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What is This?
Auditory localization poses the nervous system a challenge fundamentally different from localization through other sensory modalities. For instance, visual and somatosensory receptors are organized so that stimuli in adjacent spatial locations activate adjacent sensors on the retina or the skin. The spatial organization of these sensors is mirrored by cortical neurons, the result being a topographical map of sensory space. This type of neural representation is often called a place code. In contrast, the auditory system is characterized by tonotopical representation, that is, topographical organization according to sound frequency, starting from the auditory receptors in the inner ear and continuing all the way up to the auditory cortex. In this tonotopical representation, information on the location of a sound source is embedded in the form of localization cues (Middlebrooks and Green 1991). These cues are the interaural differences in timing and level of the sound as well as spectral cues arising from the direction-dependent filtering effects of the pinnae, the head, and the body (Fig. 1).

The extraction of localization cues in the auditory brainstem nuclei was long believed to result in a place code of sound source location (for a review, see Joris and others 1998). This view has, however, been abandoned in the absence of evidence for the required computations taking place in the auditory brainstem of small mammals (Grothe and others 2010). Furthermore, attempts to find a topographical map of auditory space in the cat and monkey cortex have consistently failed (Rajan and others 1990; Clarey and others 1994; Werner-Reiss and Groh 2008). These results have given rise to suggestions of alternative population coding strategies for extracting and representing auditory spatial information (Fig. 2).

In the human auditory cortex, sound source location is represented by a population rate code: the hemifield code (Salminen and others 2009, 2010; Fig. 2). This is a major deviation from the topographical representations of visual and somatosensory space in cortex and implies that audition has its own unique solutions for spatial processing distinct from those implemented by other sensory modalities. The aim of this review is to outline how various auditory spatial tasks are achieved in the human cortex with the use of the hemifield code. To this end, the authors consider how various implementations of the hemifield code may exist within the auditory cortex and how these may be modulated by the stimulation and task context. As a result, a coherent set of neural strategies for auditory spatial processing emerges.

Auditory Spatial Processing in the Human Cortex

Nelli H. Salminen¹, Hannu Tiitinen¹, and Patrick J. C. May¹

Abstract
The auditory system codes spatial locations in a way that deviates from the spatial representations found in other modalities. This difference is especially striking in the cortex, where neurons form topographical maps of visual and tactile space but where auditory space is represented through a population rate code. In this hemifield code, sound source location is represented in the activity of two widely tuned opponent populations, one tuned to the right and the other to the left side of auditory space. Scientists are only beginning to uncover how this coding strategy adapts to various spatial processing demands. This review presents the current understanding of auditory spatial processing in the cortex. To this end, the authors consider how various implementations of the hemifield code may exist within the auditory cortex and how these may be modulated by the stimulation and task context. As a result, a coherent set of neural strategies for auditory spatial processing emerges.

Keywords
auditory cortex, sound localization, space perception, auditory perception, human

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outline strategies by which the hemifield code can adjust to varying contexts and task demands.

**Spatial Receptive Fields in Auditory Cortex: A Hemifield Code**

Converging evidence from single-unit recordings in non-human primates and from human neuroimaging and behavioral studies points to a representational strategy of auditory space that relies on neurons widely tuned to spatial location. Specifically, spatial receptive fields of single neurons in the monkey auditory cortex are wide, often covering nearly half of the auditory space, and are not organized topographically on the cortical surface (Benson and others 1981; Ahissar and others 1992; Woods and others 2006; Werner-Reiss and Groh 2008). The most common type of spatial receptive field found in the auditory cortex of cats and monkeys is one comprising an entire hemifield, either the left or the right one. These hemifield-tuned neurons constitute the majority of all spatially

