Perception and Psychophysics. Vol. 62(5), pp. 1099–1111.

Suggested running head: AUDITORY MOTION AFTEREFFECT

The Auditory Motion Aftereffect: its Tuning and Specificity in the Spatial and Frequency Domains

Chang-Jiang Dong[*], Nicholas V. Swindale[*], Pierre Zakarauskas[*], Vincent Hayward[#] and Max S. Cynader[*]

[*]University of British Columbia, Vancouver, CANADA

[#]McGill University, Montreal, CANADA

Author contact:

Dr. Max Cynader
Department of Ophthalmology
University of British Columbia
2550 Willow Street
Vancouver, B.C.
Canada V5Z 3N9

Tel: (604)875-4353
Fax: (604)875-4663
E-mail: cynader@cs.ubc.ca

Perception and Psychophysics. Vol. 62(5), pp. 1099–1111.

ABSTRACT

In this paper, the auditory motion aftereffect (aMAE) was studied by using real moving sound as both the adapting and test stimulus. The real moving sound was generated by a loudspeaker mounted on a robot arm which was able to move quietly in three dimensional space. Seven subjects with normal hearing were tested. Results from Experiment 1 showed a robust and reliable negative aMAE in all the subjects involved. After listening to a sound source moving repeatedly to the right, a stationary sound source was perceived to be moving to the left. The magnitude of the aMAE tended to increase up to the highest velocity tested (<30°/sec). The tuning and specificity of this aftereffect was further studied in the spatial and frequency domains. The strength of the aftereffect depended on matching both the spatial location and the frequency content of the adapting and test stimuli. Offsetting the locations of adapting and test stimuli by 20° reduced the size of the effect by about 50%. A similar decline occurred when the frequency of the adapting and test stimuli differed by one octave.

Perception and Psychophysics. Vol. 62(5), pp. 1099–1111.

The Auditory Motion Aftereffect: its Tuning and Specificity in the Spatial and Frequency Domains

In vision, the motion aftereffect is a common phenomenon that can be often observed in the natural environment and easily demonstrated in the experimental settings. The well known waterfall illusion and the spiral aftereffect are just two examples. After a few minutes of viewing an object moving in a single direction (adaptation), a stationary object appears to move in the opposite direction (test). This visual motion aftereffect (vMAE) has been extensively studied for more than a century and has been taken as psychophysical evidence for the existence of specialized motion detection channels in the visual system (e.g. Wohlgemuth 1911; Gates 1934; Wade 1994). A commonly held_theory is that during prolonged exposure to one direction of motion, neurons sensitive to that direction of motion adapt (Barlow and Hill 1963; Sekuler and Pantle 1967; Pantle and Sekuler 1968; Marlin, Hasan & Cynader 1988; Saul & Cynader 1989 a & b; Giaschi, Douglas, Marlin & Cynader 1993). Then, when a static stimulus is presented, the activities of the neurons sensitive to the opposite direction dominate, causing the stationary object to be perceived as moving in the direction opposite that of the adapting motion.

Perception and Psychophysics. Vol. 62(5), pp. 1099–1111.

To date, there have been only a few studies of the aMAE (Grantham and Wightman 1979; Grantham 1989; Reinhardt-Rutland 1992; Ehrenstein 1994). In these studies, simulated moving sound was used as the stimulus (i.e. as adapting and test stimuli or just as a test stimulus), which was generated by dynamically changing interaural time and/or intensity differences. The aMAE elicited under these conditions was weak and unstable (Grantham and Wightman 1979; Grantham 1989), or even absent (Reinhardt-Rutland 1992; Ehrenstein 1994). For example, in the study by Grantham (1989), an aMAE was observed only for two out of four subjects when the adapting velocity was below 30°/sec. In the Reinhardt-Rutland (1992) and Ehrenstein (1994) studies, after adaptation to simulated moving sound presented over headphones, subjects reported a loudness aftereffect or a displacement aftereffect, but no motion aftereffect. Simulated moving sound may be an unsatisfactory stimulus to use because it can only provide the auditory system with incomplete motion cues. Thus, the auditory motion detection channels may not be adequately stimulated. However, a real moving sound can provide a more natural stimulus and potentially more localization cues, including a time-varying frequency spectrum, as well as intensity and phase information, to the auditory system for motion detection. Here we report the results of experiments in which a real moving sound was used as stimulus. Sound stimuli were generated by a loudspeaker

Perception and Psychophysics. Vol. 62(5), pp. 1099–1111.

mounted on a robot arm which can move smoothly and quietly on the surface of an imaginary sphere centered on the subject's head at velocities up to 30°/sec. Using this stimulus, a robust and repeatable aMAE was demonstrated in all subjects tested. Experiment 1 demonstrates the existence of the aMAE, and the tuning and specificity of the aMAE in the spatial and frequency domains are further studied in Experiments 2 and 3, respectively.

General Method

Subjects

A total of seven subjects (T.S., R.C., M.H., M.L., J.Q., P.Z. and C.D.) with clinically normal hearing participated in these three experiments. All subjects, aged 23 - 39 years, were recruited from members of the Ophthalmology Research Lab or were students at the University of British Columbia. Except for the two authors (P.Z. and C.D.), all subjects were unaware of the purpose of the experiments.

Apparatus

In order to study the aMAE, an acoustical stimulus system (fig. 1) has been established in our laboratory which allows a sound source to move with a given velocity (up to 30˚/sec) and along a specified trajectory. The stimulus system consists of a robot arm and control

Perception and Psychophysics. Vol. 62(5), pp. 1099–1111.

circuits and software. The robot arm was designed and constructed in the Department of Electrical Engineering at McGill University specifically for our purpose. The control of the robot arm was fulfilled in the Department of Ophthalmology at the University of British Columbia. In this system, a loudspeaker (LCS-150, Labtec) is mounted at the 'tip' (the end effector) of the robot arm which is a servo controlled mechanism of a closed loop kinematic chain. It is interfaced to an IBM PC computer through a PC motion control interface card (MFIO-3A, Precision MicroDynamics Inc.) (fig. 2). The system was designed to move the loudspeaker smoothly, quietly, and safely so that the trajectory of the loudspeaker is constrained to lay on the surface of a sphere with a radius of 0.8 m. When the subject’s head is located at the center of this sphere, during any movement, the orientation of the loudspeaker is constrained toward the subject's head. The design of the system was governed by the following list of requirements: maximum coverage of the acoustical space, minimization of acoustical emissions, high speed of motion, high acceleration, high structural resonant modes, safety of operation, low visual intrusion and bulk, and of course, low complexity and cost. The design takes advantage of a 'five bar' closed loop spherical mechanism. In this type of mechanisms, all five joint axes meet at one point. It is a property of these mechanisms that all points of their links are constrained to move on the surface of spheres

Perception and Psychophysics. Vol. 62(5), pp. 1099–1111.

centered at a common point. This was taken advantage of in the design of the robot arm to ensure proper motion of the speaker and to achieve a high level of safety so that no part of the mechanism can penetrate the space in which the subject is located. It is known that, with proper design, the workspace can cover the entire sphere (save the 'antipodes') if the first two joint axes have coinciding axes. This condition can be achieved when the actuators are either coinciding or placed at the antipodes of the sphere. For reasons of mechanical simplicity and reduction of bulk, the two actuated joints in our system were placed 20 degrees apart, so closely approaching the 'coinciding' condition. The angular design of the other links was optimized to maximize the 'dexterous' workspace, that is the work range within which the system preserves high acceleration capabilities. With these constraints in mind, a large portion of the sphere could be covered. The device is simply constructed of aluminum, and yet could achieve fairly high structural resonance despite the long reach. Much improvement could be achieved in the future with a more extensive structural design effort.

In this device, one link, the base link, is mechanically grounded and supports two actuated and instrumented joints. The other three joints are free. The base link is supported by a rigid overhead gantry and is located behind and above the subject’s head. It includes

Perception and Psychophysics. Vol. 62(5), pp. 1099–1111.

two sound proofed motion reduction boxes driven by DC motors via elastomeric belts, achieving a reduction of about 1:60. This number maximizes the acceleration capability of the device since it is roughly the square root of the ratio of the mechanism inertia to that of the motors. By control, arbitrary speaker trajectories can be programmed. Reference trajectories are synthesized by the control computer for the need of an experiment, converted into joint trajectories, which in turn are tracked by joint servo control.

