and entire testing lasted several weeks for each listener.

III. RESULTS AND DISCUSSION

A. Effect of adaptor hemifield and motion direction on the aMAE

In the following analyses, data were averaged across all 8 listeners, across the two repetitions of each experimental block for each listener, and across the 9 repetitions of each test stimulus movement level within a single block. The eight numbered subplots in Fig. 2 present the mean results of the experiment for each combination of hemifield (*left* = subplots *1–4*; *right* = subplots *5–8*), adaptor duration (*columns*), and adaptor direction (*rows*) in terms of percent "right" responses as a function of the test probe movement level. Line types represent different delays of the test probe presentation (*solid* = 0 s; *dashed* = $\frac{2}{3}$ s; *dotted* = $1\frac{2}{3}$ s).

In theory, aftereffects should be seen as an increase (decrease) in percent "right" responses after exposure to leftward (rightward) moving adaptors. This increase (decrease) should result in a shift of the mean (50% point) of the "right" psychometric function leftward (rightward) from the zero degree point indicating no directional response bias. The most immediate impression from Fig. 2 is that such
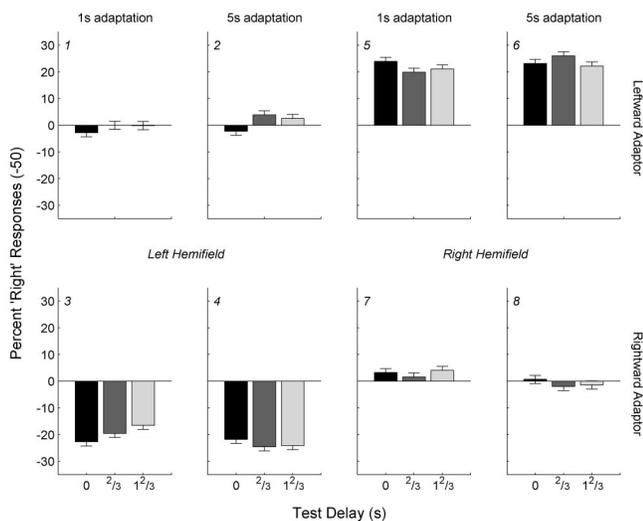
FIG. 3. Mean results presented as percent "right" responses after averaging across the test probe movement level, with an estimate of the pooled standard error. Test delays are presented along the abscissa (*shading*). Columns and rows are otherwise the same as for Fig. 2.

FIG. 4. Effect of 1 vs 5 seconds of motion adaptation, with an estimate of the pooled standard error. Data are presented as percent "right" responses averaged across all levels of test motion and delays for the two adaptor directions and hemifields.

aftereffect shifts away from 0 degrees are apparent for only four of the 8 experimental conditions: for rightward adaptation in the left hemifield (subplots *3*, *4*) and leftward adaptation in the right hemifield (subplots *5*, *6*). This result is supported by a significant 3-way interaction in the omnibus 5-factor within-subject ANOVA testing for hemifield, adaptor direction, and test probe movement level [$F(5,35) = 7.31$; Greenhouse–Geisser corrected $p < 0.005$]. No other interactions of equivalent or higher order were significant.

Another view of this result is presented in Fig. 3 which graphs percent "right" responses after averaging across test probe movement level. In this view, the lack of an aftereffect should result in average percent "right" responses of 50% (i.e., unbiased responses to test motion on average), while leftward (rightward) adaptation should result in mean aftereffect biases greater (less) than 50%. To better view potential aftereffect shifts, 50 is subtracted from all results before presentation. Error bars represent an estimate of the pooled standard error. The hemifield×adaptor direction×test motion interaction is quite evident in this depiction of the data.

The pattern of results in Figs. 2 and 3 can be described generally as follows: strong aftereffects occur only for adaptor movement *toward* the midline, while no aftereffects appear for adaptor movement *away* from midline, regardless of the hemifield of auditory presentation. Though this result was unexpected given previous reports of aMAE uniformity across ±35 degrees of the frontal midline (Dong *et al.*, 2000), it may be explainable in light of recent physiological studies into the cortical neural effects of exposure to auditory motion. These explanations are postponed for now and discussed more thoroughly at the end of this section.