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**Figure 1.** The importance of spatial hearing in everyday life. (A) We are often in situations in which multiple conversations take place concurrently. Yet, we are able to focus on one speaker at a time and ignore the rest. (B) Sound waves arrive to our ears from several sources, and these are multiplied by reverberations (only a subset is depicted). The delineation between sound sources relies heavily on spatial information. (C) The perception of sound source location is based on the extraction of localization cues embedded in the sound. The most important cues for localizing in the horizontal plane are the interaural differences in time and level (ITD and ILD, respectively). The sound reaches the ear closer to the sound source earlier and this gives rise to ITD. ILD is created by the shadowing effect of the head.
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selective neurons, with only a small minority tuned to frontal directions. That is, nearly all of the spatially sensitive neurons in the auditory cortex fall into two categories, either right-tuned or left-tuned, and both types of neurons can be found in each cortical hemisphere. This discovery has led to the suggestion of a population rate code of auditory space in which horizontal sound source location is represented in the relative levels of activation in the two opponent populations (Fig. 2; Stecker, Harrington, and Middlebrooks 2005; Werner-Reiss and Groh 2008). Here we refer to this strategy as the hemifield code.

In recent neuroimaging studies, the hemifield code was confirmed to be the primary form of spatial representation also in the human auditory cortex (Salminen and others 2009, 2010). Studying receptive field properties in the human brain is challenging because the non-invasive measurements aggregate the activity of large neural populations into a single signal. The recent magnetoencephalography (MEG) results were obtained through the use of a stimulus-specific adaptation paradigm (Fig. 3A). In this paradigm, sounds are presented from two alternating locations: a probe and an adaptor. When the probe and the adaptor are presented in the same location, they repeatedly activate the same spatially selective neurons, leading to attenuated activity and a diminished contribution to the MEG signal. However, when a spatial separation is introduced between the probe and adaptor sources, these activate different sets of neurons. Then, each neuron exclusively responding to either the adaptor or the probe is activated less frequently, and this leads to less attenuation and larger MEG response amplitudes. In the MEG recordings, probes and adaptors were presented either within the same hemifield or in opposite hemifields (Fig. 3A), and the amplitude of the response to the probe was recorded (Fig. 3B). When the sounds were in opposite hemifields, little attenuation of auditory cortical activity occurred. However, when the two sound sources were placed within the same hemifield, attenuation was strong even with extensive spatial separations (45-90 degrees) between the source locations. This is consistent with the hemifield coding strategy (Fig. 3C). Sound sources within the same hemifield activate the same hemifield-tuned neural population, and therefore strong adaptation is to be expected. Conversely, when the two sound sources fall into different hemifields, they activate primarily different hemifield-tuned neurons and little adaptation occurs.

Interestingly, a spatial coding strategy based on wide rather than narrow spatial receptive fields was suggested by psychophysical studies (Phillips and Hall 2005; Phillips and others 2006; Vigneault-MacLean and others 2007) before its discovery in recordings of brain activity. In these studies, subjects were first exposed to prolonged adaptor sounds in either the left or the right hemifield, and the influence of this exposure on the perceived location of a subsequent probe sound was evaluated. The laterally presented adaptors biased the perceived locations of the probe sounds toward the hemifield opposite to the one where the adaptor was presented. Importantly, this biasing effect applied to probes far away from the adaptor. If the perceptions of sound source location were based on narrow spatial tuning, the effect would be expected to occur locally only for probe sounds in the immediate vicinity of the adaptor location. However, the influence of the adaptor even on the perceived locations of probe sounds far away is parsimoniously accounted for by wide spatial receptive fields, such as those in the hemifield code.

