

How Plastic Is Spatial Hearing?

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Key Words

Sound localization · Plasticity · Superior colliculus ·
Auditory cortex · Virtual acoustic space · Behaviour ·
Monaural · Binaural

Abstract

The location of a sound source is derived by the auditory system from spatial cues present in the signals at the two ears. These cues include interaural timing and level differences, as well as monaural spectral cues generated by the external ear. The values of these cues vary with individual differences in the shape and dimensions of the head and external ears. We have examined the neurophysiological consequences of these intersubject variations by recording the responses of neurons in ferret primary auditory cortex to virtual sound sources mimicking the animal's own ears or those of other ferrets. For most neurons, the structure of the spatial response fields changed significantly when acoustic cues measured from another animal were presented. This is consistent with the finding that humans localize less accurately when listening to virtual sounds from other subjects. To examine the role of experience in shaping the ability to localize sound, we have studied the behavioural consequences of altering binaural cues by chronically plugging one ear. Ferrets raised and tested with one ear plugged learned to localize as accurately as control animals, which is consistent with previous findings that the representation of auditory space in the midbrain can accom-

modate abnormal sensory cues during development. Adaptive changes in behaviour were also observed in adults, particularly if they were provided with regular practice in the localization task. Together, these findings suggest that the neural circuits responsible for sound localization can be recalibrated throughout life.

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Introduction

Locating the source of a sound is one of the most important tasks performed by the auditory system. This is also one of the most complex, because, in contrast to the visual and somatosensory systems, sound source location cannot be read directly from the array of cells at the receptor surface. Instead, it is derived from the activity of central auditory neurons that are sensitive to direction-dependent cues generated by the head, torso and external ears [King et al., 2001].

The most familiar of these cues are binaural differences in sound level and time of arrival, which, in mammals, underlie localization in the horizontal plane, as well as contributing to the ability of listeners to detect and discriminate sounds of interest against a noisy background [Moore, 1997; King et al., 2000]. Additionally, spectral cues for sound location arise from the filtering properties of the head and external ears. These monaural localization cues are particularly important for making elevation judgements and in front-back discrimination, as well as

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for providing unilaterally deaf subjects with some ability to localize sounds [Slattery and Middlebrooks, 1994]. The relative importance of different spatial cues varies with both the location of the sound source and with other parameters, such as the frequency content and level of the sound. Furthermore, the computation of a consistent and accurate estimate of sound source location requires that information derived from different frequency channels is combined and coordinated with spatial information provided by other sensory systems.

Individual Differences in Auditory Spatial Cues

The monaural and binaural cue values corresponding to a particular direction in space will depend on the size, shape and separation of the ears. Acoustical measurements made from adult humans [Shaw and Teranishi, 1968; Middlebrooks and Green, 1990; Middlebrooks, 1999a] and other species [Xu and Middlebrooks, 2000; Schnupp et al., 2001] have shown that these values can vary markedly from one individual to another. They also undergo pronounced changes during the course of development as the head and external ears grow [Clifton et al., 1988; Carlile, 1991; King et al., 2001]. These observations suggest that the relationship between acoustic cue values and the sound directions to which they correspond must be learned with the aid of experience. Evidence for this is provided by studies in which virtual acoustic space (VAS) signals, which incorporate all the spatial information associated with free-field sources, are presented over headphones [King et al., 2001]. Human listeners localize VAS stimuli more accurately when these are based on their own ears than on the ears of other individuals [Wenzel et al., 1993; Middlebrooks, 1999b]. Indeed, the degradation in performance appears to be correlated with inter-subject differences in spectral localization cues [Middlebrooks, 1999b].

We have shown that similar effects can be observed at the level of individual neurons by recording from the primary auditory cortex (A1), which is thought to play a key role in sound localization [Masterton, 1997]. The spatial response fields of ferret A1 neurons can change significantly in shape and/or location when mapped with VAS stimuli based on the ears of another ferret (fig. 1) [Mrsic-Flogel et al., 2001]. As with the human psychophysical data, the magnitude and direction of the observed changes in A1 spatial tuning are consistent with individual differences in the available acoustic cue values.