Remaining analyses further investigate this significant 3-way interaction by examining in more detail only those conditions which produced clear aftereffects. Specifically, 4 of the 8 conditions tested in this experiment (subplots *3*, *4*, *5*, and *6* of Fig. 2) produced aftereffect shifts whose intersections significantly deviated from the unbiased 50% point. Therefore only data from rightward adaptors in the left hemi-
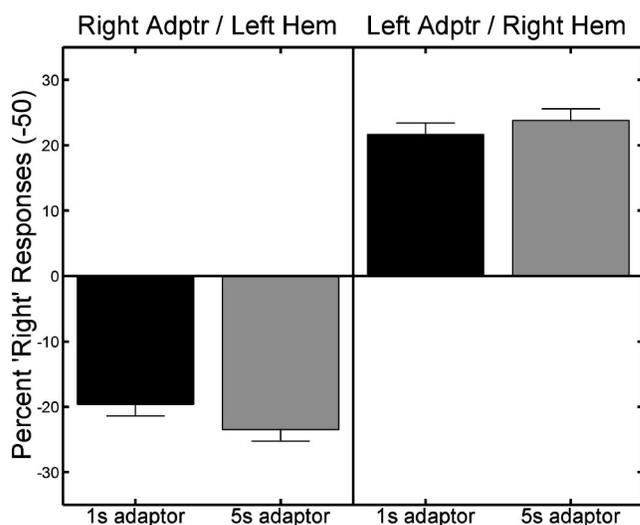
field and leftward adaptors in the right hemifield are further considered unless otherwise noted.

B. Effects of adaptor duration on the aMAE

1. Effect of 5 vs 1 second of motion adaptation

This experiment was designed to investigate two fundamental issues regarding the auditory motion aftereffect: the effect of adaptor duration on the resulting aMAE, and the decay of the aftereffect after adaptation ends. One question raised by the first issue is whether the amount of aftereffect shift differs after 5 seconds versus 1 second of adaptation. For the data from rightward adaptation in the left hemifield and leftward adaptation in the right hemifield, the adaptor direction x duration interaction is significant [$F(1,7) = 5.66$; Greenhouse–Geisser corrected $p < 0.05$] and is presented in Fig. 4.

This significant interaction contrast is clearly due to the differences in adaptor movement direction between the two hemifields, rather than due to the adaptor durations. Hence, another method for analyzing these data is to equalize the aftereffect shifts across hemifield/direction; that is, to measure their magnitudes due to adaptor motion toward the midline regardless of the hemifield. This would then allow aftereffect shifts for the same adaptor duration to be combined across the two adaptor hemifields/directions without their opposing directions canceling out, and thus increase the statistical power of the comparison between 1 and 5 s adaptation.

To equalize aftereffect shifts, the percent "right" responses for rightward adaptation in the left hemifield are converted for each listener to their corresponding shift if the adaptor had been moving leftward instead. Specifically, a reflection in the psychometric scatter is made about the zero test probe velocity point on the abscissa, and then complemented about the ordinate axis.[1] Data from rightward adaptation in the left hemifield were converted for all listeners in this manner and then analyzed with data for leftward adaptation in the right hemifield. A 4-factor

TABLE I. AMAE magnitudes resulting from 1 second of adaptation.

	Rightward motion in left hem			Leftward motion in right hem		
	0 s delay	$\frac{2}{3}$ s delay	$1\frac{2}{3}$ s delay	0 s delay	$\frac{2}{3}$ s delay	$1\frac{2}{3}$ s delay
Listener 1	6.32°/s	7.05	7.98	−5.42	−6.73	−5.85
2	2.57	1.97	0.53	−4.95	−4.01	−3.50
3	0.74	4.08	1.95	0.89	1.63	−1.00
4	5.05	3.26	1.82	−9.01	−5.00	−3.62
5	12.99	11.21	10.02	−12.27	−8.96	−9.11
6	12.37	4.47	6.19	−44.41	−7.26	−10.23
7	3.82	2.80	1.88	−4.27	−3.56	−4.98
8	14.69	8.50	6.38	−10.93	−8.43	−8.56

ANOVA (hemifield/direction×adaptor duration×test delay ×test motion)[2] on these results revealed a significant main effect of adaptor duration [$F(1,7)=5.66$; Greenhouse–Geisser corrected $p<0.05$]. Hence, when aftereffects are equalized for an adaptor direction, 5 seconds of adaptation does produce a slightly greater aMAE shift than does 1-second adaptation (mean of 5 s adaptation=73.63% equalized "right" responses; mean of 1 s adaptation=70.62% equalized "right" responses).