At first glance, the hemifield coding strategy may appear to be at odds with behavioral sound source localization. Often areas of space with better perceptual resolution, for instance, the tips of the fingers or the central visual field, are represented by large numbers of neurons maximally activated by stimuli at these locations. The ability of humans to localize sound sources is best for sounds presented directly in front (Middlebrooks and Green 1991). Therefore, one might expect maximal tuning to sound sources in front to be a common feature of auditory cortical neurons. However, in the hemifield code, neurons are maximally activated by lateral rather than frontal locations. This apparent discrepancy can be resolved by considering the contribution of the slope of

**Figure 2.** The place code and the hemifield code. Two alternative neural strategies for representing sound source location have been proposed. In the place code, sound source direction is represented by neurons narrowly tuned to location. The hemifield code consists of two neural populations widely tuned to location: one tuned to the left and the other to the right hemifield.
the spatial tuning curve to perceptual acuity. In a wide tuning curve, the best discrimination power of the neuron is far away from the location causing maximal activity (Kim and Bao 2008). The top of such a tuning curve is relatively flat, and therefore two nearby stimuli elicit similar levels of activity. However, when these two stimuli fall onto the slope of the tuning curve, they elicit unequal levels of activity. In the hemifield-tuned neurons, the steepest slopes of the tuning curves are associated with spatial locations in front (Leiman and Hafter 1972; Eisenman 1974; McAlpine and others 2001; Stecker, Harrington, and Middlebrooks 2005). This property of the tuning curves coincides with the usefulness of the localization cues: they vary more as a function of sound source location in front than in lateral locations. This may explain why behavioral localization accuracy is at its best for frontal locations.

**Specialization in Spatial Processing in Posterior Auditory Cortex**

Imaging studies of the human brain suggest that posterior auditory cortical areas are specialized in spatial processing. In these experiments, hemodynamic activity elicited...
by a sound source in a single location is contrasted to activity following the presentation of sounds from multiple as opposed to only one spatial location. When sounds are presented only from a frontal location, the sound activates both the left- and right-tuned neurons of the hemifield code only moderately (top). When sounds are presented from multiple locations within the left and right hemifields, both neural populations are activated to a higher level (bottom).

Figure 4. Posterior specialization to space arising from the hemifield code. (A) Human brain imaging studies have found increased levels of activity in the posterior end of the human auditory cortex when sounds are presented from multiple as opposed to only one spatial location. (B) This increase can be explained by the presence of hemifield-tuned neurons. When sounds are presented only from a frontal location, the sound activates both the left- and right-tuned neurons of the hemifield code only moderately (top). When sounds are presented from multiple locations within the left and right hemifields, both neural populations are activated to a higher level (bottom).

Cortical Representations of Auditory Motion

Sound sources are rarely static with respect to the ears. Therefore, the ability to integrate location information over time is important for creating a coherent perception of the auditory environment. In a topographic map of space, motion perception could be achieved by neurons detecting sequential activation in adjacent locations of the map. In the hemifield code this is not possible, and therefore an alternative strategy is needed for constructing neural detectors for auditory motion.

Human brain imaging studies have tried to identify areas specialized in motion processing in auditory cortex. In fMRI recordings, the planum temporale is activated to a higher level during the presentation of moving sound sources than during stationary ones (Baumgart and others 1999; Pavani and others 2002; Warren and others 2006). In all areas, the majority of spatial receptive fields display hemifield tuning; that is, they are wide and centered to left or right. However, there are subtle differences between the anterior and posterior areas in the way the hemifield code is implemented, and these differences might account for the results of human brain imaging studies showing spatial selectivity specifically in the posterior auditory areas. First, cat and monkey studies have shown that spatially selective neurons are more numerous in the posterior than anterior or primary areas (Recanzone 2000; Tian and others 2001; Stecker and others 2003). If this difference also applies to the human brain, it implies that in the posterior auditory cortex, a larger number of hemifield-tuned neurons take part in generating the location-dependent effects than in the anterior auditory cortex. This larger number of neurons would then lead to a larger overall size of the effect found in MEG and hemodynamic signals.

