Adapting to Remapped Auditory Localization Cues:

A Decision-Theory Model

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ABSTRACT:

This paper describes a model of adaptation to remapped auditory localization cues based on previous decision-theory models of psychophysical performance. The current model extends earlier work by explicitly assuming that past experience affects subject perception and by quantifying how training causes subject responses to evolve over time. The model makes quantitative predictions of total sensitivity, bias, and resolution for subjects involved in experiments investigating spatial auditory adaptation. One assumption of the model is that subjects cannot adapt to nonlinear rearrangements of localization cues, consistent with previous experimental reports in both audition (Shinn-Cunningham, Durlach & Held, 1998b) and vision (Bedford, 1993). The model assumes that in spatial adaptation experiments subjects learn to interpret a continuous internal decision variable differently than normal; they do not learn to associate discrete stimulus/response pairs. This view is consistent with previous analysis of results from experiments investigating adaptation to visual rearrangement as well as the McCullough effect in vision (Bedford, 1993; Bedford, 1995).

There are many studies investigating the effect of altering, or rearranging, sensory localization cues. In vision, most such studies investigate the perceptual effects of viewing the world through prisms that rotate the visual field. In audition, the majority of such studies investigate how mean localization judgements change when the interaural axis is effectively rotated (e.g., see Day & Singer, 1967; Kalil & Freedman, 1967; Mikaelian, 1969; Mikaelian, 1972; Mikaelian, 1974; Recanzone, 1998; Willey, Inglis & Pearce, 1937; Young, 1928). (For a review of auditory adaptation, see Shinn-Cunningham, Lehnert, Kramer, Wenzel & Durlach, 1997; for a review of adaptation studies in general, see Welch, 1978).

In all such studies, naïve subjects mislocalize sources in a direction predicted by the transformation imposed on the sensory stimuli reaching the eyes or ears. If the subject is given appropriate training, however, these localization errors decrease with time. Most studies of sensory rearrangement achieve this training by allowing the subject to interact freely with the environment while observing the transformed sensory stimuli (e.g., by viewing their hand as they reach for a stimulus or by listening to sounds as they walk toward or away from a sound source). To date, models of adaptation to both auditory rearrangements and rearrangements in other modalities have set out to describe qualitatively the changes in response error that occur with training. In general, these models (e.g., see Ebenholtz, 1970; Ebenholtz, 1973; Welch, 1978; Welch & Warren, 1980) do not allow quantitative predictions of changes in response error, nor do they address how resolution might be affected by changes in the adaptive state of the subjects. Instead, these models enumerate the factors that are thought to influence localization errors.

Conversely, signal-detection-theory models for one-dimensional stimulus sets have been used to make quantitative predictions of both resolution and bias for a variety of stimulus types [e.g., intensity perception (Braida & Durlach, 1988; Braida et al., 1984; Durlach & Braida, 1969; Luce, Green & Weber, 1976; Luce, Nosofsky, Green & Smith, 1982), auditory localization (Searle, Braida, Davis & Colburn, 1976), auditory lateralization (Koehnke & Durlach, 1989), and speech perception (Macmillan, 1987; Macmillan, Braida & Goldberg, 1987; Macmillan, Goldberg & Braida, 1988)]. Such models allow quantitative predictions of resolution and/or bias for given

experiments. However, these models generally assume that performance is stable and thus that

resolution and bias have reached asymptotic values. These models do not describe the *changes* in

resolution and bias over time that are seen in typical spatial-rearrangement experiments.

This paper briefly reviews a set of experiments that investigated the effect of auditory

rearrangement on mean localization judgements as well as on response bias and resolution of

source locations. A previous psychophysical model (Durlach & Braida, 1969) is extended in order

to describe the empirical results of these "supernormal" localization studies. The model is then

evaluated by comparing predicted and empirical results.

SUMMARY OF EXPERIMENTS

A number of experiments investigating adaptation to remapped auditory localization cues have

been reported previously (Durlach, Shinn-Cunningham & Held, 1993; Shinn-Cunningham,

Durlach & Held, 1998a; Shinn-Cunningham et al., 1998b). The goal of this work was to

determine if subjects could learn a new correspondence between spatial acoustic cues and reported

azimuthal position that might enhance auditory spatial resolution (see Durlach et al., 1993). To this

end, subjects were trained to identify the azimuthal location of an auditory source whose physical

cues normally correspond to a different source position.

Methods

Subjects were presented with auditory localization cues simulated over headphones using Head

Related Transfer Functions (HRTFs). HRTFs are empirically-determined filters that describe how

to simulate (over headphones) the acoustic cues that would arise from a free-field sound source

located at a specific angular location relative to the listener. In particular, the original source signal

is convolved with a pair of filters (an HRTF filter pair) to generate a binaural signal whose

interaural differences and spectral content are appropriate for the desired source at the simulated

location. HRTF-based simulations are an increasingly common method for controlling spatial

auditory cues in order to investigate the physiological and perceptual bases of spatial auditory

perception (e.g., see Brugge et al., 1994; Wightman & Kistler, 1997). For a more complete

discussion and review of these techniques, see Wenzel (1992) or Carlile (1996).

Normally, to simulate a source at azimuth   and elevation , one simply uses the empirically measured HRTF pair for that position, denoted in the frequency domain by H(, ,), where corresponds to frequency. In our experiments, the correspondence between HRTFs and azimuth position was remapped such that H (, ,), the HRTF pair used to simulate a source at position [,], is given by:

$$ H\left(\ ,\ ,\ \right) = H\left(\ ,f_n(\ ),\ \right), \tag{1} $$

where $f_n(\ )$, the family of mapping functions used to transform azimuth cues, is given by:

$$ f_n(\ ) = \frac{1}{2}\tan^{-1}\frac{2n\sin(2\ )}{1 - n^2 + \left(1 + n^2\right)\cos(2\ )}\ . \tag{2} $$

With this transformation, a source whose position is "supposed" to be at [,   ] is simulated by presenting the cues normally associated with a position of $[f_n(\ ),\ ]$. The parameter n corresponds to the slope of the transformation at   = 0. "Normal" localization cues are presented when n = 1 [i.e., the function $f_1(\ )$ is a straight line of slope one through the origin]. This mapping is shown in Figure 1 for the values of n used in the experiments.

--------------------------------------- insert Figure 1 about here ---------------------------------------

In order to determine whether subjects could adapt to the remapping of HRTF cues, they were repeatedly tested over the course of experimental sessions lasting roughly 2 hours, first using the "normal" mapping (n=1) and then an altered mapping (n>1). At the end of the experimental session, testing with the "normal" mapping was repeated to look for after-effects of the learned remapping. Every subject performed 8 identical 2-hour long sessions over the course of two to three weeks. Data from each run within a session was combined with the data from the same run in

the other sessions to yield a total of 16 judgements of each source location from each subject in each run.

Subjects were seated inside a 5-ft radius arc of 13 light bulbs, spaced every 10 degrees in azimuth from -60 to +60 degrees, which were labeled (left to right) with the numbers 1-13. In each run, a 500-ms long wide-band click train was simulated from each of the possible locations exactly twice, in random order. Subjects were asked to identify the source azimuth corresponding to the simulated source position while facing straight ahead. For the experiments reported here (Experiments F_3, F_{3mid}, F_2, F_{4a}, and F_{4b}), training was achieved by turning on the light at the "correct" or nominal location for 500 ms after each response. Each subject performed 2 "normal-cue" runs (using n = 1), 30 "altered-cue" runs (using n > 1), followed by 8 post-training runs. In all but one experiment, the post-training runs all used normal cues (i.e., using n = 1). In Experiment F_{4b}, the 8 post-training runs consisted of 4 runs in which n = 0.5 followed by 4 "normal-cue" runs.

Results

Previous reports (Shinn-Cunningham et al., 1998a) showed that the amount by which subject responses change during an experimental session depends primarily on the strength of the transformation (i.e., the value of n) and the range/number of source positions presented (Shinn-Cunningham et al., 1998a). Current analysis will focus on the results from experiments that differed only in these parameters. The transformation strengths and the number of source positions used in each experiment are summarized in Table 1. In Experiments F_3, F_2, and F_{4a}, all 13 source positions were presented and the transformation strength was varied (equal to 3, 2, and 4, respectively, as denoted by the subscript). In Experiment F_{3mid}, the transformation strength equaled 3, but only the middle 7 positions were presented (from -30 to +30 degrees). Finally, Experiment F_{4b} was identical to Experiment F_{4a}, except that in the post-training runs, subjects were given both an inverse transformation (n=0.5) and normal cues (n=1.0), as mentioned above. A more detailed explanation of the experimental methods and the rationale behind all of the chosen experimental

conditions is given in Shinn-Cunningham et al. (1998a).