2. AMAE magnitude for 1-second adaptation

The previous result indicates that aftereffect strength is a positive function of adaptor duration. However, the small percentage difference between the two durations (as measured in the average equalized percent "right" responses) suggests at first glance that the aMAE grows compressively with adaptor duration, with most of the effect arising after a single pass of a moving adaptor. This raises the question of how the aftereffect magnitude created from exposure to a single moving source compares to those generated in previously published studies after much longer adaptation periods.

The aMAE magnitude provides a single summary measure of the strength of the aftereffect in terms other than percent "right" responses. Two published measures of the aMAE magnitude are (1) the percentage area difference between the psychometric functions created by moving and stationary adaptors (Grantham, 1998); and (2) the bias parameter estimated from functions fitted to the psychometric curves (Neelon and Jenison, 2003). The later technique expresses the aMAE magnitude as the speed of a hypothetical moving test sound which should appear stationary to the listener after adaptation. For example, Dong *et al.* (2000) adapted listeners to broadband noise moving in a horizontal arc between ±15° for a period of 2 minutes. Using probit analysis (Finney, 1971) to estimate the point at which listeners should respond to a moving test stimulus leftward or rightward equally often, the authors reported for four listeners an average aMAE magnitude of near 3 deg/sec created by an adaptor speed of 20 deg/sec.

For comparison with the results of Dong *et al.*, magnitudes for our listeners were estimated from the bias parameters of logistic fits to the psychometric functions. This function is described by

$$f(x)=100\times 1/(1+e^{-(X-a)/b}), \quad (1)$$

where a and b are free parameters minimized to best fit the observed data, and X is the vector of test stimuli motion values (±10, 6, and 2 d/s). a represents the test stimulus which should appear stationary after adaptation (i.e., the 50% performance point, or the overall bias in listeners' responses) and is used as a summary measure of the magnitude of the motion aftereffect for each listener. If a motion aftereffect is present, then adaptation to leftward motion should produce negative aMAE magnitudes; that is, a slightly leftward moving test stimulus should appear stationary after adaptation (vice versa for rightward adaptor motion).

Bias terms were estimated for 1 s second adaptation at the 3 test delays for rightward motion in the left hemifield and leftward motion in the right hemifield (i.e., the quadrants in which aftereffects were present) for all data over the relevant blocks. These values are presented in Table I.

To calculate the grand average aMAE magnitude across all listeners and all irrelevant experimental conditions, these terms were first averaged across test delays (the subcolumns in Table I). The resulting values were then averaged again for each listener across the adaptor direction/hemifield (supercolumns in Table I) by reversing the sign of the aMAE magnitudes for leftward motion in the right hemifield. This process combined results across the two directions while preserving individual differences in degree and sign of the magnitudes (Neelon and Jenison, 2003). The end result was a single estimate of the aMAE magnitude for each listener for 1 s adaptation, averaged across hemifield, direction, and test delay. Averaged once more across all 8 listeners (rows in Table I), the grand mean aMAE magnitude produced by 1 second of motion adaptation in this study was 6.63 deg/sec (4.52 deg/sec standard deviation).

