

TUTORIAL

Cortical codes for sound localization

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Abstract: It is well known that there is a point-to-point map of auditory space in the midbrain: each neuron is tuned to a particular sound-source location, and neurons' preferred locations are topographically represented in a neural structure. In the auditory cortex, however, researchers have consistently failed to demonstrate evidence for such an auditory space map, despite the well-known necessity of the auditory cortex for normal sound localization. Cortical neurons show generally broad spatial tuning, and the preferred locations are not systematically organized on the cortex in a topographical fashion. An alternative hypothesis is presented here: Individual single neurons represent auditory space panoramically by space-specific characteristics of their spike patterns. Information about any particular sound-source location is distributed across a large population of neurons, and we predict accurate localization judgement by combining information across those neurons. In our analyses of experimental data using an artificial neural network algorithm, we were able to recognize spike patterns of single neurons to identify sound-source locations throughout 360° of space. The amount of information carried by a moderate size of neural ensemble appeared sufficient to account for the accuracy of location judgements by behaving animals.

Keywords: Sound localization, Auditory cortex, Neural coding, Distributed code

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1. INTRODUCTION

One of the elementary attributes of a sound source is its location in space. The ability of the auditory system to localize sound sources enables animals to locate prey or to avoid predators. Sound localization can improve the detection and identification of sounds of interest in the presence of spatially distinct competing sources.

An intact auditory cortex is essential for normal sound localization, as demonstrated by localization deficits that result from cortical lesions in humans [1–4] and experimental animals [5–7]. Numerous studies have explored the neurophysiological mechanisms for location coding in the auditory cortex. One straightforward hypothesis is that the auditory cortex contains a point-to-point map of auditory space. This *topographical code* hypothesis assumes that each neuron is selective for a particular sound-source location, that the preferred locations of neurons vary according to cortical location, and that the location of a sound source is coded by the location in the cortex of a restricted population of maximally active neurons. Topographical representation of auditory space has been

demonstrated in the optic tectum in the barn owl [8] and in the superior colliculus in mammals (guinea pig [9], cat [10], monkey [11], and ferret [12]). In the auditory cortex, however, researchers consistently have failed to demonstrate such a spatial map, at least not in the topographic form found in the midbrain.

In this article, we will begin by describing the spatial sensitivity of neurons in the auditory cortex and will cite some limited evidence for spatial topography, but will argue against the presence of a map of space in the auditory cortex. Then we will present an alternative view of auditory spatial coding, in which individual neurons code locations throughout space and in which information about a particular point in space is distributed among a large population of neurons. We will consider some specific ways in which neural populations (or “ensembles”) might represent sound-source locations. This article focuses on cortical physiology in the cat because that species has been studied in most detail. Nevertheless, we will conclude with a brief note on a recent model pertaining to non-human primates.

2. NEURONAL SPATIAL TUNING AND CORTICAL TOPOGRAPHY

In the cat, the spatial sensitivity of neurons has been studied in the primary auditory cortex (area A1) [13–16], area A2 [17–19], the anterior ectosylvian area (area AES) [17–20], and to a limited degree in the anterior auditory area (area AAF) [20]. There are good reasons to assume that cortical areas A1, A2, and AES are involved in sound localization. In the case of A1, Jenkins and Merzenich [6] observed that lesions restricted to area A1 impaired cats' localization of sounds presented contralateral to the lesion. In the case of A2, the neurons generally have favorable features for sound-location coding, such as broad frequency tuning [21], and spatial sensitivity that parallels psychophysical responses to sounds that produce spatial illusions [22]. In the case of area AES, Meredith and Clemo [23] found that area AES is the only auditory cortical field in cats that sends strong anatomical projections to the superior colliculus, which contains an auditory space map. Nevertheless, among the cortical areas in which spatial coding has been studied physiologically, no area stands out as obviously containing more spatially selective units or a more consistent spatial topography.