-------------------------------------- insert Table 1 about here --------------------------------------

Various aspects of performance, including bias, resolution, and mean response were estimated separately for each run of the experimental session as subjects learned the remapping. In general, bias (a measure of mean response error in units of standard deviation), decreased as subjects were exposed to the remapped cues, consistent with subjects learning the new mapping of physical cue to source location (Shinn-Cunningham et al., 1998a). However, some bias remained, even after performance had stabilized. In addition, the size of the localization bias was not uniform, but varied with stimulus azimuth. The ability to resolve adjacent response locations changed abruptly when the remapping was introduced, as expected. Resolution improved for stimuli that were physically more distinct with the remapped cues than with the "normal" mapping (sources in the front region, as seen in Figure 1) and decreased for stimuli that were more similar than normal (for n>1, this occurs for sources at the edges of the range). As subjects adapted to the remapped cues, however, their ability to resolve the *same* physical stimuli showed an overall decrease, indicating that subjects confused adjacent stimuli more often following training than prior to training. Response bias and resolution are discussed in greater detail when compared with predictions from the adaptation model (see Figures 5 and 6, respectively).

Analysis and Discussion

Previous analysis of changes in mean response (Shinn-Cunningham et al., 1998b) showed that subjects did not adapt exactly to the transformations shown in Figure 1. Over time, mean responses did change, but these changes were consistent with subjects learning a linear remapping of azimuthal cues instead of the nonlinear remapping that was actually imposed. The observed behavior implies that during run r, the mean perceived position of a source whose nominal location equals   is given by

$$p(\ ,r) = k(r)f_n(\ ) \tag{3}$$

where $k(r)$ is a dimensionless slope that varies with run r and $f_n(\ )$ is the location *normally* associated with the localization cues presented (see Equation 2). For normal cue presentations, $n = 1$ and $f_n(\ ) = \ $. Thus, for normal-cue runs, the mean perceived azimuthal position of a stimulus equals the nominal location ( ) scaled by $k(r)$. For naïve subjects, prior to any training with the rearranged acoustic cues, $k(r)$ was roughly equal to one, as expected. That is, for the initial normal-cue runs at the beginning of each session, $p(\ , r) = \ $: subjects heard sources at the position normally associated with the HRTFs employed and this location was the nominal location. For the altered-cue conditions, the mean perceived azimuth equals $f_n(\ )$ (the azimuth to which the physical stimulus normally corresponds) scaled by the slope $k(r)$. According to equation 3, "complete" adaptation to the transformed cues does not occur, because there is no value of $k(r)$ for which $p(\ , r)$ equals $\ $ for all possible locations unless n equals one.

Equation 3 implies that changes in perceived location depend only on changes in $k(r)$, the slope relating mean perceived location and the normal azimuthal locations of the stimuli. The effect of the exposure to the altered cues is to change the slope $k(r)$. When a transformation was first introduced (i.e., n was changed from 1 to a value $n > 1$), the subjects interpreted the new set of physical cues as they normally would (i.e., slope, k, near unity), resulting in mean errors in their location judgements. As subjects were trained, $k(r)$ decreased gradually, causing the average size of the judgement errors to decrease. However, since the nominal responses are not linearly related to the "normal" locations corresponding to the physical cues presented, systematic response errors persisted.

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This is shown schematically in Figure 2, which plots the perceived position as a function of $f_n(\ )$, the location normally associated with the physical stimulus presented. The open circles in the figure represent the ideal mapping of physical cue to position during normal-cue runs. The open

squares show the ideal mapping for runs when n = 3. Note that in both cases, there are 13 points

plotted, corresponding to the 13 available responses (-60, -50, … 60) along the y dimension.

However, the normal-cue locations at which these values are plotted along the x-dimension are

different for normal and altered cues, since the physical stimuli presented depend upon the imposed

transformation. Prior to adaptation, subjects interpret normal cues correctly with a slope k = 1 (the

dashed line connecting the open circles). When the physical stimuli are transformed, the physical

stimuli span a range normally associated with locations from roughly –80 to +80 deg. In addition,

the nominal responses are no longer linearly related to the locations normally associated with the

physical stimuli presented. When the transformation is first imposed, subjects interpret the stimuli

in the "normal" way (i.e., k is approximately equal to 1) and therefore make large localization

errors. As subjects adapt, the slope of the mapping between stimulus and perceived position

decreases to approximate the nonlinear transformation. Averaged across all source positions, the

mean response error is reduced when the slope decreases, although systematic errors remain as a

function of position. When the normal cues are reinstated at the end of the experiment, k(r)

increases back toward k = 1.

The observed changes in slope k(r) were roughly exponential, from an initial value towards an

asymptotic value denoted by T. Mathematically, if the transformation changed in run r_c, k(r) is

given by

$$k(r) = T + \left[k(r_c - 1) - T \right] e^{-b(r-r_c)} \tag{4}$$

for r $\geq$ r_c (and up until the next change in cue transformations), where b is a parameter (in units of

run^{-1}) governing the rate of change in k(r) and $k(r_c - 1)$ is the slope value prior to the change in the

auditory cues. The rate of change in k(r) was roughly independent of how the cue transformation

changed; all data were fit well using b = 0.84 run^{-1} (Shinn-Cunningham et al., 1998b).

The adaptation rate, b, was independent of the change in transformation; however, T, the

asymptotic value of k(r), varied with n (the strength of the transformation) as well as the range of

positions presented in each experiment. In particular, it was shown that for all experiments, T was

roughly equal to k_A, the value of k(r) that minimizes the mean-squared difference between $k(r)f_n(\ )$

and , the nominal position of the source. (The solid line in Figure 2 shows the best-fit line for the

example with k_A equal to 0.61.) For runs in which the cues are nonlinearly transformed, the mean

response errors (across the stimuli presented) decrease to the minimum achievable given the linear

constraint of Equation 3.

Adaptation to the nonlinear transformation is summarized by an exponential change in the slope

k(r). The slope exponentially approaches the best *linear* approximation of the transformation

presented to the subjects. The value of the slope k(r) summarizes the adaptive state of the subject

during the course of the experiment. This finding implies that there are limits on the types of

auditory spatial cue transformations that subjects can accommodate, and that subjects may not be

able to adapt to nonlinear transformations of localization cues. This type of constraint is similar to

constraints that have been observed in visual spatial rearrangement experiments (Bedford, 1993;

Bedford, 1995).

THE PRELIMINARY MODEL OF AUDITORY ADAPTATION

The preliminary model of adaptation to remapped auditory localization cues is based on the

preliminary model of intensity perception by Durlach, Braida, and associates (Braida & Durlach,

1972; Braida & Durlach, 1988; Durlach & Braida, 1969). This model focused primarily on

predicting resolution results for various experimental paradigms measuring intensity perception.

However, the underlying assumptions of the model are easily applied to experiments investigating

resolution in other stimulus dimensions, including stimulus location.

The Preliminary Model of Intensity Perception

In the preliminary model of intensity perception (described fully in Durlach & Braida, 1969)

every stimulus I gives rise to an internal sensation Y which is a Gaussian random variable with

mean (I) and variance ^{2}. This sensation is then further transformed into a decision variable

along an internal axis to produce a Gaussian random variable Q which has mean (I) and variance

$\sigma^2 + \sigma^2$. In this model, internal noise arises from two independent sources. *Sensation noise* (with variance σ^2) depends only upon the stimulus presented and, therefore, causes a fixed limit on the best performance that can be achieved in any experiment. *Memory noise* (with variance σ^2) affects the transformation from the sensation Y to the internal representation of the decision variable Q and depends upon the type of experiment. For single-interval experiments like those in the current study, memory noise is assumed to be proportional to the total range of stimuli presented in the experiment and is termed "context-coding" noise. Thus, $\sigma^2 = G^2 R^2$ where G is a constant, $R = \phi(I_{max}) - \phi(I_{min})$, and I_{max} and I_{min} are equal to the extreme values of the stimuli used in the experiment. The addition of context-coding noise allows the model to account for the fact that subjects may confuse two stimuli in large-range tasks (such as identification tasks) even when the same stimuli are perfectly resolvable in tasks where the range is small (such as in JND-type tasks).