It is impressive that the grand average aMAE magnitude for 1 second of adaptation in this experiment is almost twice as large as that reported in Dong *et al.* (2000) for 2 minutes of adaptation to a real moving source. There are at least two explanations for this larger magnitude rather than concluding 1 second of motion adaptation is equivalent to 120 seconds. First is the slightly faster adaptor speed used in this experiment compared to that used by Dong *et al.* (30 deg/sec vs. 20 deg/sec, respectively). However, they also found that aMAE magnitudes increased as a negatively accelerating function of adaptor speed, suggesting that the aMAE magnitude reported here should not be 100% larger for an adaptor only 50% faster. This raises a second, perhaps more likely explanation
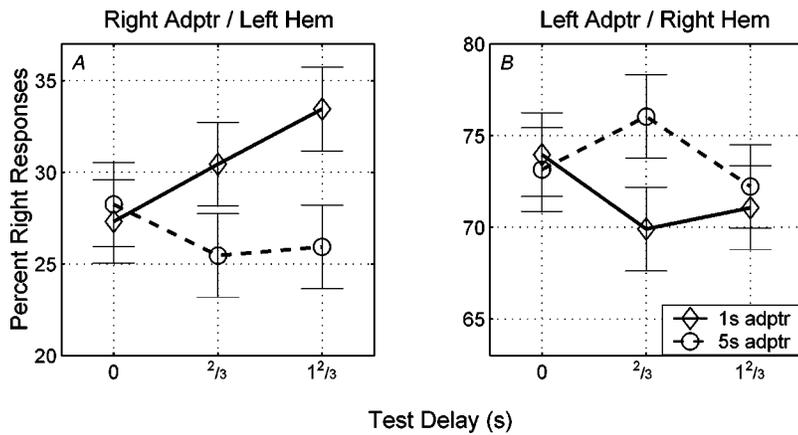
FIG. 5. Percent "right" responses as a function of adaptor duration (*line type*) and test delay (*abscissa*) for rightward adaptation in the left hemifield (*a*) and leftward adaptation in the right hemifield (*b*), averaged across test stimuli movement, with an estimate of the pooled standard error.

for this difference: that adaptation builds up over the entire course of the 10 minute long block for the 1-second adaptor duration to create the observed motion aftereffects. This question is addressed in more detail later.

It is also apparent from Table I that there were large individual differences in the data reported here. This may be one consequence of the briefer adaptation durations used here, or it may also stem from the limited number of test probe movement values. Nonetheless, it seems that for many listeners a single pass of a moving sound is enough to create dramatic biases in subsequent auditory motion judgments, which suggests a very quick onset of the modulating effect of preceding motion on subsequent motion perception. This rapid modulating effect appears to be consistent with findings in the physiological literature that only a brief exposure to auditory motion is necessary to dramatically alter the receptive fields of brainstem and cortical auditory neurons, and by extension, the possible perception of auditory motion (Spizter and Semple, 1998; McAlpine *et al.*, 2000; Malone *et al.*, 2002).

C. Effect of test delay on aMAE

The second fundamental question this experiment investigated was whether the measured strength of the auditory motion aftereffect would change as the presentation of the test stimulus was progressively delayed after cessation of the moving adaptor. As discussed in the Introduction, there are data showing that IC neurons may exhibit auditory motion direction selectivity only for very brief durations (500 ms or less) (McAlpine *et al.*, 2000): if the units are given time beyond this amount to recover from their initial response to sounds moving into their receptive fields, skewed responses for particular motion directions disappear. These data suggest that potential aMAEs would be strongest immediately after exposure to auditory motion, and should decay if measured more than 500 ms after exposure.

On the other hand, psychophysical experiments have shown that the effects of adaptation after minutes-long exposure to auditory motion may themselves last on the order of minutes or longer (Ehrenstein, 1994; Dong *et al.*, 1999). These behavioral results are complemented by recent physiological data showing that the neural adaptation to dynamic auditory stimuli may grow over time and last longer than 500 ms (Sanes *et al.*, 1998; Malone *et al.*, 2002). The current

experiment was designed to explore these issues by delaying the presentation of the test stimulus by 0, $\frac{2}{3}$, or $1\frac{2}{3}$ seconds after the adaptation ended.

