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# Models of Plasticity in Spatial Auditory Processing

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## Key Words

Neural plasticity · Spatial hearing · Learning · Auditory models · Interaural time differences · Interaural level differences · Spectral cues

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## Abstract

Both psychophysical and physiological studies have examined plasticity of spatial auditory processing. While there is a great deal known about how the system computes basic cues that influence spatial perception, less is known about how these cues are integrated to form spatial percepts and how the auditory system adapts and calibrates in order to maintain accurate spatial perception. After summarizing evidence for plasticity in the spatial auditory pathway, this paper reviews a statistical, decision-theory model of short-term plasticity and a system-level model of the spatial auditory pathway that may help elucidate how long- and short-term experiences influence the computations underlying spatial hearing.

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## Introduction

While the computations underlying normal sound source localization are partially ‘hard-wired’, accurate sound localization depends upon systematic calibration

of these computations through everyday experience. Both physiological and behavioral studies demonstrate that the spatial auditory system adapts in order to learn and maintain accurate sound localization. Developmentally, such plasticity can overcome individual differences in the shape of the head and ears and changes in the size of the head as an animal matures [Clifton et al., 1988]. The auditory system must also recalibrate on a short time scale in order to allow accurate localization when a listener moves from one acoustic environment to another [Shinn-Cunningham, 2000b]. Experimental results show that both long- and short-term experience affects the perceived location of an auditory source. While the spatial auditory system exhibits a robust ability to recalibrate, there are limits to this plasticity. Any comprehensive model of spatial auditory plasticity describing the effects of experience on spatial perception must account for how such limitations manifest as a result of both long- and short-term training with altered spatial cues.

## Long-Term Plasticity

Many studies have examined how long-term rearrangements affect physiological responses [e.g., see Knudsen et al., 1987; King and Moore, 1991; Rauschecker, 1999]. These studies show that development of normal neurophysiological responses depends upon appropriate audi-

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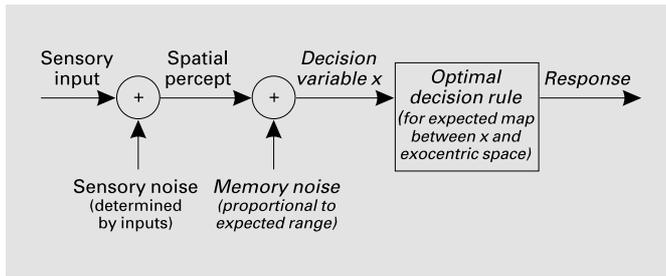
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**Fig. 1.** Decision-theory model of short-term spatial plasticity. Only italicized components change with short-term training.

tory/visual experience during a critical developmental period [e.g., see King and Carlile, 1993; Knudsen et al., 1994]. Adult animals also exhibit plasticity in the face of long-term training, but the plasticity is less complete [Knudsen et al., 1994]. Plasticity to long-term exposure has been observed at and below the inferior colliculus [Brainard and Knudsen, 1993b; Mogdans and Knudsen, 1994]; studies of higher levels of the system also show changes with experience [Korte and Rauschecker, 1993].

A few human studies have examined how localization performance changes with long-term training. With weeks of training, subjects can adapt to unilateral hearing loss [Florentine, 1976] or to rearranged spectral elevation cues [Hofman et al., 1998]. However, subjects who undergo surgery to correct congenital aural atresia (in which one ear canal is blocked, producing monaural attenuation of 45–60 dB) do not fully recover [Wilmington et al., 1994]. Even months after surgery, such patients perform poorly on some spatial auditory tasks, although they have normal sensitivity to basic spatial cues such as interaural time and level differences.

Both behavioral [Hofman et al., 1998] and physiological [Brainard and Knudsen, 1993a] evidence suggests that with long-term training, more than one set of spatial cues can represent one position in exocentric space. After adapting to altered elevation cues, subjects correctly indicate source elevation using either normal or altered cues [Hofman et al., 1998]. Physiologically, when long-term training alters receptive field tuning, the receptive fields do not shift gradually from old to new locations. Instead, the spatial tuning first becomes bimodal (with peaks in sensitivity for both old and new locations) before evolving to encode only the new location [Brainard and Knudsen, 1993a].

## Short-Term Plasticity

Studies of short-term adaptation show that subjects rapidly adapt (i.e., overcome response bias, defined as the mean localization error) to changes in the spatial cues encoding exocentric source position; however, the adaptation is only partial for complex remappings of space [Durlach et al., 1993; Shinn-Cunningham et al., 1998a, b, 2000a]. Resolution (a measure of how reliably subjects can discriminate between two nearby sources that is inversely related to responses variability) is affected both by the stimuli and by the experience of the subject [Shinn-Cunningham et al., 1998a]. When the acoustic cues representing source locations are inconsistent with any ‘normal’ source position, short-term training also decreases bias, but resolution with these inconsistent cues is worse than with normal cues [Kassem, 1998]. In this study, Kassem [1998] created spatial auditory cues to simulate those that would arise if the head were physically scaled to twice its ordinary size (leading to larger-than-normal interaural time and level differences, interaural level differences and spectral notches at lower-than-normal frequencies, and novel combinations of interaural and spectral cues). He found that when using ‘big-head’ cues, spatial resolution was generally lower than expected. These results suggest that the auditory system is ‘optimized’ for computing spatial location from normal spatial cues, and that short-term training cannot influence how spatial position is computed internally, but only how spatial percepts are mapped to exocentric space.