The preliminary intensity perception model further assumes that subject responses are based on the value of the decision variable Q using a Thurstonian decision model. With these assumptions, the decision axis along which Q falls is assumed to be divided into n contiguous regions by n+1 criteria $\{C_j\}$ (with $C_0 = -\infty$ and $C_{n+1} = \infty$). Each region corresponds to one of the n possible responses for the experiment being performed. In a single interval task, the means of the underlying probability distributions $P(Q|I_i)$ depend only upon the stimulus presented (I_i), and the variance (which is constant, independent of the stimulus value) depends only on the range of stimuli used in the experiment. The underlying discriminability between two stimuli I_i and I_j in a one-interval experiment can then be written as

$$d'_R\left(I_i, I_j\right) = \frac{\phi\left(I_i\right) - \phi\left(I_j\right)}{\sqrt{\sigma^2 + G^2\left[\phi\left(I_{max(R)}\right) - \phi\left(I_{min(R)}\right)\right]^2}}, \tag{5}$$

where R is the range of stimuli used in the experiment, σ and G are constants, $I_{max(R)}$ and $I_{min(R)}$ are the maximum and minimum stimulus intensities in the range R, and $\phi(\bullet)$ is a monotonic

transformation which relates the physical stimulus values to values along an internal decision axis. It can be seen from Equation 5 that the ability to resolve two stimuli depends only on the range of stimuli used in the experiment, and the stimulus values.

An Internal Representation of Azimuth

Many of the ideas used in developing the preliminary model of intensity perception have been used to model perception of other stimulus dimensions, including speech (Macmillan, 1987; Macmillan et al., 1987; Macmillan et al., 1988), auditory localization (Searle et al., 1976) and auditory lateralization (Koehnke & Durlach, 1989). However, no previous work quantified how auditory localization resolution depends upon absolute position. In the preliminary model of intensity perception, relative sensitivity is taken into account by the mapping function (•), which is responsible for converting values from the stimulus space to a dimension in which distance is directly proportional to discriminability between stimuli. For the current model, the function ( ) was roughly fit using data from an early free-field study Mills (1958, pp. 37-50) of the minimum audible angle (MAA). Details in the methodology for fitting ( ) are given in Shinn-Cunningham (1994). The resulting function is given by

$$( ) = \text{sign}( )\left(1 - e^{-a| |}\right) \qquad (6)$$

where a = 0.02 degrees^{-1}. The form of this function reflects the fact that the MAA is small around a reference position of 0 degrees azimuth and grows rapidly for reference locations to either side of the listener. As a result of this mapping, when a pair of stimuli at and + deg are mapped to a pair of probabilistic distributions of the internal decision variable, the distance between the means of the distributions decreases as the magnitude of grows. Since the model assumes that the standard deviation of the noise in the internal decision variable is independent of the stimulus value, the model predicts that sources to the side are less easily resolved than are sources near zero azimuth.

Extending the Model to Adaptation Paradigms

In order to account for changes in performance that occur in adaptation paradigms, the preliminary intensity perception model of Durlach and Braida is extended in two important ways:

  1) The effective range R depends both on the stimuli being presented at a given point in time and the past experience of the subject. R is no longer determined exclusively by the stimuli used in an experiment.

  2) The criteria {C_j} are not assumed to be optimally positioned for the given stimuli; their placement depends on the past experience of the subject.

Intuitively, it is unlikely that subjects immediately change their behavior when the physical stimuli change abruptly. Therefore, when the stimulus range changes in the adaptation experiment, it is unlikely that the memory noise in the underlying decision space will be determined by the range of the physical cues being presented immediately after the change. Instead, the model predicts that the range of cues that the subject *expects* to hear determines the internal decision noise. Just after a change in stimulus range, the *expected* or *effective* range should roughly equal the range of cues presented in the previous run (assuming performance was stable prior to the change in cues). Over time, the effective range should approach the actual range of cues being presented. Similarly, the model assumes that just after the remapping is introduced, subjects make their response decisions based on the positions of the decision-axis criteria *prior* to the change. Over time, the criteria shift to new positions, more appropriate for the current stimulus-response mapping. The adaptation model assumes that both of these gradual changes (in the effective range and in the placement of the decision criteria) are governed by changes in an internal mapping maintained by the subject. This internal representation describes how physical stimuli are related to the available range of responses at a given point in time.

The model assumes that the slope k(r), which relates the normal-cue position of a physical stimulus to the mean subject response, summarizes the state of the posited internal map throughout the experiment. During the adaptation experiments, a subject knows that the range of possible

responses is restricted, usually from -60 to +60 degrees. During a given run r, however, the

subject maps that same range of responses to a different range of physical cues, as described by

Equation 3. Thus, in run r, the minimum physical cue that the subject expects is equal to $\frac{\theta_{min}}{k(r)}$ and

the maximum physical cue he expects equals $\frac{\theta_{max}}{k(r)}$ (where θ_{min} and θ_{max} are the azimuthal angles of

the minimum and maximum allowed responses, respectively). These physical cue values

correspond to values along the internal decision axis of $\frac{\mu_{min}}{k(r)}$ and $\frac{\mu_{max}}{k(r)}$, respectively.

Thus, in run r, the model assumes that R_{eff}, the effective stimulus range in run r, is given by

$$R_{eff} = \frac{\mu_{max}}{k(r)} - \frac{\mu_{min}}{k(r)} . \qquad (7)$$

Similarly, the subject *expects* to hear a set of physical stimuli that are different from the actual

stimulus values presented. In particular, from equation 3, the subject expects the stimulus θ_j to

map to physical stimulus $\frac{\theta_j}{k(r)}$. Thus, in the underlying decision space, the subject expects the

mean value of the stimulus whose nominal response is θ_j to equal $\frac{\mu_j}{k(r)}$. However, the

stimulus whose nominal location is θ_j is the same physical stimulus whose "normal" location is

$f_n(\theta_j)$. Thus, in the underlying decision space, the actual stimulus has a mean value of $\left(f_n\left(\theta_j\right)\right)$.

If the subject tries to place decision criteria ideally, he will place them midway between the

expected mean locations, not midway between the mean locations of the values actually presented.

The model predicts that, in run r, the decision-axis criterion C_j will equal

$$C_j(r) = \frac{1}{2}\left[\frac{\mu_j}{k(r)} + \frac{\mu_{j+1}}{k(r)}\right], \qquad (8)$$

while the optimal placement (independent of run) is given by

$$C_j{}^{opt} = \frac{1}{2}\left[\left(f_n\left(\theta_j\right)\right) + \left(f_n\left(\theta_{j+1}\right)\right)\right].$$ (9)

-------------------------------------- insert Figure 3 about here --------------------------------------

Figure 3 illustrates how the internal decision variable and the criteria change in the model for an experiment similar to Experiment F_{3mid} (in which seven stimuli, ranging from $\theta=-30$ deg to $\theta=30$ deg, were presented). In the figure, panel a) shows the distributions of the internal decision variable that would arise for the seven normal-cue stimuli presented to a naive subject. In this condition, there is no discrepancy between the stimulus values expected by the subject and the values presented, so the subject places his criteria (the dashed vertical lines) at optimal locations along the decision axis. The variance in the distributions is determined by the internal decision noise that in turn depends on the effective range. For this condition, there is no discrepancy between the effective range and the actual range of the stimuli presented. The second panel shows what occurs when the transformed cues are first introduced: criteria are located at their optimal locations for normal cues, not for the transformed cues. In addition, the internal sensation noise is determined by the range spanned by the normal-cue stimuli, not by the actual range of stimuli now being presented. Panel c shows the effects of adaptation. Criteria are shifted in the correct direction, but are not positioned optimally, since subjects adapt to a linear approximation of the transformation employed in the experiments. In addition, memory noise grows, reflecting the fact the effective range grows as subjects learn to expect a larger range of stimuli. Finally, panel d) shows what occurs for normal cue stimuli following training. The decision criteria are at their adapted locations, causing bias in the direction opposite that initially introduced with the cue transformation. Similarly, memory noise is determined by the range expected with transformed cues, and is thus larger than in the pre-training, normal-cue condition.

MODEL PREDICTIONS

Total Cumulative Sensitivity

There are two free parameters in the model: , the standard deviation of the sensation noise;

and $\dfrac{G}{}$, the relative importance of the context coding noise compared to the sensation noise.