Analysis once again focuses only on those adaptor hemifield/direction combinations that produced reliable aftereffects. Figure 5 graphs percent "right" responses as a function of the adaptor duration (symbol) by the test delay (*x*-axis), averaged across test stimuli movement, for rightward adaptors in the left hemifield (*A*) and leftward adaptors in the right hemifield (*B*). The interaction (hemifield/direction × adaptor duration × test delay) presented in this figure is significant [$F(2,14)=4.49$; Greenhouse–Geisser corrected $p<0.05$]. A partial interaction analysis on the data in Fig. 6(a) reveals a significant effect of adaptor duration × delay [$F(2,14)=4.68$; Greenhouse–Geisser corrected $p<0.05$]. Post-hoc analyses (Tukey's HSD) showed that performance at $\frac{2}{3}$ and $1\frac{2}{3}$ s test delays for the 5 s adaptor differ significantly from the $1\frac{2}{3}$ s test delay for the 1 s adaptor ($p<0.014$; $p<0.022$, respectively). Further, for the 1 s adaptor by itself, the difference in performance between the 0 and $1\frac{2}{3}$ s test delays is marginally significant ($p<0.074$).
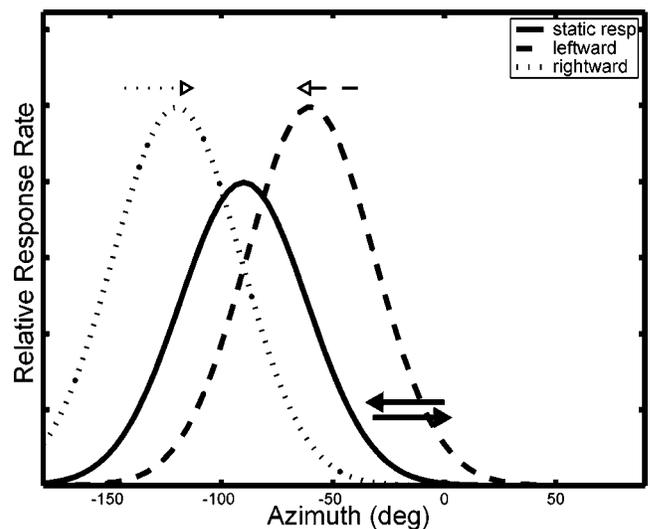

FIG. 6. Idealized response of a cortical auditory motion-sensitive neuron to static and moving sound sources (*line type*) (based upon Malone *et al.*, 2002). Solid arrows depict adaptor movement in the left hemifield from the present experiment.

The partial interaction of the data from leftward adaptor motion in the right hemifield [Fig. 6(b)], however, shows the difference between 1 s and 5 s adaptors across the test delays to be only marginally significant [$F(2,14)=3.16$; Huynh–Feldt corrected $p<0.75$]. Though the pattern of results appears to be similar to the left hemifield results for 0 and $\frac{2}{3}$ s test delays, there is little difference in the aftereffect for the two durations at the $1\frac{2}{3}$ s test delay.

As was done for the effects of adaptor duration in the previous section, the results of the two adaptor hemifields/directions were equalized to examine the overall effects of test delay. A 3-factor ANOVA on these equalized percent "right" responses confirms the significant interaction between adaptor duration and test delay [$F(2,14)=4.5$; Greenhouse–Geisser corrected $p<0.05$]. A post-hoc test (Tukey's HSD) reveals that the result for the 5 s adaptor measured at a $\frac{2}{3}$ s test delay, across the hemifield/direction, is significantly different from those for the 1 s adaptor at $\frac{2}{3}$ and $1\frac{2}{3}$ s test delays ($p<0.04$ and $p<0.013$, respectively).

This analysis of the effects of delaying the presentation of the test stimulus has produced the following results. For 1 second of auditory motion exposure, the aMAE is strongest immediately after exposure ends and declines significantly over a period of almost 2 seconds. The trend of this result initially appears to correspond with the McAlpine *et al.* (2000) finding that motion direction selectivity, and by extension a possible source of the aMAE, arises from very brief neural adaptation to auditory motion.

However, for 5 seconds of auditory motion exposure, the aMAE appears to be equally strong up to approximately 2 seconds after adaptation ends. This increasing duration of the aMAE with increasing amounts of adaptation may reflect a general trend that culminates with the prolonged aMAE that has been reported after several minutes of motion adaptation (Ehrenstein, 1994; Dong *et al.*, 1999). This result is not predicted by models of auditory motion selectivity emerging in the brainstem as a result of only brief adaptation (McAlpine *et al.*, 2000), and may therefore reflect the effects of motion adaptation across longer timescales and over greater physiological regions.

Again, it must be kept in mind that any failure to find even larger differences in the aMAE between 1 versus 5 seconds of adaptation may be the result of viewing the data over entire block lengths. The total motion exposure in the two adaptor durations over the course of an entire block may be much more similar than that caused by 1 versus 5 seconds of adaptation in isolation. This possible effect of block length is explored in the next section.

D. Effects of first versus last third of blocks

As noted earlier, experimental blocks lasted between 10–12 minutes on average for 1-second adaptor durations, and between 21–23 minutes for 5-second adaptor durations. Listeners were thus exposed to substantial amounts of auditory motion by the end of any single experimental block regardless of the number of moving stimuli heard on each individual trial. This raises the possibility that the lack of

more obvious differences between 1 and 5 seconds adaptor durations is due to the overall adaptation incurred over an entire block.