The second difference between the hemifield-tuned neurons in the posterior and anterior areas is related to the extent to which the level of neural activity is modulated by sound source location. In the cat, the modulation depth of neural activity as a function of sound source location is larger in the posterior auditory field and the dorsal zone than in other auditory fields (Stecker and others 2003; Stecker, Harrington, Macpherson, and others 2005). Also in the monkey auditory cortex, differences in spatial receptive fields between caudal belt and primary auditory cortex have been found (Recanzone 2000). Compared with neurons in the primary auditory cortex, the caudal belt neurons have a steeper slope for sound sources directly in front. Both the larger modulation depth found in cat posterior field and the steeper slope in the monkey caudal belt translate into a larger variation in neural activation level due to changes in sound source location. If these qualities applied also to the human posterior auditory cortex, they would potentially explain why the above-described indications of spatial selectivity are larger in the posterior than in the anterior auditory cortex.
others 2002). However, it is not clear whether this increase in activity reflects genuine specialization in motion processing. In the studies reporting auditory motion areas, activity elicited by a sound source moving from one side of the auditory space to the other is contrasted with that elicited by the presentation of a single stationary sound source in front. In light of the results on specialization in spatial processing of posterior areas (see previous section), it is possible that the increased activity in planum temporale is due to sounds appearing in multiple locations in the motion condition as opposed to the single frontal one in the control condition (Fig. 4). That is, the increase in planum temporale activity would reflect the range of sound source locations spanned by the stimulation rather than auditory motion as such. This possibility has been investigated by including a more appropriate control condition consisting of stationary sound sources in multiple locations (Smith and others 2004, 2007). When compared with this condition, no increase in activity of planum temporale or other auditory cortical areas appeared in response to auditory motion. Therefore, doubt is cast on the existence of auditory areas specialized in motion processing.

In animal studies, neurons selective to the motion direction of a sound source are encountered at several stages of the auditory pathway, including the auditory cortex (Ahissar and others 1992; McAlpine and others 2000; Malone and others 2002). These neurons respond more strongly to sound source motion from either left to right or vice versa than to motion in the opposite direction. Sensitivity to the direction of sound source motion is often systematically related to the selectivity of the neuron to stationary sound source locations. Typically, these neurons respond with a higher firing rate when a sound source approaches their preferred hemifield than when a sound source is moving away from it (Fig. 5; Ahissar and others 1992; McAlpine and others 2000; Ingham and others 2001; Malone and others 2002). For instance, neurons activated by stationary sound sources in the left hemifield respond at a higher rate when a sound source moves toward the left hemifield than when the motion covers the same range of locations but is directed toward the right. Such sensitivity to the stimulation history is a common feature of auditory cortical neurons (Phillips and others 2002; May and Tiitinen 2010). For the spatially selective neurons, sensitivity to the history of activity gives rise to selectivity to motion direction (Spitzer and Semple 1991, 1993; McAlpine and others 2000; Ingham and others 2001; Malone and others 2002).

In the human brain, responses to auditory motion are in line with the above-described properties of single neurons. In a recent electroencephalography (EEG) study, brain responses were recorded for changes in source location between the midline and a lateral location either in the left or the right hemifield (Magezi and Krumbholz 2010). The transition was either from the midline to the lateral location or in the opposite direction but always covered the same range of spatial locations. Movement from the midline gave rise to more prominent brain responses than movements toward the midline. This is consistent with the behavior of the hemifield-tuned neurons found in single-neuron studies (McAlpine and others 2000; Ingham and others 2001; Malone and others 2002). For example, the EEG responses to motion within the left hemifield would be expected to arise primarily from the left-tuned population of the hemifield code. For these neurons, the sound source moving toward the location on the left approaches the receptive field and leads to a large response (McAlpine and others 2000; Ingham and others 2001; Malone and others 2002). The sound moving from the left to the front in turn moves away from the receptive field and a smaller response occurs. Together these findings suggest that motion detection in the human brain is implemented by neurons that also contribute to the coding of stationary sound source locations. The lack of separate neural populations for representing sound source location and motion direction could explain why areas specialized specifically in the processing of auditory motion have not been found in the human brain.
Task- and Context-Induced Modulations in Auditory Spatial Receptive Fields