Model parameters were estimated by examining the total cumulative sensitivity '. Total

cumulative sensitivity measures the total distance along the internal decision axis between the mean

values of the minimum and maximum stimuli used in an experiment, measured in units of the

standard deviation in the decision variable.[1] Thus,   ' is given by:

$$' = \frac{\left[f_n\left(\ _{max}\right)\right] - \left[f_n\left(\ _{min}\right)\right]}{\sqrt{\ ^2 + G^2 R(r)^2}} = \frac{\left[f_n\left(\ _{max}\right)\right] - \left[f_n\left(\ _{min}\right)\right]}{\sqrt{\ ^2 + G^2 \left(\ \frac{_{max}}{k(r)} - \ \frac{_{min}}{k(r)}\right)^2}}. \tag{10}$$

For each subject, the values of   and $\dfrac{G}{}$ that minimized the mean square difference between

predicted values of ' and the individual data were estimated. These values were averaged across

subjects. The resulting values are   = 0.06 and $\dfrac{G}{}$ = 1.43 (nearly identical results were found

using a minimum mean-square error criteria in log ' space). It should be noted that for the

experiments considered here, the model is not extremely sensitive to the exact values of   and $\dfrac{G}{}$.

In particular, for the experiments considered (in which $_{max} = -\ _{min}$ and $\ ^2 << 4G^2 \ ^2 \ \dfrac{_{max}}{k(r)}$),

Equation 10 can be approximated by:

$$', \quad \frac{\left[f_n(\beta_{max})\right]}{\dfrac{G}{k(r)}\,\beta_{max}}. \tag{11}$$

Thus, as long as the product of the estimated parameters and $\dfrac{G}{}$ is constant, predictions are

roughly comparable for the identification experiments considered. This product varied from subject

to subject, consistent with the idea that different subjects have different overall levels of

performance (i.e., different levels of internal noise). Despite the fact that there are differences

across subjects (and that different subjects performed each experiment), only the average parameter

values are used for all subsequent model predictions. This choice was made in part because all data

to which the predictions will be compared are across-subject averages and in part because it

reduces the number of free parameters in the model. Thus, the model predictions presented in this

paper represent the performance expected of a "typical" subject rather than of the subjects who

performed any specific experiment.

-------------------------------------- insert Figure 4 about here --------------------------------------

Figure 4 plots predictions of total cumulative sensitivity (using Equation 9 and the best-fit

values of and $\dfrac{G}{}$) and the empirically determined total cumulative sensitivity as a function of

run. In each panel, the filled circles show the predicted values of '(r) for the corresponding

experiment. Also plotted is the mean value of the empirical estimates of ' averaged across

subjects, plus or minus one standard deviation.

As stated above, intersubject differences in the magnitude of ' are large within each

experiment (a difference for which the model could account by allowing the internal noise to vary

from subject to subject). This intersubject variability accounts at least in part for discrepancies

between the estimated and actual magnitude of ' in the different experiments (e.g., results for

Experiments F_{4a} and F_{4b}, which present identical stimuli for runs 1-32, show large differences in mean values of ' for these same runs). Overall, the observed level of performance is better than predicted in Experiment F_3, worse in Experiment F_{4a}, and in good agreement for the remaining three experiments.

Even more important than the overall magnitude of the predictions are the details of how ' changes with run. In all cases, whenever the localization cues change there are two effects: an immediate effect on the actual range of stimuli being discriminated (numerator in Equation 10) and a gradual growth of the effective stimulus range (and in the internal noise in the model; i.e., the denominator in Equation 10). In the current experiments, when the cue transformation is first introduced (e.g., in run 3 for all experiments), the physical cue range increases slightly, causing an immediate increase in predictions of '. These predicted changes are not obvious in the empirical data; however, the predicted changes are small relative to the variability in the underlying data. As subjects adapt, the internal memory noise increases and there is a concomitant decrease in predictions of ' until performance stabilizes and reaches a steady-state value.

Steady-state predictions of ' are approximately equal across all the experiments. This result is easily understood by examining the numerator and denominator in Equation 11. For the reported experiments (in which internal noise is dominated by context coding noise), ' is roughly proportional to the ratio of the actual stimulus range divided by the expected range. While the expected range varies with k(r), its steady-state value (when k(r) has approached its asymptote) is roughly equal to the actual range. Thus, for all experiments reported here, G^{-1} in the steady-state.

When the cue transformation changes at the end of the session, predicted values of ' change again. In particular, in all experiments, the actual range of stimuli (numerator in Equation 10)

decreases abruptly between runs 32 and 33. At the same time, the internal noise (denominator in Equation 10) begins to decrease towards its asymptotic value when the cue transformation changes. In most experiments, there is little discernable change in the empirical values of σ' between runs 32 and 33. However, in two experiments, empirical values of σ' showed a significant change between runs 32 and 33: in Experiment F_{3mid}, σ' was significantly lower for normal-cue runs ($n = 1$) following adaptation to transformed cues ($n = 3$); and in Experiment F_{4b}, σ' was significantly smaller for the runs in which $n = 0.5$ following training with $n = 4$. The model predicts similar changes for both experiments. In the model, these decreases arise because the range of physical cues presented to the subject decreases drastically with the change in cue transformation. At the same time, the starting value of the effective range is relatively large immediately after the change in cues (i.e., the denominator in Equation 10 is initially large). The model predicts qualitatively similar effects for Experiments F_3, F_2, and F_{4a}. However, for these experiments the percentage change in range is much smaller and the predicted effect is small compared to the intrasubject variability (i.e., compared to the random, nonsystematic variations in estimates of σ' for each subject as a function of run). In Experiments F_{3mid} and F_{4b}, the magnitude of the predicted decrease in σ' at run 33 was slightly smaller than seen in the actual data; however, in both cases the fit was relatively good.

Finally, in Experiment F_{4b}, the model predicts an abrupt increase in σ' in run 37 compared to run 36. This prediction arises because the range of stimuli increases between these runs, causing an immediate increase in the numerator and a slow decrease in the denominator in Equation 10. The empirical results also show an immediate increase in σ' in run 37; however, the increase is larger than predicted by the model.

Response Bias

The bias, β_j, is one of the performance metrics investigated in a previous paper (Shinn-Cunningham et al., 1998a).[2] β_j is equal to the difference between the optimal and actual placement of the jth decision criteria. Bias is related to absolute localization accuracy; when criteria are placed optimally, the probability of responding correctly on a given trial is maximized (if all stimuli are equally likely) and any response error is due to internal noise in the decision variable. Thus, from Equations 8 and 9, bias in the placement of the jth criterion is given by

$$B_j(r) = \frac{C_j^{opt} - C_j(r)}{\sqrt{\sigma^2 + G^2 R(r)^2}}$$

$$= \frac{\frac{1}{2}\left[\left[f_n(\theta_j)\right] + \left[f_n(\theta_{j+1})\right]\right] - \frac{1}{2}\left[\frac{\theta_j}{k(r)} + \frac{\theta_{j+1}}{k(r)}\right]}{\sqrt{\sigma^2 + G^2\left[\frac{\theta_{max}}{k(r)} - \frac{\theta_{min}}{k(r)}\right]^2}},$$ (12)

where θ_j is the nominal source position for the jth stimulus.

--------------------------------------- insert Figure 5 about here ---------------------------------------

Empirical results and model predictions of bias are shown in Figure 5: the left half of each panel shows empirical estimates of bias for sources to the left of center and the right half of each panel shows the model predictions for sources to the right of center. The model parameters used in this figure (and in resolution predictions, shown in Figure 6) are identical to the values chosen to fit δ' in Figure 4. The experimental bias was first estimated individually for each subject.[3] These values were then normalized by subtracting the average bias in the first normal-cue run to remove any bias effects not due to training. The normalized estimates of bias were then averaged across all subjects and then further collapsed by assuming left-right symmetry to yield the data plotted in Figure 5.

Focusing first on the experimental results, we see that, because of the normalization performed, initial bias with normal cues is identically equal to zero for all positions. Without this normalization, some initial bias was seen for many subjects; however, the magnitude of this initial bias was small relative to the bias seen in all other runs. When transformed cues are first introduced a large bias results in the direction expected on the basis of the transformation (i.e., subjects tend to place the criteria too close to the zero-azimuth stimulus location).[4] The bias is reduced with exposure to the altered cues to roughly 50% of the initial bias observed. When returning to normal cues, there is a negative aftereffect in the direction opposite the initial bias. The magnitude of the initial bias and negative aftereffect appear to be directly related to the strength of the transformation, with greater initial bias and aftereffect for more extreme transformations. In Experiment F_{4b}, the bias for the initial run with the transformation $n = 0.5$ resulted in a larger reverse bias than was seen using normal cues ($n = 1$), as expected. By the final run with these cues, the effect diminished. The effect of this training on the bias in run 37 (using normal cues) was to decrease the negative aftereffect seen when returning to normal-cues following exposure to the "opposite" transformation $n = 0.5$.