The area of the surface which can be reached by the loudspeaker is about 63% of the total surface area of the sphere, covering almost all the subject's frontal hemifield. The loudspeaker was connected to a soundblaster card (Sound Blaster 16, Creative Labs, Inc.) which was programmed to generate different kinds of sound, including white noise, band-pass noise, pure tones and clicks. These sounds were synchronized with the movement of the robot arm by a computer program developed in our laboratory. In this way, the sound is activated only when the loudspeaker moves into a given spatial region. This acoustical stimulation system was positioned in an acoustically treated sound-proof chamber, which was modified from an IAC sound-insulated chamber (Industrial Acoustics Company, Inc.). Taking advantage of this unique sound stimulator, a series

Perception and Psychophysics. Vol. 62(5), pp. 1099–1111.

of psychoacoustical experiments was carried out to study the aMAE.

Procedure

A two-alternative forced choice (2-AFC) paradigm was used to measure the aMAE. After listening to a sound source moving in a single direction for two minutes, subjects were asked to indicate the direction (i.e. left or right) of a brief test sound by pressing one of two buttons. In each test, the direction and velocity of the test stimulus were randomized. Following each test, the adapting stimulus was presented again for 2 seconds to maintain the adaptation (fig. 3). A total of 64 test and reinforcing presentations was given on each test of adaptation. The range of test velocities was always centered on zero and was chosen so that the extremes of the range were almost always correctly identified by the subject. Probit analysis (Finney 1971) was used to estimate the 50% response rate on the resulting psychometric function. This is the stimulus velocity which sounds stationary to the subjects. If there is an aMAE, the subjective mean velocity will shift in the direction of adaptation. In our studies, this mean velocity was used as a measure of the magnitude of the motion aftereffect.

Close inspection of the experiments done by Grantham and his colleague (1979, 1989) reveals a potential drawback

Perception and Psychophysics. Vol. 62(5), pp. 1099–1111.

in their experimental design. In their studies, test stimuli moved symmetrically about the midline. Therefore, the direction of motion of a test stimulus could be decided based on the start or end position of the test stimulus relative to midline. For example, if the start position of a test stimulus is on the right side of midline, the test stimulus will definitely move to the left. The subjects in these studies might have used the localization cues for the start or end position of a test stimulus to judge the direction of the moving test stimulus. To overcome this potential drawback in our experiments, for each start position, a test stimulus could move randomly in either direction, left or right. Thus, the start and/or end positions could no longer provide direction cues for the subjects.

All experiments were conducted in the darkened sound-proof chamber described above. Subjects were seated at the center of the sphere defined by the motion of the loudspeaker, and were instructed to keep their eyes closed and maintain a steady upright posture through the course of experimentation. A head rest was provided to prevent the subjects from tilting their heads either sideways or forward. Before data were collected, at least two hours of training was provided to each subject until the performance of the subject was stable. The order of tests with different stimulus parameters (i.e. adapting velocity,

Perception and Psychophysics. Vol. 62(5), pp. 1099–1111.

stimulus frequency or spatial region) was randomized for each of three experiments in order to minimize any order effects. Each test session lasted about one hour, which typically included three individual tests. For example, in Experiment 1, each test session consisted of three tests with different adapting velocities, +20°/sec, 0°/sec (control) and -20°/sec, where the sign '+' indicates that the direction of a moving stimulus is to the left, while the sign '-' to the right. After each test, a 5-minute break was provided in order to prevent the subject from fatiguing. Each experiment was spread over three weeks.

Experiment 1

This experiment was designed to demonstrate the aMAE and to analyze the magnitude of the aMAE as a function of adapting velocity.

Method

Four subjects (T.S., R.C., P.Z. and C.D.) were tested in this experiment. White noise was used as both the adapting and test stimulus. The average level of each sound, presented from a stationary loudspeaker at 0° azimuth at the subject's ear level and measured at the subject's head position (0.8 m distant) was about 75 dBA. During adaptation, the adapting stimulus repeatedly traversed an arc of 30° (±15° centered on the midline) at

Perception and Psychophysics. Vol. 62(5), pp. 1099–1111.

the subject's ear level with one of six velocities (±10, ±15 and ±20˚/sec). In each test of adaptation, the adapting velocity was constant throughout trials. In the control condition, the adapting stimulus was a stationary sound (i.e. with a velocity of 0˚/sec) presented directly in front of the subject (0.8 m distant). For each adapting velocity, the same test was repeated at least three times for each subject.

Results and Discussion

In figure 4, the magnitude of the aMAE from all four subjects in Experiment 1 is plotted as a function of adapting velocity. Different panels represent results from different individual subjects. The results showed clear aMAEs for all the subjects involved, although the adapting velocities used in this experiment were below 30˚/sec. After adaptation, the subjective mean velocity shifted in the expected direction. That is, when the adapting velocity was positive (i.e. to the left), the subjective mean velocity changed in a positive direction. Thus, a positive velocity was judged by the subject as stationary and correspondingly a stationary sound was heard as moving to the right.

Compared to the study by Grantham (1989), in which only 50% of subjects reported the aMAE when low adapting

Perception and Psychophysics. Vol. 62(5), pp. 1099–1111.

velocities (<30˚/sec) were tested, our results suggest that by using real moving sound as both adapting and test stimuli, a more robust aMAE can be demonstrated. In the Grantham study (1989), higher adapting velocities (50 ~ 200˚/sec) were also tested, and the magnitude of the aMAE was analyzed as a function of adapting velocity. Large inter-subject variation was observed in the form of the function measured by Grantham. For two out of four subjects in his study, the magnitude of the aMAE first increased with the adapting velocity, and then leveled off or slightly decreased. For the other two subjects, the magnitude of the aMAE changed nonmonotonically as the adapting velocity increased. Our experiment explored the effects of relatively low adapting velocities (10 ~ 20˚/sec) on the aMAE. Our results showed that the magnitude of the aMAE tended to increase with the adapting velocity up to the highest velocity tested, and this trend was consistent for all of our subjects. Due to different adapting velocity ranges used in Grantham’s and our experiments, the results from these two studies can not be directly compared. But our results at least extended Grantham’s observation of the aMAE from high adapting velocities to low adapting velocities.

In figure 5, the aMAE averaged over all four subjects tested in Experiment 1 is displayed as a function of adapting velocity. In the top panel, as in figure 4, the

Perception and Psychophysics. Vol. 62(5), pp. 1099–1111.

magnitude of the aMAE is measured as a perceived stationary mean velocity; whereas in the bottom panel, in order to analyze the aMAE in terms of gain, the aMAE is expressed as a percentage of the adapting velocity. Although, as expected, in the top panel of figure 5 the magnitude of the aMAE increased with the adapting velocity, the results in the bottom panel show that_the gain of the aMAE decreased from 17% to 12.8% as the adapting velocity increased from 10˚/sec to 20˚/sec.

Experiment 2

This experiment was designed to study the tuning and specificity of the aMAE in the spatial domain.

Method

Three subjects (M.H., T.S. and C.D.) participated in Experiment 2, two of whom were also subjects in Experiment 1. In this experiment, the stimulus was the same as that in Experiment 1, except that only one adapting velocity, i.e. 20˚/sec, was used. An arc of 70˚ (±35˚ centered on the midline) at the subject's ear level was divided into 7 equal sub-regions, each 10˚ of arc (-35° ~ -25°, -25° ~ -15°, -15° ~ -5°, -5° ~ 5°, 5° ~ 15°, 15° ~ 25°, 25° ~ 35°). Two

Perception and Psychophysics. Vol. 62(5), pp. 1099–1111.

experimental conditions were used. In Condition 1, in order to obtain the spatial tuning of the aMAE, the adapting and test regions overlapped and the magnitude of the aMAE was measured as a function of spatial region. In Condition 2, in order to determine if the aMAE is spatially specific, the adapting and test stimuli were presented in separate spatial regions, and the magnitude of the aMAE was analyzed as a function of the distance between the two separate loci. In this condition, the region swept by the adapting stimulus was a 10° arc (±5° centered on the midline), whereas the test region was chosen from one of six separate regions (-35° ~ -25°, -25° ~ -15°, -15° ~ -5°, 5° ~ 15°, 15° ~ 25°, 25° ~ 35°).