### Decision-Theory Model of Short-Term Spatial Plasticity

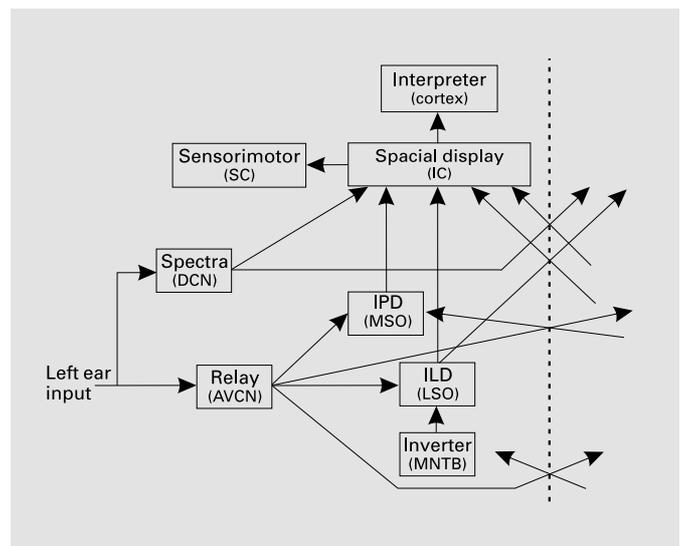
Our initial work on modeling spatial plasticity focused on short-term training effects. We developed a statistical decision-theory model [Shinn-Cunningham, 2000a] to explain the observed changes in both spatial bias and resolution (fig. 1). The model is similar to the decision-theory model of intensity perception [Braida and Durlach, 1988], but extends the intensity-perception model to account for effects of listener experience on bias and resolution. The model assumes that physical stimuli presented to a listener give rise to internal neural representations that are corrupted by stochastic noise. This peripheral, sensory noise is always present and is not affected by short-term experience. Instead, sensory noise depends only on the spatial cues in the physical stimuli and how they are extracted and integrated to form a spatial percept

of the acoustic object. The resulting spatial percept is assumed to vary monotonically with the position of the physical stimulus. The subject processes this spatial percept to generate an appropriate response; such processing depends upon past short-term experience. The spatial percept is further degraded by the addition of noise ('memory noise') whose standard deviation is proportional to the range of positions to which the subject is attending (which, in turn, depends on the experience of the subject). The resulting internal decision variable is then processed using what would be the optimal decision rule, given the expected mapping between the decision variable and exocentric space. In order to model the observed constraints on adaptation, the expected mapping between the internal decision variable and exocentric space (which determines what decision rule is used to generate responses) is assumed to be linear.

The model structure makes accurate quantitative predictions of mean response as well as resolution as subjects adapt to complex transformations of acoustic space [Shinn-Cunningham, 2000a]. It also qualitatively explains why resolution is degraded when subjects encounter novel combinations of spatial cues [Kassem, 1998]; in this case, the sensory noise in the spatial percept is greater because the sensory inputs are ambiguous. While the model is very powerful in its ability to explain short-term adaptation results, it does not address longer-term effects and is not tied to known physiological results.

### System Model of Spatial Plasticity

More recently, we have developed a preliminary, system-level model of spatial auditory processing that incorporates results from physiological as well as psychophysical experiments investigating both ordinary auditory spatial processing and plasticity in this processing. Results from psychophysical and physiological studies are consistent with the view that spatial auditory information is processed hierarchically. In particular, data show that all of the 'basic' cues for source location (e.g., spectral cues; interaural phase and level differences or IPDs and ILDs, respectively, as a function of frequency) are computed relatively peripherally, then integrated to form a spatial representation. Our preliminary model assumes that this integration approximates a maximum likelihood estimation of source position based on all of the evidence accumulated in the lower processing stages. Some cues (e.g., low-frequency IPD information) are weighted more heavily because they are more reliable than other cues.



**Fig. 2.** System-level model of spatial auditory processing (one side of the symmetrical model). Short-term training only affects highest processing stages, long-term training affects all stages. DCN = Dorsal cochlear nucleus; AVCN = anteroventral cochlear nucleus; MSO = medial superior olive; LSO = lateral superior olive; SC = superior colliculus; MNTB = medial nucleus of the trapezoid body.

Cells encoding peripherally computed spatial attributes excite higher-level cells whose receptive fields are consistent with their encoded information and inhibit higher-level cells that are inconsistent. The resulting representation of space projects to even higher centers responsible for generating appropriate behavioral responses.