Predictions for all experiments are in good agreement with the data (to the extent that the panels are symmetric about the line $y = -x$, the data and model predictions are equal). A large bias is evident with the first altered cue run which decreases by the end of the training. A negative aftereffect occurs when first tested with normal cues after the altered-cue exposure. In the experimental data, the size of the bias and negative aftereffect varies with the transformation strength. The predictions capture not only the general trends in the bias results, but also show the same dependence of the magnitude of the induced bias with changes in cue transformation.

While the agreement between the predicted and actual bias results is quite good, there are a few discrepancies worth pointing out. The actual data show artifacts of the response method (whereby bias tends to be positive for the leftmost position and negative for the rightmost position) that is less evident in the model predictions. In addition, the size of the predicted negative aftereffect is generally larger than the negative aftereffect in the empirical data. This discrepancy may be due to a

tendency to "readapt" to normal cues more quickly than it takes to adapt to the altered cues. On the whole, data from all five experiments are fit well by the model.

Resolution

The metric $d'_j = d'(_{j+1},\ _j)$ is the resolution with which stimulus j+1 and j can be discriminated. The model predicts that d'_j is given by

$$
d'_j(r) = \frac{\left[f_n(_{j+1})\right] - \left[f_n(_j)\right]}{\sqrt{^2 + G^2 \left(\frac{max}{k(r)} - \frac{min}{k(r)}\right)^2}} \,.
\tag{13}
$$

-------------------------------------- insert Figure 6 about here --------------------------------------

Figure 6 plots experimental and predicted values of d'_j for various runs in the experiments. Again, focusing first on the experimental results, the first test with altered cues yields a large increase in resolution for sources in front of the listener compared to the first test with normal cues.

However, in all the experimental results, d'_j showed a tendency to decrease as the subjects adapted to the altered cues. A similar decrease is seen in the final (post-training) test with normal cues compared to the initial resolution test with normal cues. In Experiment F_{4b}, dramatically decreasing the range of stimuli in run 33 resulted in a large decrease in resolution. There was little effect of this exposure on resolution in run 37 (using normal cues).

The overall magnitudes of the actual and predicted results are reasonably close for all five experiments. In the predictions, a similar decrease in resolution is seen with training, but the decrease tends to be smaller than that shown in the experimental results. The decrease in the predictions arises because the effective range increases as subjects adapt, causing an increase in memory noise with training. As in the actual results, the predicted decrease is largest in Experiment F_{3mid}. This occurs in the predicted results for two reasons: 1) a smaller range was used in Experiment F_{3mid} than in the other experiments, so that the percentage increase in the effective range

is largest when changing from altered to normal cues, and 2) the absolute increase in the range with

transformed cues is larger for positions closer to the center of the range [both because of the

transformation employed and because of the shape of   ( )].

DISCUSSION

Other unidimensional decision models

   The preliminary model of adaptation is based on the preliminary model of intensity perception

of Durlach and Braida (e.g., see Durlach & Braida, 1969); however, this is not the only

quantitative model of perception of unidimensional stimulus sets. Two other prominent, alternative

psychophysical models of resolution are considered here (for a short note reviewing these and

other unidimensional stimulus models, see Shiffrin & Nosofsky, 1994).

   Luce and his colleagues (Green, Luce & Duncan, 1977; Luce et al., 1976) suggested that

intensity resolution changes with stimulus range as a result of shifts in a fixed-width "attention

band." The posited "attention band" was assumed to cover a limited range of intensities at any

moment. Stimuli with values falling inside the attention band were expected to be resolved more

easily than stimuli outside the attention band. The recent history of stimuli presented to a subject

determined the location of the attention band at any point in time. The attention-band model predicts

that resolution in small-range intensity experiments is, on average, better than resolution in larger-

range tasks because a stimulus is more likely to fall inside the attention band. Further, the model

predicts that there should be observable sequential effects in resolution, whereby resolution is

enhanced when two subsequent stimuli are similar in value (Luce et al., 1982).

   A number of investigators have shown that, in a large range experiment, the value of a

preceding stimulus significantly reduces the variability in response to a subsequent stimulus when

the two are close in value (Green et al., 1977; Luce et al., 1982; Purks, Callahan, Braida &

Durlach, 1980; Ward & Lockhead, 1970). However, analysis suggests this effect is caused by a

shift in response criteria (in a Durlach/Braida style decision-theory model) rather than a change in

underlying sensitivity (as predicted by the attention-band model; e.g., see Luce et al., 1982; Purks

et al., 1980).

Other experiments demonstrate that with an appropriate experimental design (for instance, if the stimulus order is controlled so that subsequent presentations are always close in value), underlying sensitivity does improve (Luce et al., 1982; Nosofsky, 1983). Both the attention-band model and the preliminary adaptation model predict that recent history affects resolution. The attention-band model predicts these effects because past history affects the location of the fixed-width attention band. In contrast, the current model posits that the range of stimuli across which subject attention is allocated evolves over the course of tens of trials. In effect, by assuming that the *expected range* of stimuli determines memory noise, the adaptation model combines elements of the attention-band model with the basic structure of the preliminary model of intensity perception.

Braida and Durlach refined the preliminary model of intensity perception to account for systematic changes in relative intensity resolution with stimulus range. The preliminary model of intensity perception predicts that sensitivity is uniformly scaled up or down with changes in range. However, careful examination of the shape of the cumulative sensitivity functions observed in experiments using different ranges of stimulus intensity reveals that stimulus sensitivity is relatively better at the edges of the range than in the middle of the range (Berliner, Durlach & Braida, 1977; Luce et al., 1982). Durlach and Braida developed the *anchor model* of intensity perception to account for this discrepancy (Braida & Durlach, 1988; Braida et al., 1984). The anchor model assumes that resolution is influenced by the location of *perceptual anchors* located at the edges of the range of the set of physical stimuli. Judgements of intensity are made by judging the distance between an observed internal decision variable and these internally-maintained anchors. Distance judgements for values relatively close to the anchors are more accurate, leading to improved sensitivity for stimuli near the anchors.

Analysis of the cumulative sensitivity function in the current experiments did not reveal any systematic changes in relative sensitivity as a function of the stimulus range (Shinn-Cunningham, 1994). In particular, results from all experiments were consistent with the assumptions of the preliminary model of intensity perception. Thus, the simpler, preliminary model was used as the

basis for the current adaptation model. Although results in the current experiments suggest that the range of stimuli used in an experiment does not affect relative sensitivity, this does not necessarily imply that there are not internal anchors or reference positions that are important in auditory spatial perception. One alternative is that spatial perception is qualitatively different from perception of other stimulus dimensions, and that any perceptual anchors occur at fixed values, independent of the stimulus range. In particular, since it is important in everyday life to make absolute, egocentric judgements of source location, it is conceivable that subjects constantly maintain a set of fixed anchor locations (such as "straight ahead" or "directly to the left" of the head). If spatial resolution is governed by comparisons with such fixed anchors, the observed shape of the cumulative sensitivity function should show little, if any, dependence on the stimulus range. In other words, the current results do not negate the possibility that perceptual anchors are at play in the current experiments. Instead, they suggest that the locations of any *spatial* perceptual anchors are constant, independent of the experimental paradigm.

What changes during spatial adaptation?

Even though subjects are trained to associate a finite set of stimulus/response pairs, the model assumes that subjects do not learn the specific associations used during training. Instead, the model assumes that training causes subjects to alter an internal map relating physical acoustic cues to sound source location. This internal map is constrained: only linear relationships between stimuli/responses are learned. This assumption is consistent with the ideas of "dimension learning" (e.g., see Bedford, 1993) and "function learning" (e.g., see Koh & Meyer, 1991).

In contrast to most rearrangement studies, the work of Bedford (e.g., Bedford, 1993) examined whether subjects can adapt to complex, nonmonotonic remappings. Her results imply that subjects adapt to complex remappings by fitting a roughly linear function to all of the stimulus/response pairs presented. Mean localization errors persist when the stimulus/response pairs used to train the subjects do not obey a linear relationship. Bedford demonstrated that training with even a single stimulus location causes subjects to alter their localization responses to sources

from many different locations (Bedford, 1993). She interpreted her results as indicating that localization-rearrangement experiments cause subjects to alter entire stimulus/response dimensions, rather than learning explicit stimulus/response pairs.