Results and Discussion

Results obtained from Condition 1 and 2 for all the subjects in Experiment 2 are displayed in figure 6 and 7 respectively. In these figures, results from different subjects are shown in different panels. In figure 6, the magnitude of the aMAE was plotted as a function of spatial region. Results showed that within the spatial region tested (-35° ~ 35°), the spatial tuning curves were relatively independent of positions. That the aMAE is spatially specific is clearly shown in figure 7, in which the magnitude of the aMAE was plotted as a function of location of the test region. When the test region overlapped the adapting region (-5° ~ 5°), the aMAE elicited

Perception and Psychophysics. Vol. 62(5), pp. 1099–1111.

was largest. As the distance between the test and adapting regions increased, the aMAE diminished, resulting in an inverted 'V' shape of the spatial tuning function. From the spatial tuning curves in figure 7, a space constant was determined for each subject and for the average over all three subjects tested in Experiment 2, by finding the best fitting Gaussian functions and taking the standard deviation as a measure of the space constant. These were 15.3°, 14.9° and 19.5° for subjects T.S., M.H. and C.D. respectively. The space constant obtained from the average spatial tuning curve of these three subjects was 16.4°.

Experiment 3

This experiment was designed to study the tuning and specificity of the aMAE in the auditory frequency domain.

Method

Three subjects (M.L., J.Q. and C.D.) were tested in this experiment. The adapting region and stimulus intensity were the same as those in Experiment 1. As in Experiment 2, only one adapting velocity (20°/sec) was tested. In this experiment, instead of using white noise, five 1-octave band-pass noises with different center

Perception and Psychophysics. Vol. 62(5), pp. 1099–1111.

frequencies (f_c) (i.e. 500 Hz (L), 1000 Hz, 2000 Hz (M), 4000 Hz and 8000 Hz (H)) were used as stimuli. As in Experiment 2, there were two conditions in this experiment. In the first condition, the adapting and test stimuli had the same spectrum. In order to study the frequency tuning of the aMAE, the magnitude of the aMAE was analyzed as a function of frequency band. In the other condition, in order to investigate if the aMAE is frequency specific, the adapting and test stimuli were in different frequency spectral ranges. Six combinations of the adapting and test stimuli were tested (i.e. L-M, L-H, M-L, M-H, H-L and H-H, where the first letter indicates the spectral content of the adapting stimulus and the second one indicates that of the test stimulus). Due to limited time available from each subject, each band-pass noise and each combination of adapting and test stimuli was tested only once.

Results and Discussion

Results from Experiment 3 are shown in figures 8 and 9. In figure 8, the magnitude of the aMAE was plotted as a function of frequency band. The results showed that the magnitude of the aMAE was slightly larger for low frequency (<1000 Hz) sound than for middle (2000 ~ 4000 Hz) or high frequency (>4000 Hz) sound, which is consistent with the results reported by Grantham and Wightman (1979). Sound in

Perception and Psychophysics. Vol. 62(5), pp. 1099–1111.

the middle frequency range (2000 ~ 4000 Hz) was least efficient in inducing the aMAE. The same pattern was shown in all three subjects tested. Figure 9 compares the aMAE measured with nine combinations of the adapting and test stimuli. In three panels (top right, bottom left and bottom right) of figure 9, low (f_C: 500 Hz), middle (f_C: 2000 Hz) and high (f_C: 8000 Hz) frequency sounds served as test stimuli respectively. In these three panels, the adapting stimulus was a low (f_C: 500 Hz), medium (f_C: 2000 Hz) or high (f_C: 8000 Hz) frequency sound. The results showed that the aMAE was largest when the adapting and test stimuli overlapped in frequency, that is, when both of them were low, middle or high frequency sound. When the adapting and test stimuli were different in frequency, the magnitude of the aMAE decreased. The extent of the decrease depended on the distance in frequency between the adapting and test stimuli. The farther the difference in frequency, the weaker the aMAE, suggesting that the aMAE is frequency specific. These results are summarized in the top left panel of figure 9, in which the size of the circle represents the magnitude of the aMAE averaged over all three subjects tested in nine combinations of adapting and test stimuli. In addition to the frequency specificity of

Perception and Psychophysics. Vol. 62(5), pp. 1099–1111.

the aMAE which is reflected by the larger sizes of the circles along the diagonal (lower-left corner to upper-right corner), the pattern in this panel shows an interesting asymmetry of the frequency distribution of the aftereffect. The circles below the diagonal are larger than those above it, indicating that the aMAE is stronger when the test stimulus is higher in frequency than is the adapting frequency and weaker in the opposite conditions.

General Discussion

In the present study, by using real moving sound as both adapting and test stimuli, a robust aMAE was observed even with adapting velocities as low as 10°/sec. When the magnitude of the aMAE obtained in the present study is expressed as gain, i.e. a percentage of the adapting velocity, it is comparable to that of the vMAE. By using a nulling procedure, Taylor (1963) measured the velocity of the vMAE as a function of adapting velocity. In order to compare the MAE between these two modalities, we recalculated the magnitude of the vMAE measured by Taylor (1963) in terms of gain. Consistent with our results for the aMAE, his results showed that although the velocity of the vMAE increased with the adapting velocity, the gain of the vMAE decreased from 11.1% to 3.6% or from 23.3% to 4.8%

Perception and Psychophysics. Vol. 62(5), pp. 1099–1111.
when the adapting velocity increased from 9˚/sec to 108˚/sec, and that the gain depended on the duration of adaptation. Compared to previous studies, in which simulated moving sound was used, the present study suggests that real moving sound does indeed provide robust motion cues to the auditory system, and thus more adequately stimulates the auditory motion detection channels. In order to have the aMAE explicitly expressed, not only do the auditory motion detection channels need to be adequately adapted, but also to be tested by using real moving sound as stimulus.

The existence of a motion aftereffect is often regarded as evidence for specialized motion detection mechanisms in a modality. A motion aftereffect, which is caused by adaptation to auditory spectral motion, was earlier demonstrated in our laboratory (Shu et al. 1993). After listening to a simple spectral pattern (a spectral peak or a spectral notch) moving upwards or downwards in frequency for a few minutes, the same pattern was perceived as moving in the opposite direction even though it was actually stationary. This result suggests that there exist specialized channels in the auditory system which process dynamic spectral cues. Our present results showing that

Perception and Psychophysics. Vol. 62(5), pp. 1099–1111.

the aMAE can be demonstrated if appropriate stimuli are used suggest that the auditory system contains specialized channels for detecting motion in azimuthal space. This notion is supported by a recent neurological study (Griffiths, Rees, Witton, Shakir, Henning & Green 1996), which described a patient who had a specific deficit in auditory motion detection although his ability to localize stationary sounds was much less impaired. The fMRI examination of this patient revealed damage in a cortical area which was distinct from the primary auditory cortex, suggesting that moving sound may be processed independently from stationary sound. In vision, an analogous neurological study (Zihl, von Cramon & Mai 1983) was reported on a patient who exhibited disturbances of movement vision without substantial effects on static vision. By using CT scanning and neuropsychological testing, it was found that bilateral cerebral lesions affecting the lateral temporo-occipital cortex and the underlying white matter were responsible for the observed disorder in movement vision in this patient, suggesting that visual motion processing depends on neural mechanisms beyond the primary visual cortex. The parallel findings in these two studies suggest that perception of_motion in the auditory and visual systems are mediated by specialized

Perception and Psychophysics. Vol. 62(5), pp. 1099–1111.

motion detection channels located beyond the primary sensory cortices.

The fact that the aMAE is both frequency and spatially specific indicates that these motion specific channels have specific characteristic frequencies and defined receptive fields with an average space constant of about 15˚ obtained in the present study. The results of figure 9 showing that the aMAE is stronger when adapting stimuli contain lower frequency sound relative to that contained in the test stimuli than when the frequency relation between the adapting and test stimuli is reversed suggest that the frequency tuning of the motion sensitive channels may spread farther to the high-end than to the low-end of the frequency spectrum. Further studies would be needed to confirm this suggestion. Recently, similar results were obtained in an independent study by Grantham (1998). In his study, moving sound stimuli were first recorded using two microphones put in the ear canals of the KEMAR manikin's two ears. These recorded sounds were later played back to the subject through headphones during experiments. As in the present study, Grantham's results showed that the magnitude of the aMAE was larger when the adapting and test regions overlapped than when they were

Perception and Psychophysics. Vol. 62(5), pp. 1099–1111.

separate, and that the aMAE was stronger when the adapting and test stimuli shared the same spectral content.

It is commonly held that low frequency sounds (<1300 Hz) can cause substantial interaural time differences (ITDs) at the two ears. Whereas, due to the shadow effect of the head, middle (1300 ~ 4000 Hz) and high frequency sounds (>4000 Hz) primarily generate interaural intensity differences (IIDs). During the movement of a sound source in the real world, the ITDs and IIDs change with time. These dynamic localization cues are known to be important for the auditory system to detect acoustic motion. But whether one of these cues is more efficient in inducing the perception of motion is still unclear. The present study of the frequency tuning of the aMAE provides some clues for answering this question. Our finding that the aMAE is somewhat stronger for low frequency sounds than for middle and high frequency sounds suggests that the time-varying ITDs generated by sound moving in the real world play a more important role in the auditory motion detection. However, our results showing that the aMAE can be observed even with high frequency sounds centered at 8000 Hz indicate that either IID or ITD cues can be used.