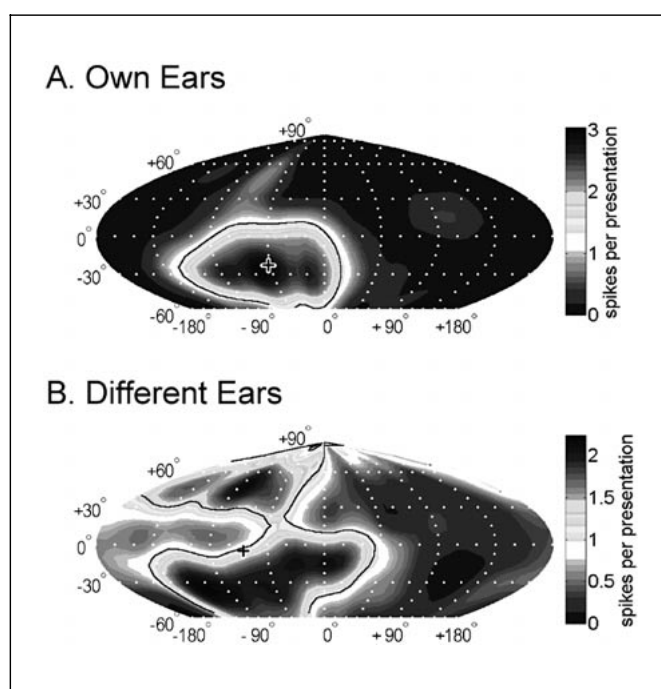


Fig. 1. Spatial response field of a neuron in the primary auditory cortex of an anesthetized adult ferret mapped using VAS stimuli. Broadband stimuli were presented from 224 virtual sound directions, covering 360° in azimuth and from -60° to +90° in elevation. **A** Responses to VAS stimuli derived from the animal's own ears. **B** Responses of the same neuron to VAS stimuli based on the spatial cues measured from another ferret. The crosses are spike-count-weighted centres of gravity calculated for all virtual sound directions and the lines indicate iso-response contours corresponding to 50% of the maximum response (spikes/presentation). Based on Mrsic-Flogel et al. [2001].

Together these findings highlight the pronounced individual differences that exist in the values of the acoustic cues that form the basis for our ability to localize sound. Accurate sound localization therefore requires that the neural code for auditory space be calibrated to these individual characteristics.

Calibrating Auditory Localization during Infancy

There is considerable evidence that the developmental emergence of the neural mechanisms responsible for sound localization is an activity-dependent process that is shaped and refined by sensory experience [reviewed in King, 1999; King et al., 2001]. Most electrophysiological studies of plasticity have concentrated on the superior col-