Koh and Meyer (1991) trained subjects to associate pairings of line length (the stimuli) and event duration (the response). Various mathematical relationships governing the trained stimulus/response pairs were tested. The results of the study imply that the easiest mapping to learn is a linear function in log-length log-duration coordinates. Since duration and length perception both obey Weber's Law for the visual stimuli used in the experiment, Koh and Meyer concluded that subjects learn most rapidly when presented with stimulus/response functions that are linear in the underlying perceptual dimensions.

The current model and the work by Bedford also imply that linear stimulus/response relationships are most readily learned; however, both of these studies imply that the stimulus/response mapping is linear in spatial dimensions, not in the internal-decision-axis dimensions. This difference may reflect qualitative differences between learning somewhat arbitrary stimulus/response relationships (such as between line length and event duration) compared with learning spatial-cue/position relationships.

Evidence for neural plasticity

The proposed model of adaptation assumes that peripheral acoustic spatial cues are mapped to some internal perceptual dimension representing source location, and that training alters how these peripheral cues are mapped to spatial responses. These assumptions lead naturally to the question of whether neural spatial auditory maps have been observed, and whether such maps demonstrate plasticity when sensory stimuli are rearranged. A brief review of these issues is presented below (for a more complete review, see King, 1993; King & Moore, 1991; and Brainard, 1994).

Spatially-tuned, topographically-organized neurons are observed at the levels of the brainstem through the inferior and superior colliculi in a variety of mammals and birds (e.g., see King, 1993; Knudsen & Knudsen, 1989). However, as yet there is little evidence for such maps in the cortex

of any species, even though spatially-sensitive cells are observed (e.g., see Middlebrooks, 1994).

   In normal adult animals, multisensory cells of the superior colliculus (SC, or its avian homologue, the optic tectum) form a topographical map in which visual receptive fields, auditory receptive fields, and/or somatosensory receptive fields are in registry (e.g., see King, 1993). The formation of spatial auditory maps in the SC is disrupted when animals are deprived of effective visual or auditory stimulation during a critical period in development (King & Carlile, 1993; Withingon-Wray, Binns, Dhanjal, Brickley & Keating, 1990; Withingon-Wray, Binns & Keating, 1990; Withington, 1992). Similarly, when owls are reared with abnormal visual or binaural cues, the tuning of the auditory map in the optic tectum (OT) is altered in a way that compensates for the externally-imposed sensory rearrangement (Brainard & Knudsen, 1995; Knudsen & Knudsen, 1986; Knudsen & Knudsen, 1989). When the owls are older than the critical period in development, the spatial maps in OT do not completely compensate for the imposed sensory rearrangement (Knudsen & Knudsen, 1985; Knudsen & Knudsen, 1990). Spatial tuning of OT cells in more mature birds does exhibits some plasticity, especially to less extreme transformations; however, the degree to which spatial tuning of OT cells changes generally decreases with age (Knudsen, Esterly & Olsen, 1994; Knudsen & Knudsen, 1990).

   Spatial tuning of cortical neurons also can be affected by sensory experience. In particular, animals deprived of visual stimulation have a larger number of spatially-selective auditory neurons with sharper-than-normal spatial tuning (Korte & Rauschecker, 1993; Rauschecker & Korte, 1993).

   In humans who suffer from congenital aural atresia, the ear canal is blocked or absent, effectively attenuating the sound to that ear by 45 – 60 dB (Wilmington, Gray, & Jahrsdoerfer, 1994). It is possible to correct this anomaly with surgery so that patients receive normal auditory stimulation, but the surgery is usually performed after the head has neared its mature size. Even months after this surgery, patients tend to perform poorly on complex spatial auditory tasks. In contrast, they have normal sensitivity to basic binaural cues such as interaural time and level differences. One interpretation of this result is that even though peripherally-computed auditory

spatial cues are available to these patients, their spatial perception is permanently disrupted by the abnormal sensory stimulation they received during early development.

These studies demonstrate that the spatial tuning of auditory neurons can be affected by long-term sensory rearrangement. This plasticity decreases with age: in particular, without appropriate early experience, spatial auditory perception may be permanently interrupted even when relatively peripheral auditory processing is intact. While the demonstrated plasticity is probably important for understanding the development of normal spatial perception, the relationship between these results and the short-term, reversible changes in behavior observed during adaptation to spatial rearrangement of auditory cues is unknown. However, taken together, these results suggest that auditory spatial perception is governed by an internal representation of external space that can be "retuned" by sensory experience, even in adult animals. Assumptions in the current model are consistent with this view: short-term adaptation in the model corresponds to a linear "retuning" of the posited neural representation of auditory space.

Summary

The preliminary model of adaptation extends the preliminary model of intensity perception (Braida & Durlach, 1972; Braida & Durlach, 1988; Durlach & Braida, 1969) by predicting changes in bias and resolution as subjects are trained with remapped auditory localization cues. In particular, the model assumes that the effective stimulus range and the placement of decision criteria are governed by changes in a linearly-constrained map relating stimulus to response. The slope of this map evolves over time as subjects adapt, causing the criteria and the effective range (and hence the internal noise) to evolve over time. The resulting model predicts that the order of stimulus presentation will affect resolution, an effect that the preliminary intensity perception model did not address.

Decision criteria are assumed to equal the perceived-optimal criteria in the subjects' decision space. However, since the mapping between physical cue and perceived position 1) changes slowly with time and 2) is constrained to be linear, the model predicts that response bias decreases

with exposure time, but never disappears. Similarly, the perceived range of positions is always assumed to equal the spatial range of the responses used in the experiments; however, the effective range in the underlying decision space changes as the mapping between perceived and normal-cue position changes. This gradual change in effective range causes a corresponding gradual change in resolution. The model predicts the observed dependence of ', bias, and d' on stimulus value and on run. Empirical results match predicted values fairly well, both qualitatively and quantitatively.

The model implies that adaptation to rearranged spatial auditory cues is characterized by changes in an internal map that determines how a noisy, internal representation of spatial location is related to positions in external space.

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NOTES

[1] Note that the model assumes that $'$ equals the sum of the distances between adjacent stimuli in the set, measured in units of standard deviation. Thus, $'$ equals the sum over all adjacent stimulus pairs of d'_j, the standard psychophysical measure of stimulus resolution. The measure d'_j is considered in detail below.

[2] In the current paper, bias is denoted by B (rather than the more usual symbol) to avoid confusion with the sensation noise in the model.

[3] Bias estimates and resolution estimates (shown in Figures 4, 5 and 6) were found using a maximum likelihood estimation approach detailed in Shinn-Cunningham et al. (1998a).

[4] Theoretically, the optimal placement for *all* criteria should be farther from the zero-azimuth location than the actual criteria placement for naïve subjects; however, bias in the first altered-cue run tends to be positive for the leftmost criterion and negative for the rightmost criterion in all experiments. This is an artifact of the identification method, reflecting the fact that subjects cannot

accurately indicate the heard location of a source when it falls outside the range of allowed

responses.