This issue had been expected during the design of this experiment and hence the presentation of the 6 test motion levels (±10, ±6, ±2 degrees) and the three test delays (0 s, $\frac{2}{3}$ s, $1\frac{2}{3}$ s) were balanced so that equal numbers of each combination were presented in three sections across the length of a single experimental block. Specifically, three exemplars of each combination of test motion and delay were presented in the first, second, and third sections of a block (within each section, however, the presentation order of the stimuli was otherwise random). This provided the opportunity to compare effects of interest after approximately 3–4 (7–8) minutes of overall motion exposure to 1-(5-)second adaptation (i.e., first third of blocks) versus effects near the end of experimental blocks. Though it is clear that the first third of a block for the 5-second adaptor is still longer than the first third for the 1-second adaptor, these sections were compared directly at this point for ease of analysis.

1. Effect of adaptor duration for first vs last 3rd of block data

Analysis once again focuses only on those adaptor hemifield/direction combinations that produced reliable aftereffects. Data from the first third of the experimental blocks that induced aftereffects were analyzed in the 4-factor partial interaction ANOVA used in the previous sections. As was found for data over entire experimental blocks (Sec. III B I), the adaptor hemifield/direction × duration interaction over the first 3rd of experimental blocks is significant, though its effect is considerably larger [$F(1,7)=21.58$; Greenhouse–Geisser corrected $p<0.01$]. When the data are equalized across the hemifield/direction, the differences between the adaptor durations in percent equalized "right" responses are indeed slightly greater than was previously found for the data over the entire experiment (mean of 5 s adaptation $=74.83\%$ equalized "right" responses; mean of 1 s adaptation$=69.16\%$ equalized "right" responses).

This effect of adaptor duration disappears, however, by the end of experimental blocks: the hemifield/direction x duration interaction is no longer significant [$F(1,7)=0.002$; $p>0.95$] and the equalized difference between the two adaptor durations has all but vanished (a mean of 5 s adaptation $=72.69\%$ equalized "right" responses; mean of 1 s adaptation$=72.57\%$ equalized "right" responses). This difference in the effect of adaptor duration between the first and last third of experimental blocks confirms what was hypothesized previously: the aftereffect created by 5 seconds adaptation is initially reliably stronger than that created from 1 second adaptation; however, the repeated presentation of moving adaptors over the course of an entire experiment eventually adapts listeners an equal amount, regardless of adaptor duration on individual trials.

2. Effect of test delay for first vs last 3rd of block data

The same ANOVAs described above indicate no significant effects of delays for either the first or last 3rd of block data at the $p<0.05$ criterion level. However, for both time periods, the interaction between adaptor duration and test delay is marginally significant ($p<0.08$). This suggests that differences in the temporal decay of the aftereffect, as measured by the effect of test delay, may only emerge for the different adaptor durations after prolonged exposure to auditory motion (e.g., over an entire experimental block). It appears that the following conclusions may be drawn considering the results presented in sections $C1$ and $C2$: auditory motion aftereffects become stronger and last longer as subjects become more adapted to auditory motion over the course of an experimental session, regardless of the duration of sound motion on individual trials.

E. Asymmetrical aMAE.

An attempt is made here to explain the asymmetrical aMAE seen in Figs. 2 and 3 using recent data on neural response in mammalian primary auditory cortex (AI) to simulated auditory motion (Ahissar *et al.*, 1992; Wilson and O'Neill, 1998; Ingham *et al.*, 2001; Malone *et al.*, 2002). These data show that the majority of neurons respond to auditory motion in the contralateral hemifield and, further, that many shift their receptive field response profiles toward the direction of source motion. For nonhuman mammals, maximal responses to static source position appear to occur at lateral azimuths near the acoustic axis (Brugge *et al.*, 1996; Malone *et al.*, 2002). Hence, for source motion near midline (such as used in this study), these units should respond more strongly to movement away from rather than toward midline, and consequently lead to greater aftereffect shifts toward the midline.