Figure 1 shows examples of spike counts of units in area A2 as a function of sound-source location in the horizontal plane (azimuth) and in the vertical midline plane (elevation) [24]. Positive azimuths are on the cat's right side, ipsilateral to the recording site, and positive elevations are above the horizontal plane. The examples roughly span the range of sharpness of tuning that we have observed. Spatial sensitivity varies among units and, to a lesser degree, among cortical areas, but one can make some generalizations. The majority of cortical units shows greater than 50% modulation of their spike counts by the location of the sound source in azimuth (area A1 [14, 15]; areas A2 and AES [18]). Spatial sensitivity tends to be broad. For instance, 58 to 97% of units in areas A2 and AES responded with more than 50% of their maximum spike rates across receptive fields spanning 180° or greater [18]; the exact percentage of units varied with cortical area and sound level. A similar breadth of sensitivity is reported for the majority of units in area A1 [13, 15, 16]. Spatial receptive fields of neurons tend to be smallest when measured with sound levels near threshold, but increases in sound levels can result in considerable expansion of receptive fields [13, 25]; Figure 1 shows examples of spatial tuning that broadened with increasing sound level. In many instances, the spatial preferences of units can change with changes in sound level. In areas AES and A2, more than half of the units that

showed measurable spatial tuning when stimulus levels were 20 dB above threshold showed substantial changes in the locations of stimuli that produced maximum responses when sound levels were increased by 20 dB. The units represented in Figs. 1B and C are examples that showed such changes in tuning. Spatial profiles of units can show two or more discrete peaks separated by well-defined valleys, as seen in Figs. 1A and B. Middlebrooks and colleagues [18] found that ~20% units in area A2 and AES had two or more peaks.

A sound source at moderate level at any location activates a sizeable fraction of the units in the contralateral auditory cortex. Figure 2 shows, as a function of sound-source azimuth, the percentage of units recorded in area A2 that were activated to more than 25, 50, or 75% of their maximum firing levels. The plots demonstrate, for instance, that a sound source at a level 40 dB above threshold located nearly anywhere on the side contralateral to the recording site would activate nearly all units to at least half of their maximal rates, and sounds at most contralateral locations would activate about 70% of units to more than 75% of their maximum rates. That is, a model that relied on spike counts to code locations in contralateral space would require that nearly all units discriminate locations with counts restricted to the maximum half of their dynamic ranges (*i.e.*, spike counts could range between 50 and 100% of maximum). Indeed, the majority of units would need to operate in the upper quarter of their dynamic ranges (75 to 100% of maximum).

A topographical model of spatial coding in the cortex would require that the spatial preferences of units vary systematically as a function of the locations of units in the cortex. In support of a topographical model, the studies described above found that units that are located close together in the cortex generally tend to show similar spatial sensitivity. For instance, Middlebrooks and Pettigrew [13] found clusters of units that showed the same receptive field class. Units within a particular receptive field class, however, often occupied multiple clusters that were separated by units within a different receptive field class. Subsequent studies have confirmed the tendency of units with similar spatial tuning to aggregate in the cortex [26, 27]. Some studies have demonstrated examples of sequences of units along as much as 1.5 mm of electrode tracks across the cortex that showed systematic changes in spatial preferences [14, 18]. Such sequences of units, however, were interspersed among sequences of units that showed very different spatial sensitivity. Investigators who have searched for spatial topography in areas A1, A2, or AES consistently have concluded that the organization that they found was not consistent with an integrated cortical map of auditory space.