TABLES

Experiment	n	Subjects	Positions
F_3	3	5	13
F_{3mid}	3	4	7
F_2	2	4	13
F_{4a}	4	3	13
F_{4b}	4, 0.5	3	13

Table 1: Summary of experiments: n gives transformation strengths used, Subjects gives number of subjects, and Positions shows number of positions used in each experiment.
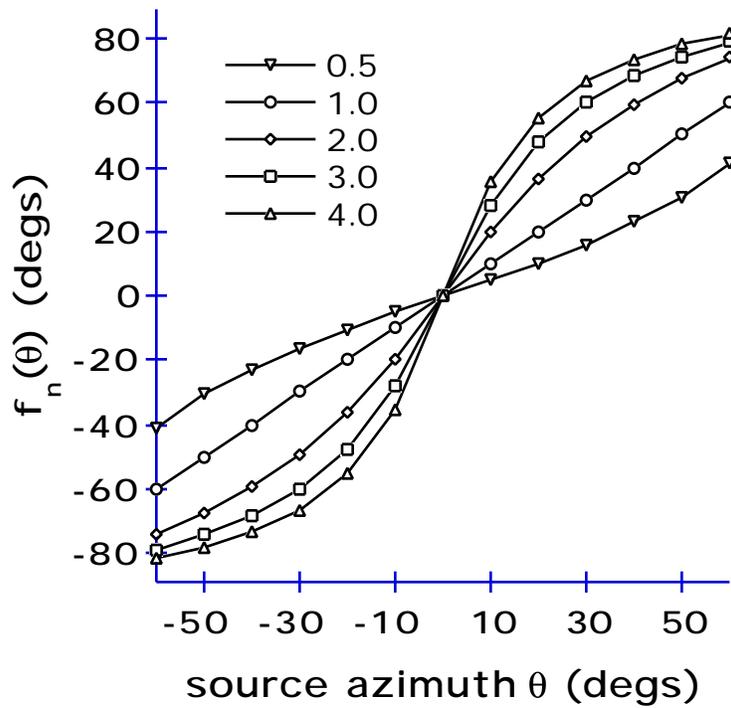
FIGURE CAPTIONS

Figure 1. The family of functions $f_n(\ )$ used to transform auditory localization cues. Using these transformations, a source from azimuth   was synthesized using the HRTF that normally corresponded to the position $f_n(\ )$.
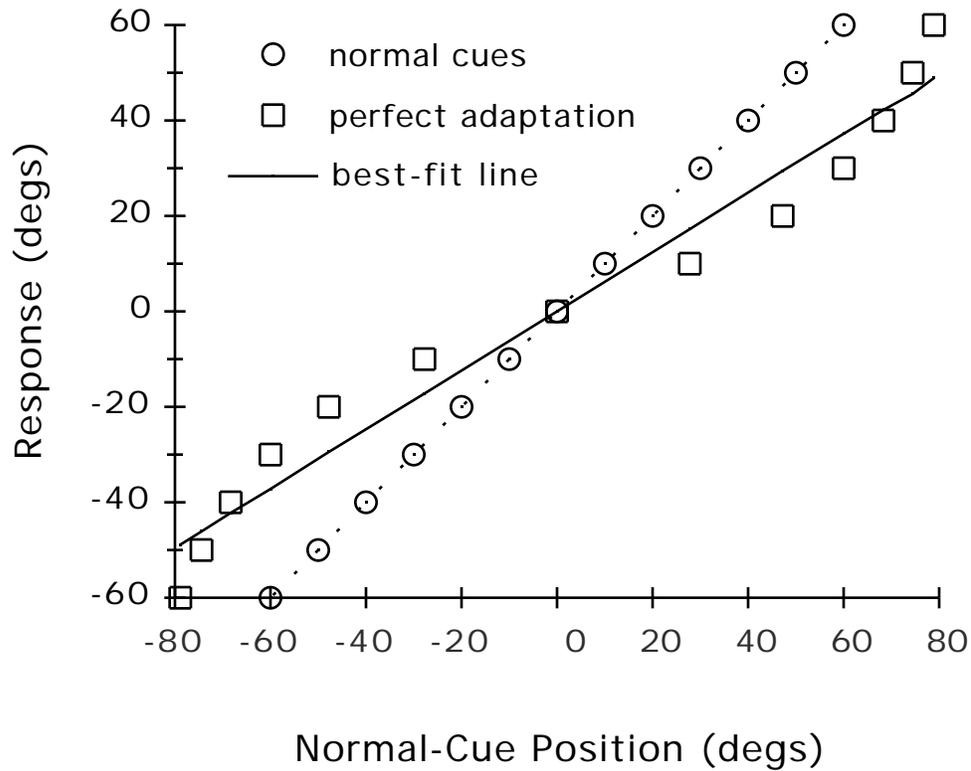
Figure 2. Schematic representation of the observed constraint on adaptation. The abscissa represents $f_n(\ )$, the location normally associated with the stimulus whose nominal location is .The ordinate represents the mean response given by the subject. In normal-cue runs, the correct responses for the cues presented (open circles) fall on a line of slope one. In altered-cue runs, the correct responses (open squares) are a nonlinear function of $f_n(\ )$. The solid line represents how subjects actually adapt to this nonlinearity.
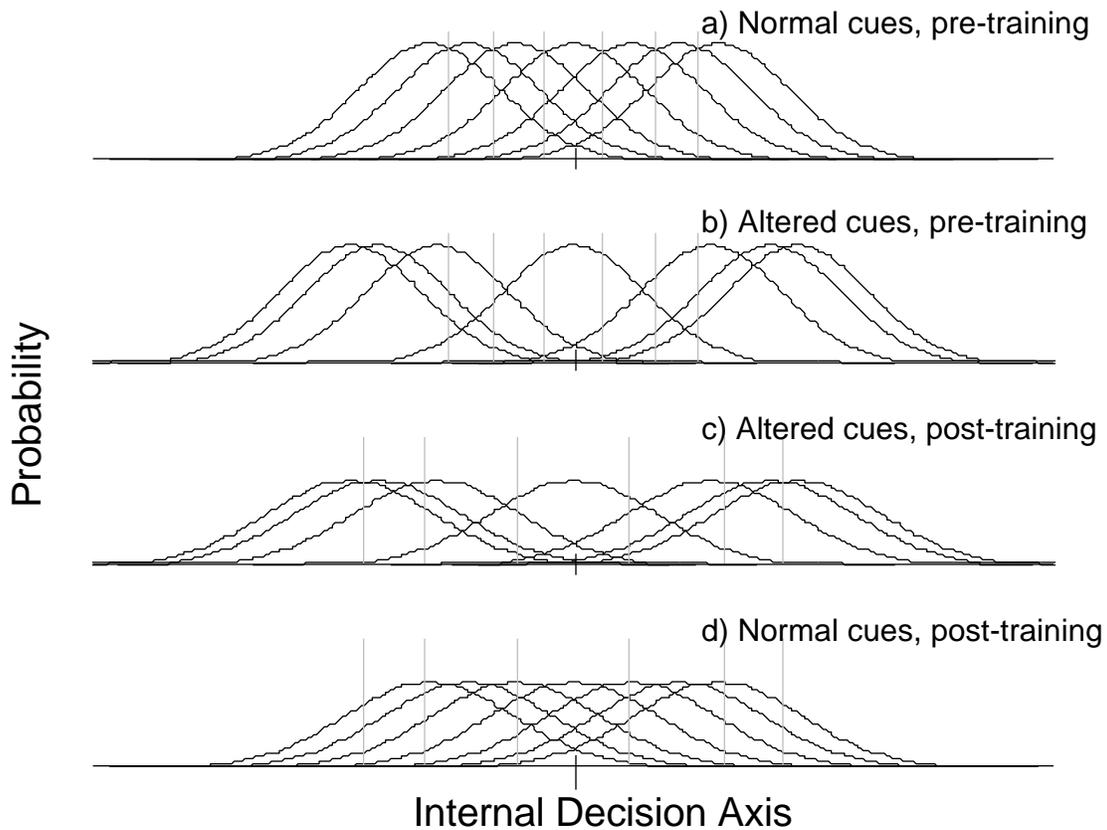
Figure 3. Representation of the internal decision axis for a seven-alternative, forced choice task similar to that in Experiment F_{3mid} (in order to emphasize model behavior, transformation strength n is equal to 6). a) initial run with normal cues, b) initial run with altered cues, c) final run with altered cues, and d) initial, post-training run with normal cues. In each panel, the probability distributions of the internal decision variable corresponding to each of seven possible stimulus values are plotted. The criteria dividing the decision axis into seven distinct regions are shown by the dashed vertical lines.
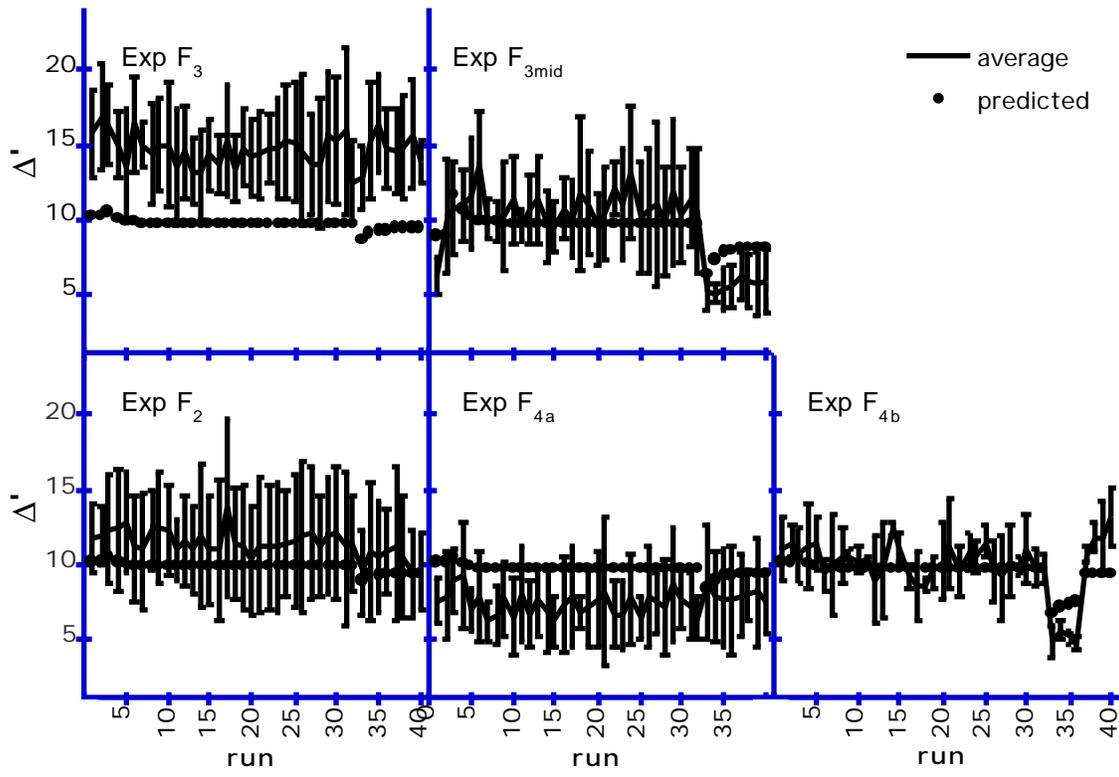
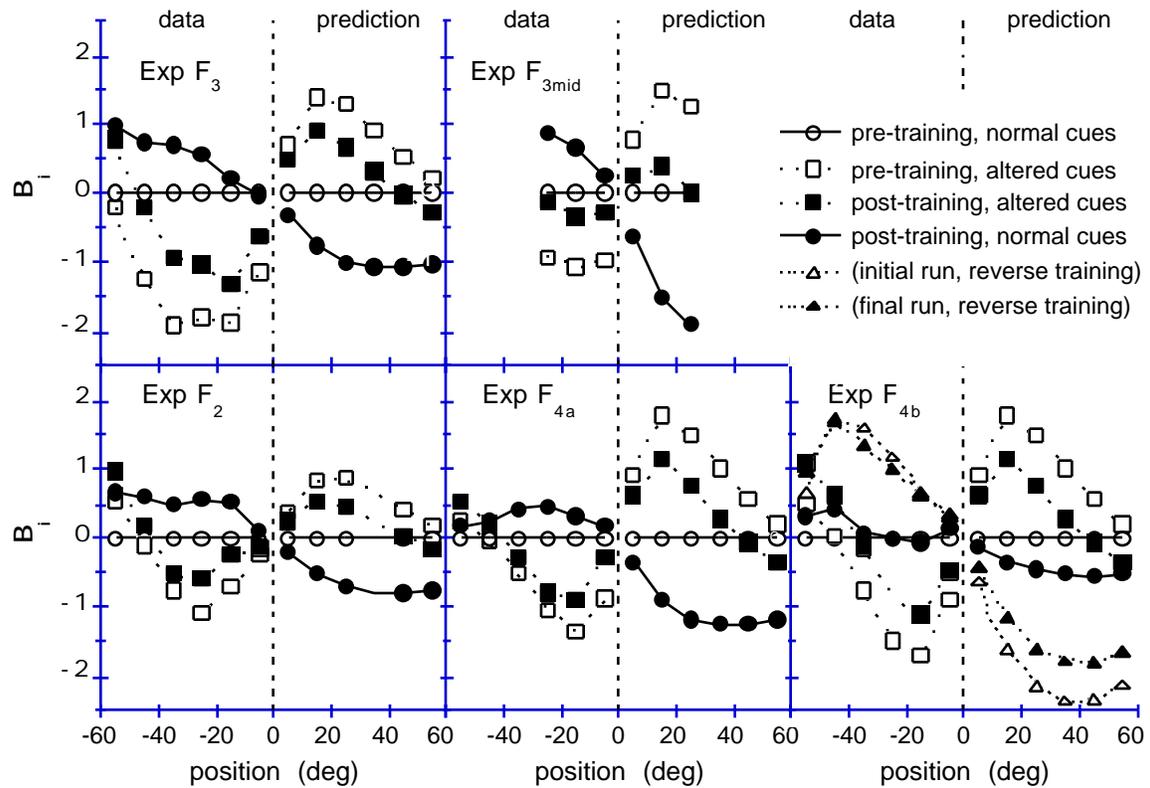Figure 4. Estimated and predicted ' as a function of run.