Figure 6 presents an idealized depiction of these response changes (*line type*) for units hypothetically recorded from right auditory cortex with maximal response to sources near $-90°$ azimuth (illustrations are based upon data from Malone *et al.*, 2002). As can be seen, a source starting at the midline and moving leftward (upper black arrow) should evoke a much stronger neural response than a sound starting at -30 degrees and moving rightward (lower black arrow). It is this response asymmetry between source motion into and out of laterally centered receptive fields that may have lead researchers to find a majority of neurons "preferring" contralateral rather than ipsilateral sound source motion (Ahissar *et al.*, 1992; Stumpf *et al.*, 1992; Malone *et al.*, 2002). This asymmetry may arise from common response adaptation as described in leaky integrate-and-fire neural models (Gerstner & Kistler, 2002), for example, rather than reflect a specialized reaction to sound motion direction. More relevant to the purposes of this work, this response asymmetry for motion near the midline could provide the basis for the asymmetrical aftereffects found in this experiment.

The difficulty with this portrayal of neural response to auditory motion is that, at first glance, it appears to predict an opposite aftereffect asymmetry to the one reported here. Spe-

cifically, for units with the best response near $-90°$ azimuth, the response to leftward motion in the left hemifield (i.e., away from midline) should evoke the greatest response in motion sensitive neurons and hence result in the greatest adaptation; in contrast, rightward motion should produce little activation and likewise little adaptation. This would imply the creation of strong rightward aftereffects (i.e., bias shifts toward the midline) for leftward motion adaptation and no leftward aftereffects for rightward adaptation. But the aMAE asymmetry reported here showed just the opposite pattern: for motion in the left hemifield, strong aftereffects appeared for rightward (toward midline) but not for leftward adaptor motion.

One possible explanation for this mismatch would be if maximal azimuthal responses in the human auditory cortex occurs nearer to $0°$ rather than at the acoustic axis. In this circumstance, motion toward the midline would create a strong increase in neural response, which should result in observable aftereffects away from the midline (and *vice versa* for ipsilaterally directed adaptation). Though data in nonhuman mammals indicate that maximal spatial responses fall at more lateral azimuths (Brugge *et al.*, 1996; Malone *et al.*, 2002), the distribution of receptive field maxima for humans remains empirically unknown. This explanation of the aMAE asymmetry must await confirmation by future data on the spatial response properties of neurons in human AI.

It should be noted that the asymmetrical aMAE seen here has not been reported in previous studies investigating the spatial extent of the auditory motion aftereffect (Grantham, 1998; Dong *et al.*, 2000). One source of this discrepancy is most certainly the briefer adaptation times used here versus those used in previous experiments. However, an asymmetrical aMAE based on the adaptor direction may be more robust to adaptation duration than implied by a superficial comparison of the cited aMAE studies. Grantham (1998) measured aftereffects after 30 seconds adaptation to pass-band noise moving toward and away from the midline in a single hemifield, though he did not test statistically for any differences of the adaptor direction on aMAE magnitude. Nonetheless, a plot of his results (Fig. 13, 1998) suggests that movement toward the midline may have produced larger aftereffects than movement away from midline.

Dong *et al.* (2000) tested adaptation regions constrained to single hemifields using only a rightward moving, 2-minute adaptor. If their results were to parallel those found here, then aMAE shifts would be seen only for adaptors in the left hemifield (i.e., movement toward the midline). However, plots of their data do not show significant differences in aMAE magnitudes for rightward motion in the two hemifields. The differences in the aMAE asymmetry between these three experiments (including this one) thus appears to be a function of the increasing adaptation periods used: a significant aMAE asymmetry after 1–5 seconds of adaptation (reported here), a slight aMAE asymmetry after 30 seconds of adaptation (suggested in Grantham, 1998), and no apparent aMAE asymmetry after 120 seconds of adaptation (Dong *et al.*, 2000). It is also possible that these differences may reflect different adaptive processes: the depicted recep-

tive field shifts underlie a true motion illusion with very short time constants of growth and decay, while bi-directional aMAEs arise from other, longer lasting response changes.

Nonetheless, the imbalanced aMAEs found here and suggested in Grantham's plots after 30 seconds of adaptation, may signify a real, robust difference in neural response to sound motion toward versus away from the midline. The fact that asymmetrical responses to sound motion have also been found in mammalian AI (Jenison *et al.*, 2001) suggests a possible cortical component to the auditory motion aftereffect. It remains to be determined whether extra-auditory cortical areas also contribute to the aMAE, as has been demonstrated for visual motion aftereffects (Culham *et al.*, 2000; Van Wezel and Britten, 2002).