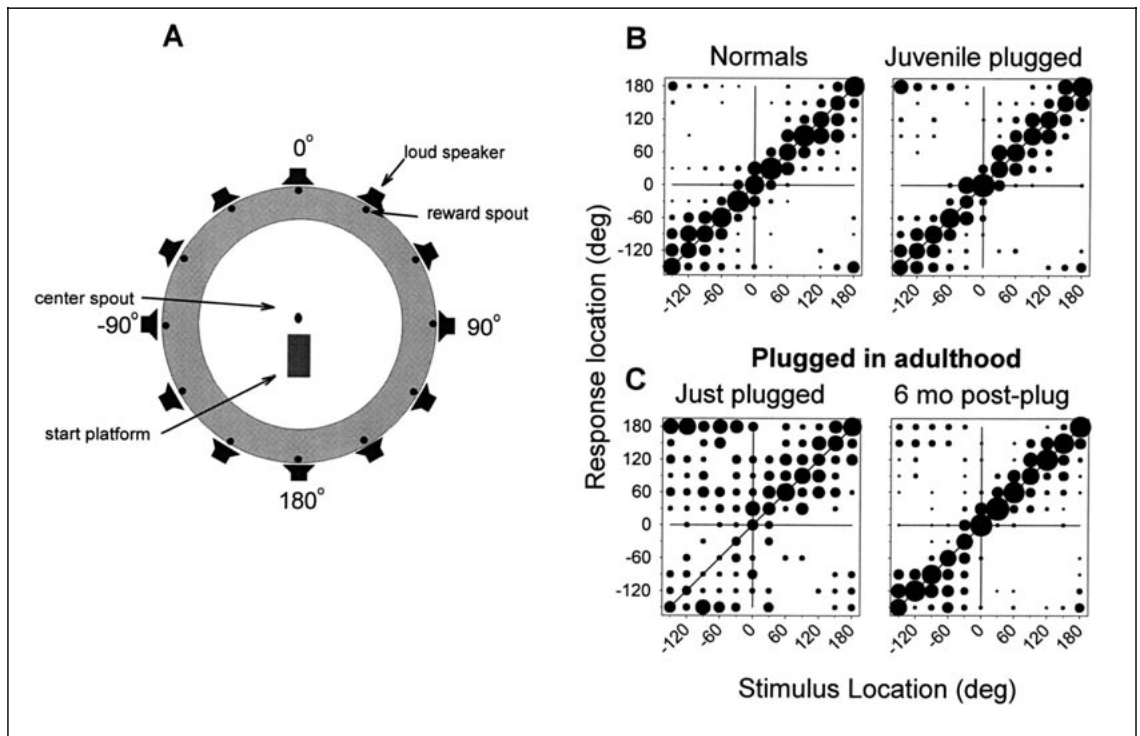


Fig. 2. Behavioural evidence for plasticity of sound localization. **A** Schematic view of chamber used to measure the spatial identification ability of ferrets. The animals were trained to stand on the start platform and initiate a trial by licking the centre spout. Each trial consisted of a broadband noise burst (100 ms duration) presented randomly from 1 of 12 speakers placed at 30° intervals in the azimuthal plane. Within each testing session, five sound levels ranging from 56 to 84 dB SPL were used to minimize loudness cues. Ferrets were rewarded for approaching and licking the spout associated with the speaker that had been triggered. **B** Stimulus-response plots showing the combined data of 3 normal, adult ferrets (normals) and 3 ferrets that had been raised and tested with the left ear occluded with

a plug that produced 30–50 dB attenuation (juvenile plugged). These plots illustrate the distribution of responses (ordinate) as a function of stimulus location (abscissa). The size of the dots indicates, for a given speaker angle, the proportion of responses made to different spout locations. The juvenile plugged ferrets could localize sound as accurately as the controls. **C** Data from 3 normally reared adult ferrets immediately (just plugged) and 6 months after (6 months post-plug) occlusion of the left ear. Prior to plugging, these animals performed as well as the normals shown in B. Following insertion of the earplug, they initially localized poorly, but showed a marked improvement when they were next tested 6 months later. Adapted from King et al. [2000].

liculus (SC), a multisensory nucleus in the midbrain, which is involved in the control of reflexive orienting movements that help to shift attention toward novel stimuli. This sensorimotor function appears to be facilitated by the presence of topographically aligned sensory and motor maps in the SC [Stein and Meredith, 1993]. Indeed, as a consequence of the presence of a map of auditory space, the mammalian SC and its homologue in the barn owl midbrain have become particularly useful systems for investigating experience-dependent plasticity in the neural coding of sound source location. Changes in the tuning of auditory neurons in the SC to free-field sound sources or to the corresponding spatial cues can be induced by experimentally altering the sensory information available to the animal. Such studies have, for exam-

ple, highlighted the role of vision in refining the auditory space map so that the neural representations of visual and auditory space in the SC become and remain aligned during the course of development [King, 1999; Knudsen et al., 2000].