Perception and Psychophysics. Vol. 62(5), pp. 1099–1111.

The finding that across the spatial range tested (-35° ~ +35° in azimuth) the aMAE was independent of horizontal position is quite interesting. It is known that for static horizontal sound localization, there is a clear azimuth dependence. Studies show that the minimum audible angle (MAA), which is the minimum arc between two static sources that can be discriminated (Mills 1958), is smallest (about 1˚) around 0˚ azimuth and increases with azimuth (e.g. about 2° and 6.5° at 35° and 75˚ azimuths respectively) (Mills 1972). In other words, the acuity of static sound localization in the horizontal plane decreases as the sound sources are moved from directly in front of the listener (0˚ azimuth) towards one ear. Since the aMAE we observed are largely invariant with azimuth, our results suggest that motion detection in the auditory system is not based on comparisons of the static localization of the sound source at different times (Middlebrooks and Green, 1991). Rather, the auditory motion detection channels appear to respond directly to the velocity and direction of a moving sound regardless of its location. That is, the sound source velocity and direction appear to serve as directly perceived attributes of moving stimuli (Lappin, Bell, Harm & Kottas 1975). This would be important, because it would allow a listener to detect motion of a sound moving

Perception and Psychophysics. Vol. 62(5), pp. 1099–1111.

directly towards or away from the listener in the midsagittal plane. In such a case, binaural cues are unavailable and sound source motion could not be inferred by a position comparison system, but could be inferred by an intensity-comparing system. Findings in neurophysiological studies render some support for this contention. For instance, units in the cat auditory cortex, which respond selectively to amplitude-modulation ramps of different speeds, a correlate of sound source velocity in three dimensional space, have been reported (Stumpf, Toronchuk & Cynader 1992). This contention gains further support from a theoretical acoustical analysis by Zakarauskas and Cynader (1991). Their study showed that the rate of change of monaural intensity function was directly proportional to the source velocity scaled by the distance of a sound source for omnidirectional sources of constant intensities. Thus, it is attractive to speculate that the auditory system may make explicit use of the rate of change of monaural intensity to detect motion directly.

In summary, compared to previous studies, a more robust and reliable aMAE was observed in the present study by using real moving sound as stimulus. Within the spatial region tested (±35° centered on the midline), the aMAE is

Perception and Psychophysics. Vol. 62(5), pp. 1099–1111.

relatively independent of position. The aMAE is larger for low frequency sound than for middle and high frequency sounds, but it can be observed for both low and high frequency stimuli. The aMAE observed is spatially and frequency specific. These results suggest that the auditory system contains specialized motion detection channels, which may directly detect the velocities of moving sound sources.

Perception and Psychophysics. Vol. 62(5), pp. 1099–1111.

References

Barlow HB and Hill RM. (1963) Evidence for a physiological explanation of the waterfall phenomenon and figure after-effects. Nature, 200:1345-1347.

Ehrenstein WH. (1994) Auditory aftereffects following simulated motion produced by varying interaural intensity or time. Perception, 23:1249-1255.

Finney DJ. (1971) Probit analysis (3rd edn.), Cambridge Univ. Press.

Giaschi D, Douglas R, Marlin S and Cynader MS. (1993) The time course of direction-selective adaptation simple and complex cells in cat striate cortex. Journal of Neurophysiology, 70(5): 2024-2034.

Grantham DW and Wightman FL. (1979) Auditory motion aftereffects. Perception and Psychophysics, 26(5): 403-408.

Grantham DW. (1989) Motion aftereffects with horizontal moving sound sources in the free field. Perception and Psychophysics, 45(2):129-136.

Grantham DW (1998) Auditory motion aftereffects in the horizontal plane: the effects of spectral region, spatial sector, and spatial richness. Acustica/Acta Acustica, 84(2): 337-347.

Perception and Psychophysics. Vol. 62(5), pp. 1099–1111.
Griffiths TD, Rees A, Witton C, Shakir RA, Henning GB and Green GG. (1996) Evidence for a sound movement area in the human cerebral cortex. Nature, 383:425-427.

Lappin JS, Bell HH, Harm OJ and Kottas B. (1975) On the relation between time and space in the visual discrimination of velocity. Journal of Experimental Psychology, 1(4): 383-394.

Marlin SG, Hasan SJ and Cynader MS. (1988) Direction-selective adaptation in simple and complex cells in cat striate cortex. Journal of Neurophysiology, 59:1314-1330.

Middlebrooks JC and Green DM. (1991) Sound localization by human listeners. Annual Review of Psychology, 42:135-159.

Mills AW. (1958) On the minimum audible angle. Journal of Acoustical Society of America, 30:237-246.

Mills AW. (1975) Auditory localization. In: Tobias (Ed.) Foundations of Modern Auditory Theory. New York: Academic Press. Vol. 2.

Pantle AJ and Sekuler RW. (1968) Velocity-sensitive elements in human vision: initial psychophysical evidence. Vision Research, 8(4):445-450.

Reinhardt-Rutland AH. (1992) Changing-loudness aftereffect follow simulated movement: implications for channel

Perception and Psychophysics. Vol. 62(5), pp. 1099–1111.
hypotheses concerning sound level change and movement. Journal of General Psychology, 119:113-121.

Saul AB and Cynader MS. (1989a) Adaptation in single units in visual cortex: the tuning of aftereffects in the spatial domain. Visual Neuroscience, 2:593-607.

Saul AB and Cynader MS. (1989b) Adaptation in single units in visual cortex: the tuning of aftereffects in the temporal domain. Visual Neuroscience, 2:609-620.

Sekuler RW and Pantle AJ. (1967) A model of after-effects of seen movement. Vision Research, 88:1-11.

Shu ZJ, Swindale NV and Cynader MS. (1993) Spectral motion produces an auditory after-effect. Nature, 364(6439): 721-723.

Stumpf E, Toronchuk JM and Cynader MS. (1992) Neurons in cat primary auditory cortex sensitive to correlates of auditory motion in three-dimensional space. Experimental Brain Research, 88: 158-168.

Wade NJ. (1994) A selective history of the study of visual motion aftereffects. Perception, 23:1111-1134.

Wohlgemuth A. (1911) On the after-effect of seen movement. British Journal of Psychology, Monograph supplement 1:1- 117.

Zakarauskas P and Cynader MS. (1991) Aural intensity for a moving source. Hearing Research, 52:233-244.

Perception and Psychophysics. Vol. 62(5), pp. 1099–1111.

Zihl J, von Cramon D & Mai N. (1983) Selective disturbance of movement vision after bilateral brain damage. Brain, 106:313-340.

Perception and Psychophysics. Vol. 62(5), pp. 1099–1111.

Author Note

Chang-Jiang Dong, Nicholas V. Swindale, Pierre Zakarauskas and Max S. Cynader, Department of Ophthalmology; Vincent Hayward, Department of Electrical Engineering.

The present study is supported by NSERC Grant #A9939 to M.C.. Part of this work was presented at the 134th meeting of Acoustical Society of America, San Diego, California, December 1997. We thank Eric De Silva for his contribution to the design and construction of the acoustical stimulation system used in the study and all the subjects who kindly volunteered to participate in the study. We recently learned that D.W. Grantham has independently carried out a similar study of the spatial and frequency specificity of the aMAE, published in Acustica/Acta Acustica. We are grateful to him for making us aware of his results before publication.

Correspondence concerning this article should be addressed to Dr. Max Cynader, who is at Department of Ophthalmology, University of British Columbia, 2550 Willow Street, Vancouver, B.C. V5Z 3N9, Canada.

Perception and Psychophysics. Vol. 62(5), pp. 1099–1111.

Figure Caption

Figure 1 A picture of the acoustic stimulus delivery system used in this study. This stimulus system is positioned in an acoustically treated sound-proof chamber. In this system, a loudspeaker (LCS-150, Labtec) mounted on a robot arm can move smoothly and quietly on the imaginary surface of a sphere with a radius of 0.8 m. In the picture, a subject is seated in the chamber with his head at the center of the sphere.