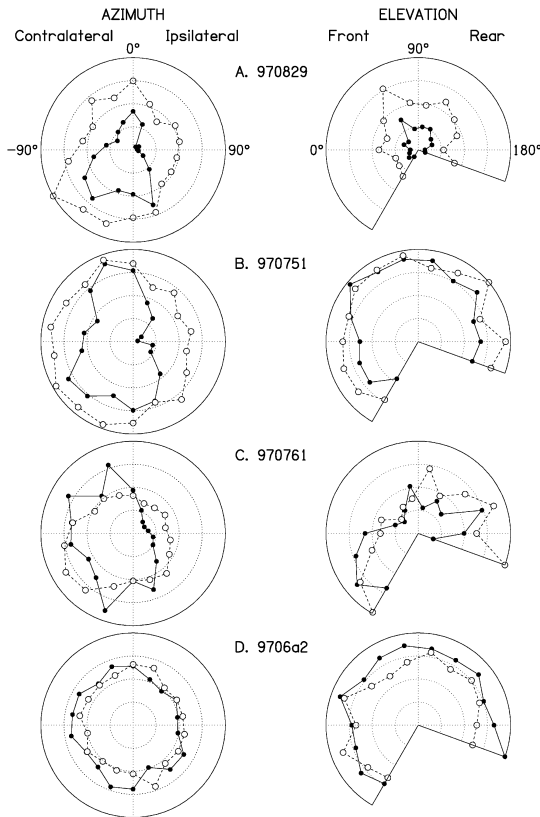


Fig. 1 Spatial tuning of spike counts of neurons recorded in area A2. Each row represents one unit. Left and right columns represent the azimuth tuning and elevation tuning, respectively. In these polar plots, the angular dimension shows the sound-source location and the radial dimension shows the average spike count normalized to 100%. Azimuth straight front of the animal is labeled as 0°, and positive azimuths indicate the right side of the animal, ipsilateral to the recorded cortical hemisphere. The elevation plots are views from the cat's left side. Filled and open symbols indicate sound levels 20 dB and 40 dB, respectively, above units' thresholds. (From Middlebrooks [24])

3. PANORAMIC CODE BY SINGLE NEURONS

In a conventional view of stimulus coding by neurons, each neuron responds maximally for some restricted range of stimuli and is relatively insensitive to other stimuli. The generally broad spatial sensitivity of the auditory cortical neurons that have been studied to date suggests an alternative view, that location-specific characteristic responses of individual neurons might signal the locations of sound sources throughout broad ranges of locations [18, 19]. Figure 3 represents the responses of a neuron in area AES to noise bursts presented from vari-

ous azimuths in the horizontal plane. Each row of dots represents the pattern of spikes recorded during one stimulus presentation; eight presentations at each azimuth are shown. One can see differences in the response patterns elicited from various locations. Most conspicuous was the tendency of stimuli at contralateral locations to elicit the greatest spike counts. Also, for both contra- and ipsilateral stimuli, stimuli at frontal locations tended to elicit temporally restricted bursts of spikes with short first-spike latencies, whereas stimuli at rear locations tended to elicit longer-latency spike patterns that were more dispersed in time.

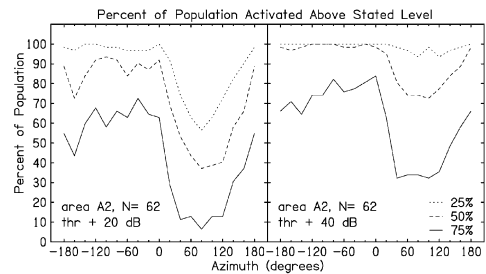


Fig. 2 Percentage of the neural population activated by sound sources at various locations in azimuth. Populations consisted of 62 neurons in area A2. Left and right panels represent stimulus SPLs of 20 and 40 dB, respectively, above units' thresholds. The three lines in each panel show the percentages of the units that were activated above 25, 50, or 75% of each unit's maximum spike count. (Modified from Middlebrooks *et al.* [18])

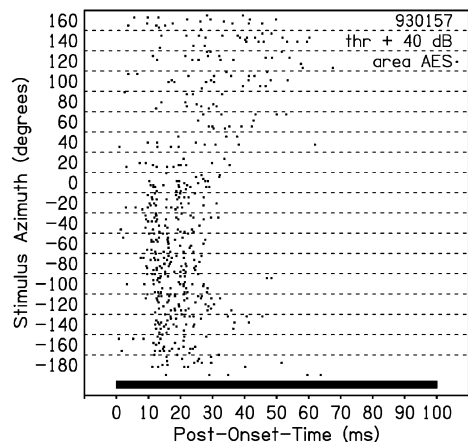


Fig. 3 Responses of a neuron to sounds at various azimuths. Each dot represents the latency of one spike from the unit, expressed relative to the stimulus onset. Each row of dots represents the spike pattern in response to one presentation of a 100-ms noise burst. Eight trials for each stimulus azimuth are shown. Sound-source azimuth is indicated on the vertical axis. (Modified from Middlebrooks *et al.* [18]).