Cortical representations of sensory information are known to adapt to task demands. For instance, selectivity to sound frequency can become sharper and neurons can change their frequency preferences in order to provide better detection of target sounds (Fritz and others 2003; Kauramäki and others 2007). The neural strategies for representing sound frequency and spatial location are fundamentally different, frequency being represented with a place code and location with the hemifield code. Thereby, also task-induced modulations can be expected to occur in the representation of auditory space in a distinct manner. Although it is unknown whether such changes take place in the spatial receptive fields of the human auditory cortex, animal studies have revealed mechanisms that may be suitable for temporarily adjusting the hemifield code according to task demands.

In the cat primary auditory cortex, some neurons change their spatial selectivity according to task conditions (Lee and Middlebrooks 2011). This was discovered in a comparison between the spatial tuning widths of single neurons during idle listening and during the performance of an auditory task. During idle listening, the spatial receptive fields ranged from approximately half the auditory space to covering nearly all locations in the horizontal plane. In contrast, while the cat was performing an auditory detection task, the average tuning width of the neurons dropped so that most receptive fields covered only half of the horizontal plane. That is, neurons that during idle listening are responsive to a wide range of spatial locations become more selective during task performance. This increase in the number of spatially selective neurons implies that more neurons take part in representing sound source location in the hemifield code, and this possibly improves the accuracy of the representation.

In some situations, there may be a need to prioritize localization accuracy in some particular direction such as when an interesting event occurs in one direction while sounds arriving from other directions are deemed less relevant. In the hemifield code, the best localization accuracy is provided by the slopes of the tuning curves coinciding with locations in front. Therefore, one strategy for targeting discrimination power to a relevant location is simply to turn the head to the target direction. A similar effect might be possible without a motor act by a modulation of auditory neural activity so that the steepest slope of the receptive field coincides with the direction of interest. A possible signal for the relevance of a sound source location is the frequency of occurrence of sounds from that location. A direction from which sounds originate frequently is likely to be a direction in which good location discrimination is needed. This signal of relevance was recently used in evaluating the context-sensitivity of hemifield-tuned neurons in the ferret inferior colliculus (Dahmen and others 2010). In this experiment, the stimulation statistics were varied so that sounds occurred more frequently in one location than in others. The spatial receptive fields of inferior colliculus neurons were found to shift so that the steepest slope of the curve migrated toward the location at which sounds occurred most frequently (Fig. 6). This modulation in the spatial receptive fields targets the best discrimination power of the spatially selective neurons to the location where the majority of sound sources occur. It is unknown whether similar adaptation mechanisms take place in the cortex or in the human brain.

Conclusions and Directions for Future Research

In this review, we have presented a set of neural strategies for processing auditory spatial information. Human neuroimaging and behavioral studies and single-unit recordings in animals show that the auditory cortex represents spatial locations with a population rate coding strategy, the hemifield code (Vigneault-MacLean and others 2007; Werner-Reiss and Groh 2008; Salminen and others 2009). This code can be found in all auditory...
cortical areas (Middlebrooks and others 2002; Woods and others 2006). However, there are quantitative differences between areas, with the posterior auditory cortex showing higher levels of spatial selectivity (Recanzone 2000; Tian and others 2001; Stecker and others 2003). In the hemifield code representation of space, sensitivity to auditory motion arises from the sensitivity of single neurons to their history of activation (McAlpine and others 2000). This leads to the representations of stationary and moving locations to be overlapping and realized by the same set of neurons. Finally, animal studies suggest that the hemifield code may also adapt to the context and task demands signaled by attention or the properties of the auditory environment (Dahmen and others 2010; Lee and Middlebrooks 2011).