Figure 2 Schematic diagram of the acoustical stimulus delivery system. A specially designed robot arm tracks the reference trajectories specified by a controlling PC computer through a motion control interface card (MFIO-3A, Precision MicroDynamics Inc.) via joint servo control. In order to generate a real moving sound, a loudspeaker (LCS-150, Labtec) is mounted on the 'tip' of the robot arm, which is connected to a soundblaster card (Sound Blaster 16, Creative Labs, Inc.). Sounds generated by the sound card are synchronized with the movement of the robot arm. In this way, sounds are activated only when the loudspeaker moves into a given spatial region.

Perception and Psychophysics. Vol. 62(5), pp. 1099–1111.

Figure 3 Time sequence of stimuli. After an initial two minutes of adaptation, a brief test sound of 1 second is presented to the subject. The subject has to respond by pressing one of two buttons to indicate the direction of motion of the test sound. Following each response, the adapting sound is presented again for 2 seconds to maintain the adaptation. A total of 64 test and reinforcing presentations are given on each test of adaptation.

Figure 4 Magnitude of the aMAE measured as a function of adapting velocity. In this study, the subjective stationary mean velocity obtained from the psychometric function was used as a measure of the aMAE. Different panels show results from different subjects. In the adapting condition, the adapting sound repeatedly traversed along an arc of 30° (±15° centered on the midline) with one of six velocities (±10, ±15 and ±20 °/sec, where the sign '+' indicates that the direction of a moving stimulus is to the left, and the sign '-' indicates rightward motion). In the control condition, the adapting sound was presented from a stationary loudspeaker (0 °/sec) directly in front of the subject (0.8m distant). Note that there is a clear aMAE for all the subjects tested. The magnitude of the aMAE tended to increase up to the highest velocity tested.

Perception and Psychophysics. Vol. 62(5), pp. 1099–1111.

In this and the following figures, the error bar indicates the standard error.

Figure 5 Grand average of the aMAE over all four subjects tested in Experiment 1 as a function of adapting velocity. In the top panel, the magnitude of the aMAE is measured as a perceived stationary mean velocity. In the bottom panel, the aMAE is expressed as a percentage of the adapting velocity, i.e. the gain of the aMAE. Note that although the magnitude of the aMAE increased with increases in adapting velocity, the gain of the aMAE tended to decrease as the adapting velocity increased.

Figure 6 Spatial tuning of the aMAE for three individual subjects and the grand average over all these three subjects tested in Experiment 2. In this experiment, only one adapting velocity (20˚/sec) was used. An arc of 70˚ (±35˚ centered on the midline) at the subject's ear level was divided into 7 equal sub-regions, each 10˚ of arc (-35° ~ -25°, -25° ~ -15°, -15° ~ -5°, -5° ~ 5°, 5° ~ 15°, 15° ~ 25°, 25° ~ 35°). The adapting and test regions were always overlapped, and the magnitude of the aMAE was measured as a function of spatial region. Note that in this experimental condition, within the spatial region tested, the aMAE was largely invariant across positions.

Perception and Psychophysics. Vol. 62(5), pp. 1099–1111.

<u>Figure 7</u> Spatial specificity of the aMAE for three individual subjects and the grand average over all these three subjects tested in Experiment 2. In this experimental condition, the adapting and test stimuli were presented in separate spatial regions. The region swept by the adapting stimulus was a 10° arc (±5° centered on the midline), whereas the test region was chosen from one of six separate regions (-35° ~ -25°, -25° ~ -15°, -15° ~ -5°, 5° ~ 15°, 15° ~ 25°, 25° ~ 35°), indicated by the abscissa. Note that when the distance between adapting and test regions increased, the magnitude of the aMAE decreased.

<u>Figure 8</u> Frequency tuning of the aMAE for three individual subjects and the grand average over all these three subjects tested in Experiment 3. In this experiment, five 1-octave band-pass filtered noise stimuli with different center frequencies (f_c) (i.e. 500 Hz, 1000 Hz, 2000 Hz, 4000 Hz and 8000 Hz) were used as stimuli. The adapting and test stimuli had the same spectrum. The magnitude of the aMAE was analyzed as a function of frequency band. Note that the aMAE was slightly larger for low frequency sound than for high and middle frequency sounds. The middle frequency stimulus was least efficient in inducing

Perception and Psychophysics. Vol. 62(5), pp. 1099–1111.
the aMAE. In this experiment, due to limited time available from each subject, each band-pass noise and each combination of adapting and test stimuli was tested only once.

Figure 9 Frequency specificity of the aMAE for three individual subjects. In the top right, bottom left and bottom right panels, low (L) (f_C: 500 Hz), middle (M) (f_C: 2000 Hz) and high (H) (f_C: 8000 Hz) frequency sounds served as test stimuli respectively. In these three panels, the adapting stimulus was a low (f_C: 500 Hz), middle (f_C: 2000 Hz) or high (f_C: 8000 Hz) frequency sound. Note that the aMAE was largest when the adapting and test stimuli overlapped in frequency, that is, when they were in the combinations of L-L, M-M and H-H, where the first letter indicates the spectral content of the adapting stimulus, and the second of the test stimulus. When the adapting and test stimuli were different in frequency, the magnitude of the aMAE decreased. The farther the difference in frequency, the weaker the aMAE.

The results for all three subjects are summarized in the top left panel, in which the vertical axis indicates the

Perception and Psychophysics. Vol. 62(5), pp. 1099–1111.

spectral content of the adapting stimulus, the horizontal axis shows that of the test stimulus, and the size of the filled circle represents the magnitude of the aMAE averaged over all three subjects tested in nine combinations of adapting and test stimuli. The numbers next to the circles show the magnitude of the aftereffect for each combination of adapting and test stimuli. Note that the size of the circles below the diagonal (lower-left corner to upper-right corner) are larger than those above it, showing that the aMAE for the combinations of L-M, L-H and M-H is stronger than that for those of M-L, H-L and H-M.

Perception and Psychophysics. Vol. 62(5), pp. 1099–1111.

Fig 1

Perception and Psychophysics. Vol. 62(5), pp. 1099–1111.

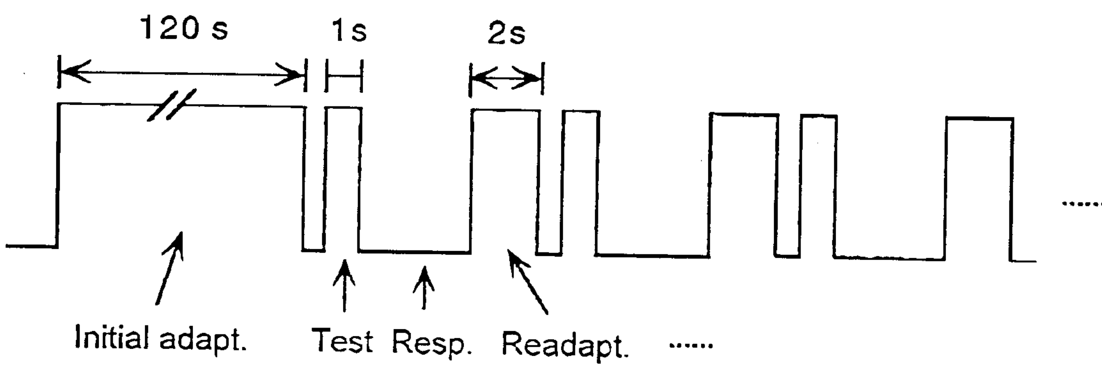

Fig 2.

Perception and Psychophysics. Vol. 62(5), pp. 1099–1111.