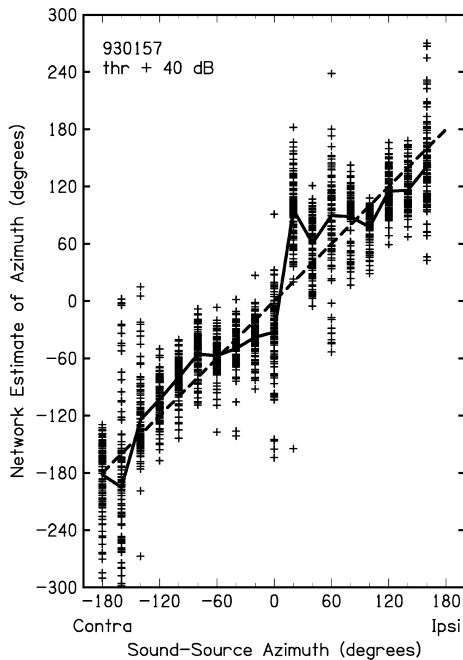


Fig. 4 Artificial-neural-network estimates of sound-source azimuth. Each plus sign represents the network estimate of azimuth based on recognition of one spike pattern. Horizontal and vertical axes represent the actual sound-source location and the network estimate of the azimuth, respectively. The solid curve represents the circular centroid (*i.e.*, the average) of the estimates at each source azimuth. The dashed line represents the loci of perfect estimates. (Modified from Middlebrooks *et al.* [18])

We measured the accuracy with which location-specific spike patterns could signal sound-source locations. An artificial-neural-network (ANN) algorithm was used to identify sound-source locations by recognizing characteristic temporal spike patterns of cortical neurons. The ANN was a two-layer feedforward perceptron with nonlinear transfer functions [28]. The ANN could recognize high-dimensional input patterns without need for a priori specification of particular information-bearing features of the patterns, such as spike counts or first-spike latencies. We interpreted the accuracy of ANN estimations as an empirical measure of the amount of stimulus-related information carried by the spike patterns. In experiments, we recorded neural responses to 40 or more stimulus presentations at each of 18 azimuths at increments of 20° in the horizontal plane. Spike patterns recorded during odd- and even-numbered trials were separated into “training” and “test” sets. Under the conditions of animal preparation and anesthesia that was used, cortical neurons typically responded to a noise burst with one or a few spikes at the onset of the sound. The sparseness of spike patterns

made it difficult to estimate sound-source locations on the basis of responses of single neurons to single sound presentations. For that reason, we formed average spike density functions by averaging multiple sets of 8 responses, drawn randomly with replacement within each of training and test sets. The network was configured to take as input the spike patterns represented with 1-ms time resolution and to produce as output an estimate of the sound source azimuth. Patterns from the training set were used to train the ANN, and then the trained network was used to classify the patterns from the test set. The procedure for analysis of each neuron is detailed elsewhere [18].

Figure 4 shows the neural-network estimates of sound-source locations based on spike patterns from the neuron represented in Fig. 3. Each symbol indicates the estimate based on one input spike pattern, and the solid line indicates the mean of the estimates of each source location. The mean-estimate line generally follows the dashed line that indicates perfect performance. This indicates that the spike patterns of this cortical neuron signaled source locations more or less accurately throughout 360° of azimuth. The progression of estimates shows a discontinuity from 0 to $+20^\circ$. This was seen in the analysis of the majority of neurons and presumably reflects the high level of neuronal sensitivity to sound-source locations around the midline. The median value of the difference between actual and estimated sound-source locations, computed on a spike-pattern-by-spike-pattern basis, was 24.7° . That is, half of the spike patterns estimated sound-source locations that were within 24.7° of the correct location. Across all the neurons that were studied, median errors averaged 38.4 and 37.5° in areas AES and A2 in a condition in which sound levels were fixed at 20 dB above neural thresholds. Median errors of neurons in both cortical areas increased by about 6° in conditions in which sound levels were fixed at 40 dB above neural thresholds or in which levels roved in 5 dB steps between 20 and 40 dB above threshold. We found no evidence for classes of units that are specialized for sound localization: median errors of units showed unimodal distributions in both areas A2 and AES.

It is common practice in studies of sensory coding to summarize the responses of neurons only by mean spike counts and to eliminate any measure of spike timing. We tested the degree to which spike counts captured stimulus-related information in spike patterns [18]. We compared the accuracy of sound localization based on recognition of full spike patterns (as described above) with recognition based only on spike counts. There were several instances in which median errors in the spike-count-only condition were as small as in the full-pattern condition. For the substantial majority of neurons, however, median errors in

the full pattern condition were appreciably smaller than in the spike-count only condition, indicating that one or more features of spike timing carried information about sound-source location.