IV. CONCLUSIONS

This study investigated the temporal growth and decay of the auditory motion aftereffect (aMAE) by manipulating how much motion listeners were exposed to during adaptation (1 versus 5 seconds) and how quickly test stimuli were presented following this exposure (0, $\frac{2}{3}$, and $1\frac{2}{3}$ seconds delay). Regarding the effects of adaptor duration, 1 second of exposure to auditory motion (i.e., a single pass of a moving sound source) produced strong biases in response to the motion direction of subsequent test stimuli. This result is taken as evidence of the rapid growth of the aMAE, and is consistent with findings in the physiological literature that only brief exposure to auditory motion is necessary to dramatically affect the receptive fields of brainstem and cortical auditory neurons and, by extension, the possible perception of auditory motion (Spizter and Semple, 1998; McAlpine *et al.*, 2000; Malone *et al.*, 2002).

However, 5 seconds of exposure to auditory motion generally produced stronger aMAEs. The apparently small increase in the magnitude of the aMAE for 5 seconds relative to 1 second of motion adaptation may also indicate that a substantial amount of adaptation builds up after an entire experimental session of motion exposure (e.g., lasting at least 10 minutes or more), regardless of adaptor duration on individual trials. This hypothesis was further supported by analyses showing that the differences in aMAE for the two adaptor durations were greatest in the initial third of an experimental block (over the course of the first 4–7 minutes), and decreased by its end.

Concerning timing of the test stimulus presentation, the aMAE was strongest immediately after adaptation ceased for 1 second of motion exposure on each trial, and decayed significantly by $1\frac{2}{3}$ seconds. However, for 5 seconds of motion exposure on each trial, the aMAE appeared as strong after $1\frac{2}{3}$ seconds as it was immediately after adaptation ends. This argues that greater amounts of motion adaptation result in longer lasting motion aftereffects (Dong *et al.*, 1999). The stronger and longer lasting aMAEs for longer exposure to auditory motion further suggest that models of motion selectivity in inferior colliculus relying on very brief forms of adaptation [e.g., <500 ms (Cai *et al.*, 1998; McAlpine *et al.*, 2000)] may not be able to completely account for all aspects

of the auditory motion aftereffect. These differences between 1 and 5 seconds of adaptation may also imply two components to the aMAE: a short time-constant motion illusion (i.e., a true motion aftereffect), and a longer time-constant motion desensitization in the direction of adaptation (i.e., response bias) (Grantham, 1998).

Finally, one of the most dramatic findings of this experiment was also one of the least expected: aftereffects arising from both adaptor durations were produced only by stimuli moving toward but not away from the midline (that is, aftereffects were only seen as shifts away from the midline). This result is not congruent with previous studies reporting equivalently strong bi-directional aftereffects for adaptation regions across ±35 deg of the midline (Dong *et al.*, 2000).

Ultimately, it is possible that the auditory motion aftereffect arises from both the long- and short-term adaptation of cells at multiple brainstem and cortical sites. One caveat that must be kept in mind when trying to explain the behavioral results seen here using neurophysiological data is that many of the aforementioned physiological studies measured neural responses using tonal stimuli varying only in phase differences (Spitzer and Semple, 1993; 1998; McAlpine *et al.*, 2000; Malone *et al.*, 2002). The experiment reported here used virtual auditory motion stimuli which incorporated all natural auditory spatial cues (ITD, ILD, monaural spectral cues). Given the convergent projections from the superior olive to the inferior colliculus and beyond, as well as the myriad cortico-cortical and cortico-collicular loops in the auditory system (Winer *et al.*, 1998; Kaas *et al.*, 1999; Thompson and Schofield, 2000), the presentation of stimuli rich in spatial cues could produce quite dramatic responses to auditory motion across the entire auditory system. A complete explanation of the aMAE must await more detailed information on how the human auditory system responds to and encodes sound motion.

[1]As an example, if a listener reported a +2 deg/sec test stimulus was moving rightward 20% of the time after rightward adaptation (i.e., a typical leftward aMAE), then the corresponding result for hypothetical leftward adaptation should be that a −2 deg/sec test stimulus would be labeled as moving rightward 80% of the time (i.e., a rightward aMAE).

[2]Even though adaptor hemifields/directions have been equalized in this analysis, there still may be differences in the aMAE between these two conditions.

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