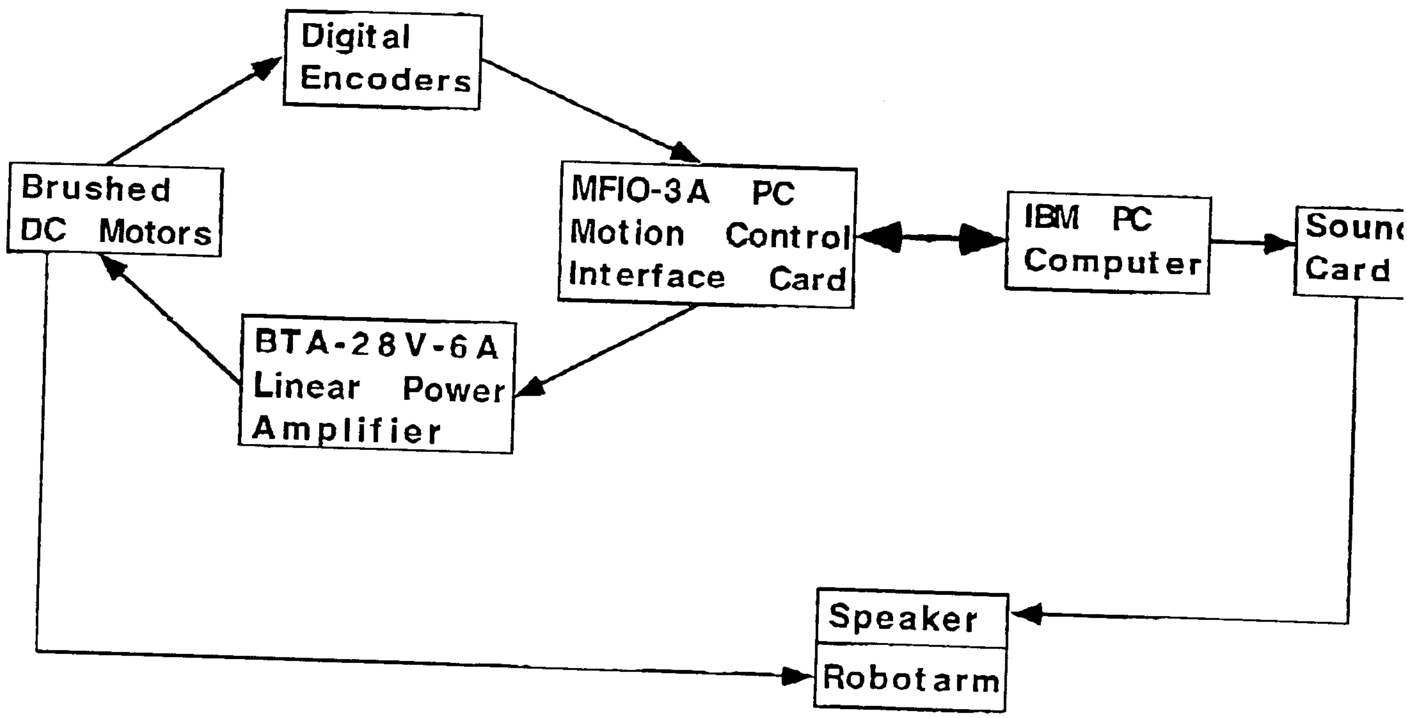

Fig. 3

Perception and Psychophysics. Vol. 62(5), pp. 1099–1111.

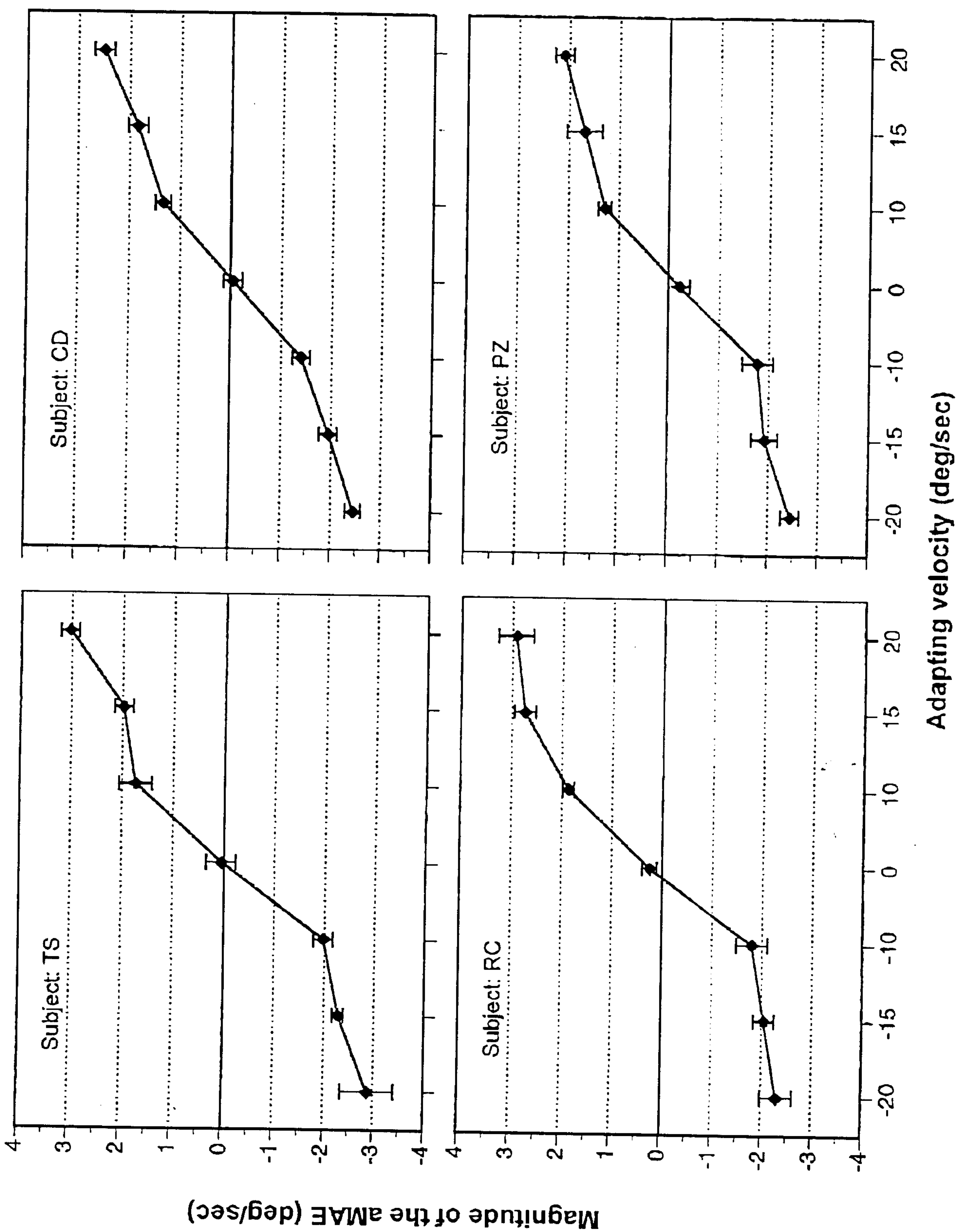

Fig 4.

Perception and Psychophysics. Vol. 62(5), pp. 1099–1111.