A similar ANN analysis revealed that spike patterns of neurons in areas AES and A2 also could signal sound-source elevations [19]. We measured responses to noise sources that varied in elevation in the vertical midline around the interaural axis, from 60° below the horizon in front, through straight overhead, to 20° below the horizon in the rear. Across all elevations and across both cortical areas, median errors in ANN estimation of elevation averaged 47.9° in the condition in which sound levels roved in 5-dB steps from 20 to 40 dB above neural thresholds. We noted a statistically significant correlation between sources on the horizontal and vertical planes in median errors of units. This correlation is not trivial because dominant acoustical cues are fundamentally different for sound localization in azimuth (inter-aural difference in sound level and sound arrival time) and in elevation (spectral envelopes). Thus, we infer that spike patterns of cortical neurons can carry information about sound-source location per se, rather than one or more specific acoustical properties that covary with source azimuth or elevation.

In summary, single units in the auditory cortex are generally sensitive to the sound-source location, and spike patterns of each unit can carry information about source locations throughout a broad range of space. Such neurons are distributed widely throughout the auditory cortex. This suggests a “distributed code” in which information about any point in auditory space is distributed across a diffuse population of neurons, in contrast to a topographical code in which each sound-source location is represented by activity at a particular cortical place. We expect that the accurate neural coding of sound-source location can be achieved by combining information across large populations of neurons. The following section describes studies in which we have begun to explore ways in which such combination of information across populations might take place.

4. CODING BY NEURAL ENSEMBLES

We have extended our analysis of stimulus coding by temporal spike patterns to include small populations of neurons, which we refer to as “neural ensembles” [29]. We employed the ANN algorithm again as a useful analysis tool that did not require any particular a priori assumption as to how the nervous system combines information across multiple neurons. We recorded from neural ensembles with multi-channel recording probes that permitted simultaneous recording of differentiated spike activity at up to 16 cortical sites. The results that we present here are

based on recordings of 5 to 19 distinct neurons or small clusters of neurons. In our analysis, we have concentrated on information that was available on single trials. That is, there was no averaging across trials. All analysis was based on conditions in which sound levels varied in 5-dB steps from 20 to 40 dB above neural threshold.

In one analysis, we measured the accuracy with which an ANN could identify sound-source locations based on recognition of the spike patterns recorded at 5 to 19 sites. The simultaneously recorded multiple-neuron spike patterns were represented as 5 to 19 sets of 25 2-ms time bins. The network architecture did not attempt to model any physiological specialization for coordinated coding by neural populations. For that reason, the results that we obtained probably underestimate the stimulus-related information contained in these neural ensembles. Nevertheless, sound localization on individual trials was remarkably accurate. Performance of the ensembles ranged from near chance levels (90°) to one ensemble that produced a median error of 22.9° . Across all 34 neural ensembles that we tested, the mean and standard deviation of the median errors were $49.21 \pm 11.9^\circ$, which compares with the mean performance of responses of single neurons averaged across 8 trials ($46.0 \pm 10.3^\circ$).

We also explored the accuracy of single-trial azimuth identification by larger neural ensembles [29]. For that purpose, we compiled spike patterns recorded non-simultaneously across multiple neurons in multiple cats. In that condition, trial-by-trial median errors averaged around 20° for ensembles of 128 neurons drawn randomly from our sample population. For the purpose of comparison with a cat behavioral study by May and Huang [30], we tested the accuracy of localization of targets in the frontal half of the horizontal plane by an ensemble of the 128 neurons that were most accurate in single-neuron tests. Figure 5 shows the localization performance by behaving cats and the ANN. In that condition, the errors of the mean azimuth estimates by the neural ensemble averaged 8.9° across sound-source locations, which was roughly half the average error of the behaving cats in the May and Huang study. The trial-by-trial standard deviation of the neural ensemble estimates was about double that of the behavior. One should not over-interpret these comparisons, since our neural-network recognition of multiple-neuron spike patterns does not incorporate any specific between-neuron comparisons that might be used by the brain and because the specific patterns of localization errors by the network differ from the errors made by the behaving cats. Nevertheless, it is encouraging that neural ensembles of modest size can signal sound-source locations with accuracy comparable to behavioral accuracy.