Manipulation of acoustic localization cues during infancy also reveals plasticity in the auditory space map in the midbrain [King et al., 2000]. As with the effects of abnormal visual experience, the neural changes observed seem to depend on the degree to which the spatial cues are altered. Thus, disruption of the spectral localization cues available to juvenile ferrets, by removal of the pinna and concha of the external ear, leads to the emergence of an abnormal auditory space map in the SC [Schnupp et al., 1998] and to less accurate localization behaviour [Parsons

et al., 1999]. On the other hand, compensatory changes are observed at both neuronal and behavioural levels in animals raised with a unilateral conductive hearing loss produced by plugging one of the ears during infancy [King et al., 2000]. Indeed, ferrets raised and tested with one ear occluded can learn to identify the location of a sound source as accurately as normal adult animals (fig. 2B), although measurements of minimum audible angles and free-field binaural unmasking reveal less adaptation for other aspects of spatial hearing [Moore et al., 1999; King et al., 2000].

Relearning to Localize Sounds in Adulthood

Examination of the effects of manipulating sensory inputs at different ages suggests that experience-induced plasticity of the auditory space map in the SC is developmentally regulated and most pronounced during the growth period when the size, shape and relative positions of the sense organs are changing. However, recent experiments on sound localization have revealed that a remarkable degree of plasticity persists into adulthood.

For example, the capacity of the barn owl's auditory system to adjust to, and recover from, altered visual cues produced by mounting prisms in front of the eyes depends not only on the age of the animal, but also on the richness of the environment in which it was raised and on previous experience of the prisms during infancy [reviewed in Knudsen et al., 2000]. Indeed, the vision-induced plasticity observed in adult birds appears to rely on the anatomical rewiring of the midbrain produced by prism rearing during infancy.

Behavioural studies have shown that adult humans can learn to associate altered acoustic localization cues with directions in space, particularly after prolonged exposure to the abnormal cues [Hofman et al., 1998; Shinn-Cunningham et al., 1998]. We have explored the capacity of adult ferrets to adapt to altered binaural cues resulting from the substantial attenuation caused by plugging one ear. As expected, their ability to localize sound is initially disrupted by monaural occlusion, indicating the importance of binaural cues in this task, but then recovers to a large extent if the earplug is left in place for several months (fig. 2C) [King et al., 2000]. In fact, pronounced improvements in performance can be observed within the first few days of plugging, suggesting that the degree and rate of adaptation may be determined primarily by experience in carrying out the localization task. Interestingly, these rapid improvements in performance in adult ani-

mals can take place in the absence of feedback or vision [Kacelnik et al., 2001].

The neuronal basis for these adaptive changes is presently unknown. Examination of the time course of adaptation and of the consequences of restoring normal auditory inputs suggests that they are unlikely to be due to an anatomical remodelling of the neural circuits responsible for sound localization. Instead it may be that a greater weighting is placed on acoustic cues that are unaffected by the manipulation used. Thus, ear-plugged ferrets may rely more on monaural pinna cues for localization in the horizontal plane than under normal binaural hearing conditions.

Future Directions

Sound localization is a complex computational task, which is calibrated by experience so that listeners can learn to localize accurately using their own ears. Until recently, the clearest evidence for experience-dependent plasticity has come from single-unit studies of the developing auditory space map in the SC. Behavioural experiments have now shown that the capacity to reinterpret acoustic cues for sound location extends into adult life, raising the possibility that hearing disorders at any age may give rise to compensatory changes in spatial hearing. A major area of future research will involve the investigation of the neural mechanisms that give rise to behavioural plasticity. Experiments in which barn owls and ferrets have been raised with altered sensory inputs have shown that experience-driven changes in the auditory space map in the midbrain can be accompanied by equivalent changes in behaviour, and progress is now being made in identifying the cellular and molecular steps involved [King, 1999; Knudsen et al., 2000]. However, behavioural and functional imaging studies indicate that the perception of sound source location in mammals is likely to rely on cortical activity. Before we can address the nature of plasticity in the cortex, it will be necessary to obtain a better understanding of the coding strategies used for representing auditory space in A1 and particularly at higher levels of the auditory system.