Figure 5. Estimated and predicted bias B_i as a function of position. In each panel, the experimental results, plotted on the left side of each panel, were found by assuming that performance was symmetric about the midline. The predictions from the model are shown on the right side of each panel. To the extent that the left and right halves of each panel are symmetric about the line $y = -x$, the model fits the experimental results.
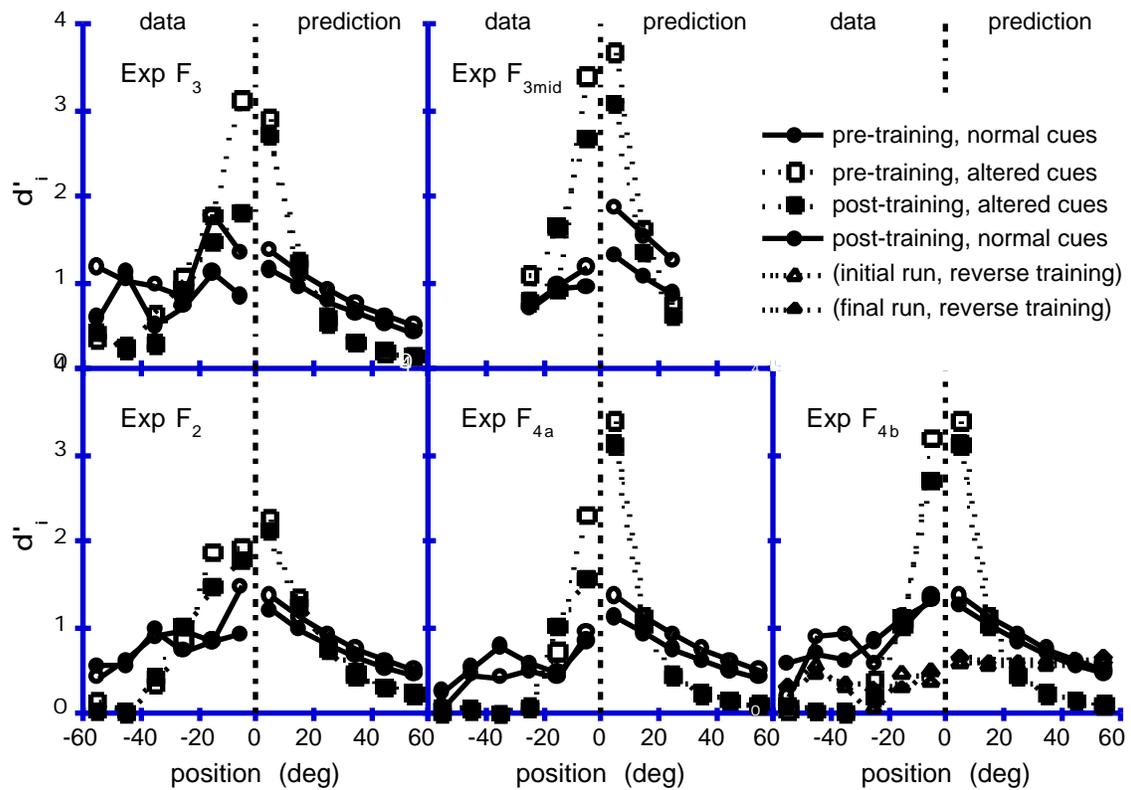
Figure 6. Estimated and predicted resolution d$'_i$ as a function of position. In each panel, the experimental results, plotted on the left side of each panel, were found by assuming that performance was symmetric about the midline. The predictions from the model are shown on the right side of each panel. To the extent that the left and right halves of each panel are symmetric about the x axis, the model fits the experimental results.