In contrast with previous models [e.g., see Stern and Trahiotis, 1997], in the proposed model, IPDs, ILDs, and spectral shape in all frequency channels are combined in one step to form a spatial representation. In particular, if IPD cues and ILD cues at one frequency are in disagreement, both of the interaural cues still have a direct influence on the activity of the neurons in the final representation. The proposed model is consistent with functional models of auditory spatial processing based on physiological studies of the owl [e.g., see Knudsen et al., 1987] and with behavioral evidence suggesting that IPD and ILD information is not averaged together to form spatial percepts, but that each cue separately influences the perception of source location [Koehnke et al., 1995].

The left half of our (symmetrical) preliminary system-level model (based on a simplified view of physiological evidence) is shown in figure 2. Left (and right) ear inputs represent frequency-tuned nerve fibers in the VIIIth nerve. These inputs go to two blocks representing antero-

ventral and dorsal cochlear nuclei. The model hypothesizes that the dorsal cochlear nucleus calculates spectral attributes of the sound important in elevation perception. The anteroventral cochlear nucleus provides ipsilateral and contralateral input to areas devoted to computing interaural cues (IPDs in the medial superior olive; ILDs in the lateral superior olive). Thus, IPD, ILD, and spectral cues are computed in parallel, in separate spatial-cue channels. These channels then converge in the inferior colliculus (IC) to form a representation of external space. The activity of neurons in the IC is assumed to approximate the probability of observing the spatial cues presented given that a source is at the location encoded by the receptive field of a particular neuron. This representation is referred to as the 'IC map' (the use of the word 'map' simply reflects the functional importance of this processing and does not necessarily imply that the neural representation is topographically organized). The IC map then innervates higher blocks, one controlling reflexive motor responses (superior colliculus) and one controlling other localization responses. The second block (corresponding to cortex) is a sort of interpreter, mapping spatial percepts (encoded in the IC map) to exocentric spatial positions [e.g., see Shinn-Cunningham, 2000a].

In the preliminary model, plasticity in neural processing can occur at a number of sites, including the stage interpreting the IC map and at lower stages. We hypothesize that short-term training does not alter how spatial cues are combined or spatial percepts computed, but only how they are mapped to external space (i.e., short-term exposure only alters the highest stages of processing, not the IC map representation). Changes in the response of the IC map, however, can occur with more extensive training, over the course of weeks. Whereas short-term training alters where in exocentric space a source is perceived, long-term training can affect how source position is computed from basic stimulus attributes. One can also relate the stages of processing in the model to the internal sources of noise in the decision theory model of auditory adaptation [Shinn-Cunningham, 2000a]. Specifically, the *sensory* noise in the decision-theory model corresponds to noise in the spatial display (in the spatial representation in IC), while the *memory* noise reflects noise in the higher processing (interpreter stage).

We hypothesize that the 'sensitive period' in development that is observed in physiological studies [e.g., see King and Carlile, 1993; Knudsen et al., 1994] is necessary to *create* a spatial representation of space at the level of the IC; however, it is possible to *alter* this representation even after the developmentally critical period. Thus, lis-

teners deprived of normal experience [Wilmington et al., 1994] can detect changes in basic spatial cues such as IPD and ILD; however, they cannot perform well on *spatial perception* tasks (which depend upon integrating these basic spatial cues to compute a spatial position). We also hypothesize that it is the complexity of the proposed maximum-likelihood computation that enables different combinations of spatial cues to map (many-to-one) onto one spatial position [e.g., see Brainard and Knudsen, 1993a; Hofman et al., 1998]. A different method for integrating spatial cues (such as averaging location estimates derived independently for individual spatial cues) would not predict this result.

In short, although the proposed model is only a preliminary, system-level description of the processing of spatial auditory information, we believe that its structure is consistent with results from diverse experiments. The model leads to a number of interesting hypotheses. For instance, consistent with suggestions from previous experiments, the model predicts that novel combinations of spatial cues will lead to measurably more diffuse, poorly resolved spatial percepts and worse spatial resolution. The postulated maximum-likelihood structure predicts that certain spatial cues at certain frequencies will be weighted more heavily and will dominate spatial perception because they vary more reliably with spatial position than other cues in other frequencies. Again, while there are some previous experiments that suggest dominance of particular cues at particular frequencies [Bilsen and Raatgever, 1973; Wightman and Kistler, 1992; Shinn-Cunningham et al., 1995], our model makes quantitative predictions regarding the relative influence of each cue that can be tested explicitly. Our model also predicts that short-term training leads to a change in how the maximum-likelihood estimate of position (which integrates information across frequency) maps to exocentric space. This view predicts that when training with narrowband stimuli and testing with broadband stimuli (or vice versa), the amount of training generalization will depend on the relative influence of the narrowband frequency cues on spatial perception.

## Conclusions

Taken as a whole, results of psychophysical and physiological experiments suggest that the computation of spatial position is a hierarchical process that exhibits plasticity at many levels. Whereas long-term training can alter how spatial cues are integrated to form spatial percepts, short-term training appears to influence how these loca-

tions are mapped to spatial behaviors. By developing a system-level view of spatial auditory processing, hypotheses can be formulated and tested to improve our understanding of the way in which experience influences the computation of sound source position.

## Acknowledgments

Portions of this work were supported by the Whitaker Foundation and the Air Force Office of Scientific Research.

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