In light of the findings reviewed here, it seems clear that the representation of auditory space in cortex is not formed by a set of static feature detectors but rather is an adaptive system sensitive to context. Here this was manifested in two ways. First, the sensitivity of the hemifield-tuned neurons to motion direction emerges from the sensitivity to the stimulation history (McAlpine and others 2000; Ingham and others 2001; Malone and others 2002). Thus, sensitivity to dynamical stimulation properties does not require a new processing stage that integrates the activity of the previous step. Instead, sensitivity to motion can be achieved within the population already sensitive to the location of stationary sound sources. Further, motion sensitivity occurs only in a subset of neurons. This could be explained by neurons integrating over different time scales and may presumably also influence sensitivity to the speed of auditory motion. Second, the frequency of occurrence of sound source locations in previous stimulation has an effect on the spatial receptive fields (Dahmen and others 2010). Spatial tuning curves can shift so that the best discrimination ability of the neuron coincides with the direction from which most sounds originate. If such mechanisms exist also at the cortical level, they could serve the purposes of, for instance, spatial selective attention. Hypothetically, the tuning curves shift so that best neural performance in sound source localization is at the direction of attention. This could provide a potential neural explanation for the improved perceptual performance brought by spatial attention.

Human brain imaging studies imply that the posterior auditory cortex is specialized in spatial processing (Zatorre and others 2002; Krumholtz and others 2005; Ahveninen and others 2006). This claim is further supported by the role of the posterior auditory cortex in the dorsal auditory processing stream, whose central function is spatial processing (Rauschecker and Tian 2000). This stream functions as a link between the auditory cortex and the multimodal parietal cortical areas. In light of this, the differences between spatial tuning properties in posterior and other auditory cortical areas found in single-unit recordings are surprisingly small. The tuning pattern is qualitatively the same in all areas, that is, in line with the hemifield code, and only small quantitative differences can be found in the steepness of spatial selectivity (Recanzone 2000; Tian and others 2001; Stecker and others 2003). This suggests that substantial differences in spatial processing may still exist for sound features that have not been considered in previous comparisons between auditory cortical areas. For instance, the posterior areas may implement the dynamical properties leading to context- and motion-sensitivity to a larger extent than other areas. Alternatively, the special role of the posterior auditory areas in spatial processing may be related to spectral analyses. Some aspects of spatial hearing involve the extraction of spectral localization cues, and these cues need to be delineated from features related to other sound properties. Therefore, the posterior auditory cortex may be the performer of these analyses (Griffiths and Warren 2002).

At some stage of spatial processing, the hemifield-coded representation of auditory space needs to be integrated with the place-coded representations of visual and somatosensory space. In the cortex, this integration presumably takes place in posterior parietal areas. These areas integrate information from vision, touch, and audition and participate in formulating motor responses (Mazzoni and others 1996; Stricanne and others 1996; Cohen and Andersen 2000; Griffiths and others 2000; Lewis and others 2000; Gifford and Cohen 2004; Schlack and others 2005). In posterior parietal cortex, spatial receptive fields to visual and auditory stimuli are not shaped like the receptive fields of the hemifield code. Instead, they are relatively narrow (~40 degrees) and peak in directions other than lateral ones (Stricanne and others 1996; Schlack and others 2005). Thus, the format of auditory spatial representation in the parietal cortex is no longer a hemifield code. Instead, the locations of sound sources appear to be related to representations of motor acts. A similar situation can be found in the subcortical superior colliculus. Here, neurons form a topographical map of auditory spatial locations, and their activity is associated with eye movements to auditory targets (Palmer and King 1982; Wise and Irvine 1983). Therefore, neurons in the superior colliculus and posterior parietal cortex appear to represent eye or arm movements needed for reaching the sound source with the gaze or the hand, and sound source location is represented as a potential target for a movement. The details of this representation or how it is transformed from the hemifield code are still unknown.