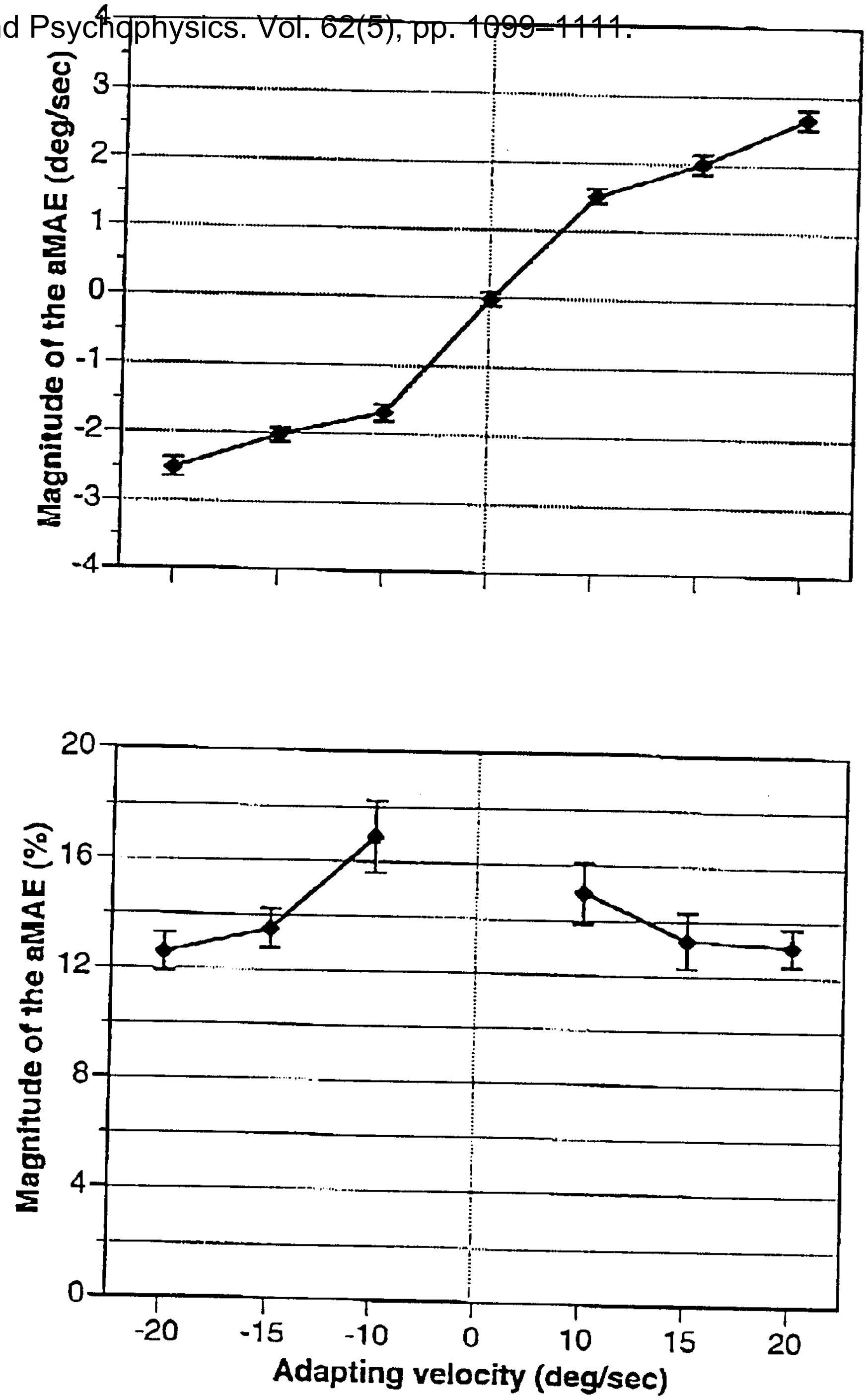

Fig 5

Perception and Psychophysics. Vol. 62(5), pp. 1099–1111.

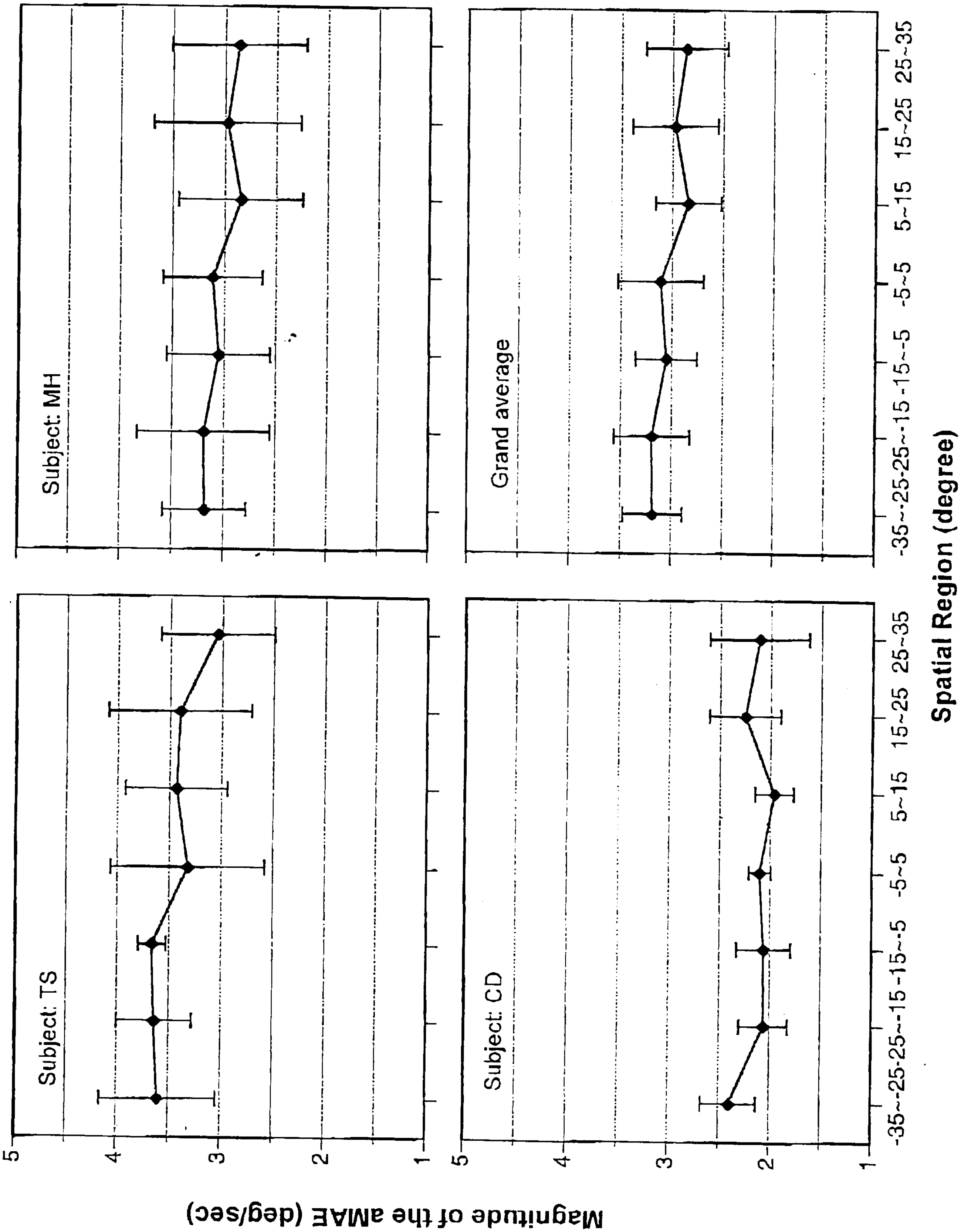

Fig 6

Perception and Psychophysics. Vol. 62(5), pp. 1099–1111.

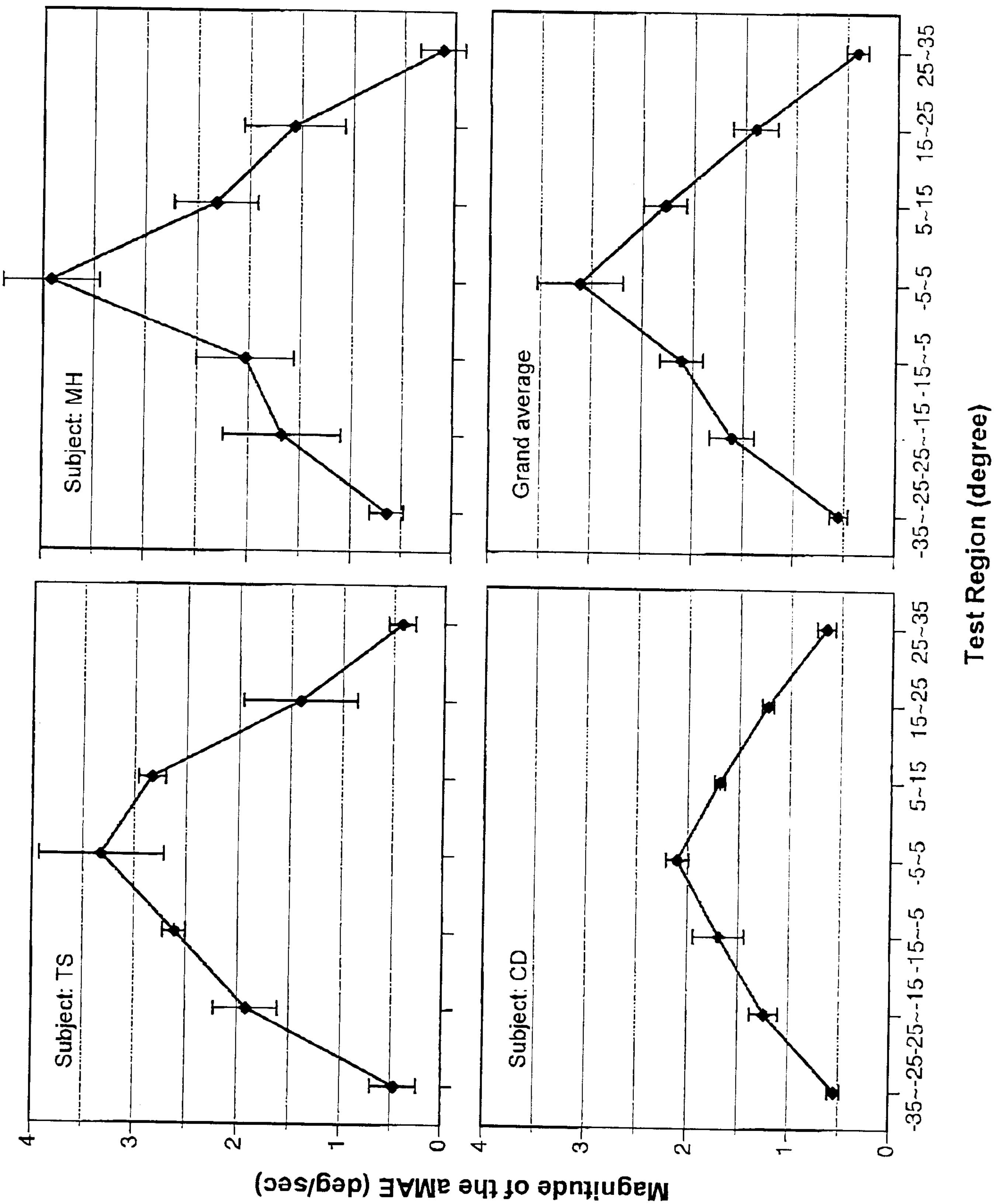

Fig 7.