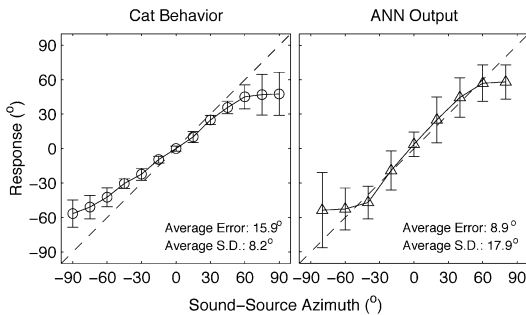


Fig. 5 Responses of behaving cats and the artificial neural network to sounds in frontal locations. In the behavioral study [30] (left panel), cats were trained to orient their heads to the sound-source location. The network responses (right panel) were based on spike patterns of 128 units. The means and standard deviations are plotted as a function of sound-source azimuth. (from Furukawa *et al.* [29]; Copyright 2000 by the Society of Neuroscience)

As was the case for single neurons, sound localization by neural ensembles was more accurate when the analysis preserved spike-timing information than when responses were represented only by spike counts. Nevertheless, performance could be quite good in some cases even when only spike counts were used. The neural ensembles that produced the most accurate sound localization tended to be those in which the constituent single neurons showed the greatest diversity in their spatial sensitivity. In terms of spike counts alone, one can think of activity shifting from one subset of neurons to another as the sound-source location was varied. When we manipulated ensemble spike patterns in various ways, performance was significantly better when the profile of the cross-population distribution of spike counts was preserved than when the profile was obliterated and only the cross-population spike-count mean was preserved. The code by cross-population spike pattern would be particularly effective in which stimulus intensity was varied. Spike counts of individual neurons often increased with increasing stimulus intensity, which would confound the location coding. The profiles of spike counts across units, on the other hand, could be relatively insensitive to intensity variation.

The cross-population profiles in spike *latency* also seemed to be an effective information-bearing feature of ensemble spike patterns. We tested the effect of expressing spike times relative to the first spike in the ensemble, effectively eliminating direct knowledge of the stimulus onset time. Although the result varied among neural ensembles, in some cases there was little or no loss of information carried by spike times. This indicates that, for those units, the location codes did not require an external

reference to the stimulus onset time.

5. CONCLUDING REMARKS

The present review can be summarized as follows:

- (1) The majority of neurons in auditory cortical areas that have been studied in cats are sensitive to sound-source location, most often preferring the sounds in the contralateral hemifield. Receptive fields typically are large (a hemifield or more) and enlarge as sound levels are increased. There is no evidence of systematic receptive-field-based cortical map of auditory space.
- (2) The spike patterns of neurons vary with sound-source location. Recognition of spike patterns by a computer algorithm can identify source locations with varying degrees of accuracy throughout up to 360° of auditory space.
- (3) Populations on the order of 100 neurons can signal sound-source locations with accuracy comparable to the accuracy measured in behavioral trials. Features in ensemble spike patterns that carry location-related information include cross-population profiles of spike counts and latencies.

It is somewhat surprising that across all cortical areas that have been studied in cats, no distinct population of neurons has stood out as specialized for sound localization. We speculate that computation of sound-source location is essentially complete by the level of the mid-brain (remember that the superior colliculus, a brainstem nucleus, contains a map of auditory space). Then, spatial information is perhaps distributed to multiple thalamo-cortical systems. It is possible that the pathways to discrete cortical areas are specialized for various aspects of hearing and that most or all such areas incorporate spatial information to some degree. One could imagine that some cortical areas might utilize auditory spatial information for an overtly spatial task, such as for directing eye movements. Other cortical areas might perform functions that are not overtly spatial, such as identification of communication sounds, but spatial information might assist those functions, such as by helping to segregate multiple sound sources. In this view, one might predict that differences between cortical areas in spatial sensitivity of neuronal responses might appear during appropriately designed behavioral tasks in experiments employing an unanesthetized preparation.

In a recent review article, Rauschecker [31] has proposed a model of parallel processing in the primate auditory cortex. He speculates, by analogy with the visual system [32], that the auditory cortex contains two processing streams, one for identifying a sound source (the “what” stream) and one for localizing it (the “where” stream). He proposes that a key element of the where stream is the caudomedial area (CM). This attractive hypothesis

awaits testing by systematic physiological experiments. One study [33] has provided partial evidence suggesting that area CM is part of the where pathway. In that study, neurons in area CM, on average, could detect changes in the location of a constant-level sound source relative to the frontal midline with somewhat greater resolution than those in area A1.

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