Lesion studies performed in cats and monkeys show that the auditory cortex is crucial for successful sound source localization (Jenkins and Merzenich 1984; Heffner 1997). In these studies, the animals are trained to approach
the location of a sound source. Bilateral ablation of the auditory cortices leads to an inability to perform this task while unilateral lesions lead to deficits specific to the hemifield on the opposite side of the lesion. Left- and right-tuned neurons can be found in both auditory cortices, which, therefore, should be able to represent sound source locations in both hemifields. It is not clear why deficits specific to the contralateral hemifield still arise. One alternative is that the lesion disrupts the functions of the posterior parietal cortex responsible for orienting responses to locations in the contralateral hemifield. Intriguingly, lesions of the human auditory cortex do not cause problems specific to the contralateral space. Instead, severe localization deficits are found in the entire auditory space as a consequence of right-hemispheric lesions (Zatorre and Penhune 2001; Spierer and others 2009). This may also be related to the functions of the parietal cortex. In humans, lesions to the right parietal cortex lead to neglect, a condition associated with severe problems in spatial orientation. Presumably, the missing or dysfunctional right-hemispheric auditory cortex could lead to disturbances in auditory spatial orienting performed by the right parietal cortex and thereby cause problems in sound source localization.

Neurons consistent with the hemifield coding strategy are numerous in the auditory cortex. This does not, however, exclude the presence of additional strategies for auditory spatial processing. Most of the evidence supporting the hemifield code considers only one aspect of the neural response, the firing rate at stimulus onset. Therefore, other forms of spatial representation could possibly be found by considering other features of the neural response. For instance, some studies have found the timing of spikes to carry information on spatial location (Middlebrooks and others 1994, 1998). Additional spatial selectivity may also reside in the firing rate during sustained activity. Often, auditory cortical neurons respond strongly to the onset of a sound but show low levels of sustained activity. However, high levels of sustained activity can be found when the properties of the stimulus such as its frequency content and temporal modulation match the preferences of the neuron (Wang and others 2005). This may reflect a higher level of selectivity to stimulus features in the sustained than in the onset response. Whether selectivity to auditory spatial location differs in the sustained and onset responses is not known.

The hemifield code accounts for various aspects of sound source localization within the horizontal plane. This is also the dimension along which sound source localization is behaviorally best. However, we have also the ability to perceive the elevation and distance of sound sources (Middlebrooks and Green 1991). These two dimensions cannot as such be incorporated in the hemifield code and therefore require another, still unknown, coding strategy. Although location perception in the left-right dimension is based on the interaural difference cues, the perception of elevation requires the extraction and correct interpretation of spectral cues (Middlebrooks and Green 1991). This implies that the extraction of elevation information is based on the analysis of the frequency spectrum of the stimulus. This needs also to be combined with previous knowledge on the sound to avoid confusion between the localization cues and other sound features. The perception of distance relies on the sound level, on changes in the sound spectrum, and, in enclosed spaces, on familiarity with the room acoustics. This process also relies on previous knowledge of sound sources and the acoustical environment. Although the hemifield code as such does not explain these aspects of spatial hearing, they may still be realized by the hemifield-tuned neurons. The hemifield code has the advantage that the left-right dimension of auditory space is represented by only two types of neurons. Therefore, representations of other stimulus features can be combined with the representation of horizontal sound source location without an explosion in the number of neurons needed for creating a complete combinatorial representation of place-coded stimulus features (see also Stecker, Harrington, and Middlebrooks 2005).

Converging lines of investigation support the hemifield code of sound source location and further emphasize that the representation of auditory space is not static but rather dynamically changes according to the auditory environment and perceptual goals. At the level of single neurons, new functionality arises from the sensitivity of the neurons to their previous stimulation and to the demands set by the listening task. In behavioral sound source localization, the context in which the sounds are presented and the previous knowledge of the listener about sound sources and the environment have a crucial role. Therefore, future research might greatly benefit from an approach that takes the auditory context and the previous experiences and current goals of the listener into consideration.

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