Fig. 7

Perception and Psychophysics. Vol. 62(5), pp. 1099–1111.

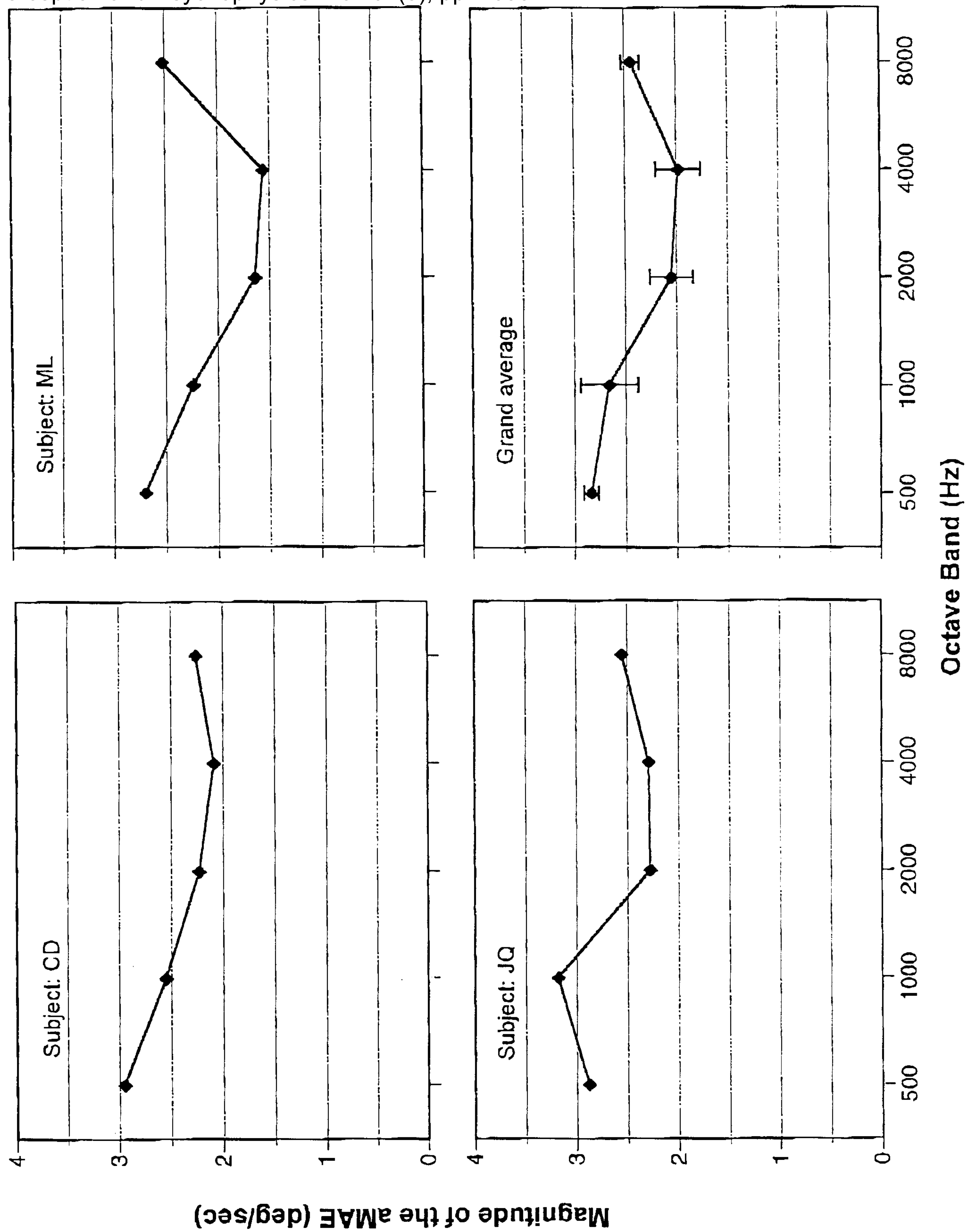

Fig. 8

Fig. 8

Perception and Psychophysics. Vol. 62(5), pp. 1099–1111.

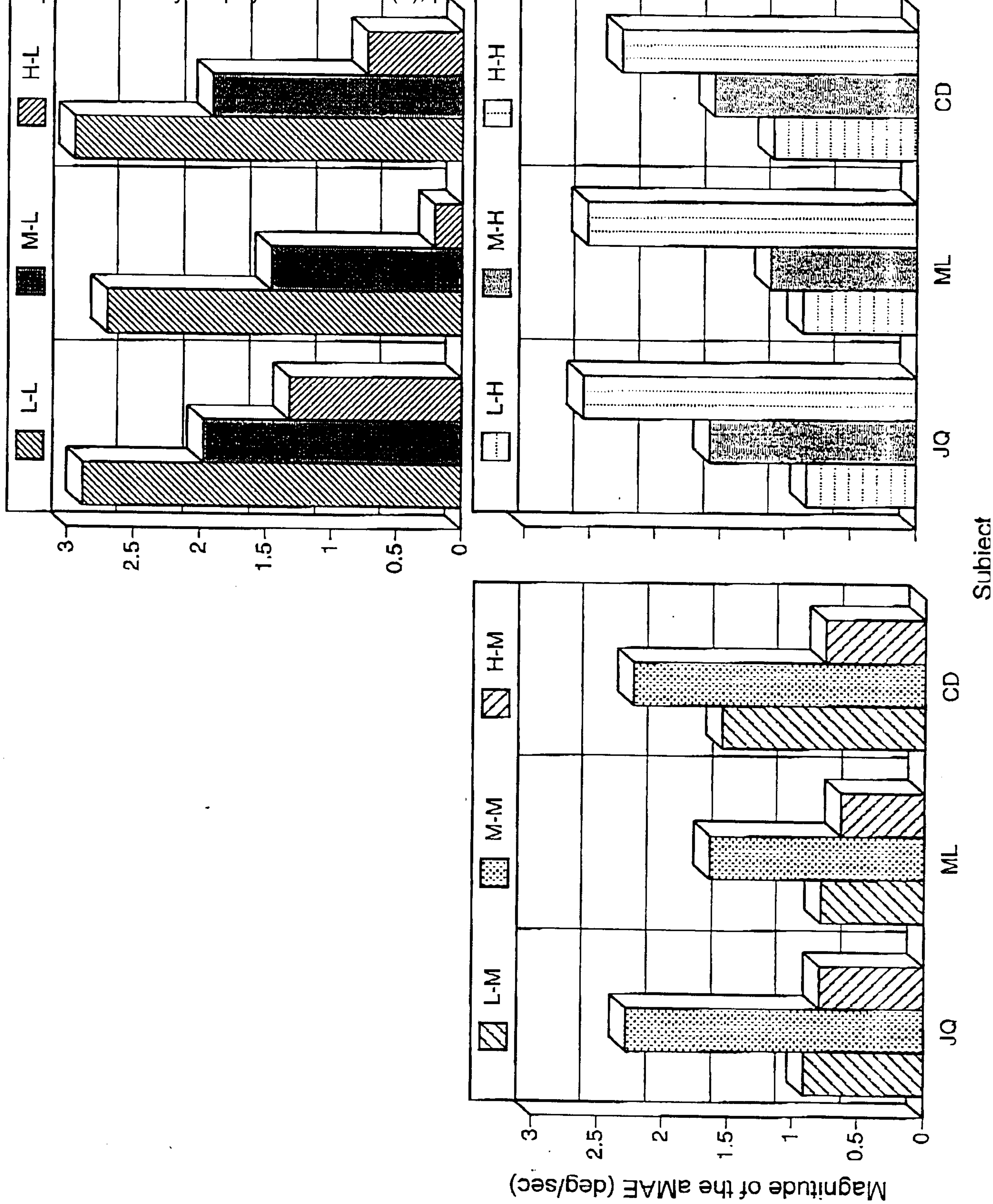

Fig. 9

Fig. 9