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References

- Carlile S: The auditory periphery of the ferret: Postnatal development of acoustic properties. *Hear Res* 1991;51:265–278.
- Clifton RK, Gwiazda J, Bauer JA, Clarkson MG, Held RM: Growth in head size during infancy: Implications for sound localization. *Dev Psychol* 1988;24:477–483.
- Hofman PM, Van Riswick JG, Van Opstal AJ: Relearning sound localization with new ears. *Nat Neurosci* 1998;1:417–421.
- Kacelnik O, Parsons CH, Moore DR, King AJ: Plasticity of auditory spatial processing in adulthood. *Abstr Assoc Res Otolaryngol* 2001;24:262.
- King AJ: Sensory experience and the formation of a computational map of auditory space in the brain. *Bioessays* 1999;21:900–911.
- King AJ, Parsons CH, Moore DR: Plasticity in the neural coding of auditory space in the mammalian brain. *Proc Natl Acad Sci USA* 2000;97:11821–11828.
- King AJ, Schnupp JWH, Doubell TP: The shape of ears to come: Dynamic coding of auditory space. *Trends Cog Sci* 2001;5:261–270.
- Knudsen EI, Zheng W, DeBello WM: Traces of learning in the auditory localization pathway. *Proc Natl Acad Sci USA* 2000;97:11815–11820.
- Masterton RB: Role of the mammalian forebrain in hearing; in Syka J (ed): *Acoustical Signal Processing in the Central Auditory System*. New York, Plenum Press, 1997, pp 1–17.
- Middlebrooks JC: Individual differences in external-ear transfer functions reduced by scaling in frequency. *J Acoust Soc Am* 1999a;106:1480–1492.
- Middlebrooks JC: Virtual localization improved by scaling nonindividualized external-ear transfer functions in frequency. *J Acoust Soc Am* 1999b;106:1493–1510.
- Middlebrooks JC, Green DM: Directional dependence of interaural envelope delays. *J Acoust Soc Am* 1990;87:2149–2162.
- Moore BCJ: *An Introduction to the Psychology of Hearing*. San Diego, Academic Press, 1997.
- Moore DR, Hine JE, Jiang ZD, Matsuda H, Parsons CH, King AJ: Conductive hearing loss produces a reversible binaural hearing impairment. *J Neurosci* 1999;19:8704–8711.
- Mrsic-Flogel TD, King AJ, Jenison RL, Schnupp JWH: Listening through different ears alters spatial response fields in ferret primary auditory cortex. *J Neurophysiol* 2001;86:1043–1046.
- Parsons CH, Lanyon RG, Schnupp JWH, King AJ: Effects of altering spectral cues in infancy on horizontal and vertical sound localization by adult ferrets. *J Neurophysiol* 1999;82:2294–2309.
- Schnupp JWH, Booth JWR, Mrsic-Flogel T, King AJ: Individual differences in ferret spectral localization cue values are reduced by frequency scaling. *Abstr Assoc Res Otolaryngol* 2001;24:262.
- Schnupp JWH, King AJ, Carlile S: Altered spectral localization cues disrupt the development of the auditory space map in the superior colliculus of the ferret. *J Neurophysiol* 1998;79:1053–1069.
- Shaw EAG, Teranishi R: Sound pressure generated in an external ear replica and real human ears by a nearby point source. *J Acoust Soc Am* 1968;44:240–249.
- Shinn-Cunningham BG, Durlach NI, Held RM: Adaptation to supernormal auditory localization cues. I. Bias and resolution. *J Acoust Soc Am* 1998;103:3656–3666.
- Slattery WH, Middlebrooks JC: Monaural sound localization: Acute versus chronic unilateral impairment. *Hear Res* 1984;75:38–46.
- Stein BE, Meredith MA: *The Merging of the Senses*. Cambridge, MIT Press, 1993.
- Wenzel EM, Arruda M, Kistler DJ, Wightman FL: Localization using nonindividualized head-related transfer functions. *J Acoust Soc Am* 1993;94:111–123.
- Xu L, Middlebrooks JC: Individual differences in external-ear transfer functions of cats. *J Acoust Soc Am* 2000;107:1451–1459.