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Perceiving sounds in the real world: an introduction to human complex sound perception

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1. ABSTRACT

Arguably sensory systems, including audition, evolved allowing animals to navigate, find prey, avoid predators, mate, and, for some species, communicate. All of these essential functions require animals to determine objects in their environment. Vibrating objects produce a sound pressure wave that has the potential of informing an animal about these objects. Such acoustic information can make the organism aware of its immediate environment, provide useful information about that environment, allow for communication, and/or provide an esthetic value. However, sound has no dimensions of space, distance, shape, or size; and the auditory periphery of almost all animals contains peripheral receptors that code for the parameters of the sound pressure wave rather than information about sound sources per se. Thus, knowledge about sound sources gleaned from the peripheral neural code for the sound produced by a source is most likely computed in the brainstem and brain by means of an auditory neural computer. How this neural computer works and what other aspects of neural processing aid the computer is a mystery that is receiving a great deal of attention by many auditory scientists.

2. THE NEED FOR AN AUDITORY NEURAL COMPUTER

As cells evolved into animals, animals had to cope with the world around them. They needed to navigate, avoid predators, find prey, and mate. Later in evolution many animal species learned to communicate. These essential elements of survival required animals to sense their environment and the objects in it. Objects that vibrate produce a sound pressure wave that travels from the object to an animal. Thus, an ability to sense sound waves is one way animals could be informed about objects in their environment.

De Cheveigne (1) borrowed a concept from vision (2) to portray a simplistic view of how a sense of hearing might have evolved. Figure 1 depicts three stages of the possible evolution of an auditory system. A simple organism may only have had to detect the presence of sound and move toward it to find food (or a mate). For instance, a sound-wave receptor on one side of a primordial fish could have triggered a motor neuron on the other side that moved a fin that propelled the fish in the direction of the sound source (Figure 1a). Such a simple system would

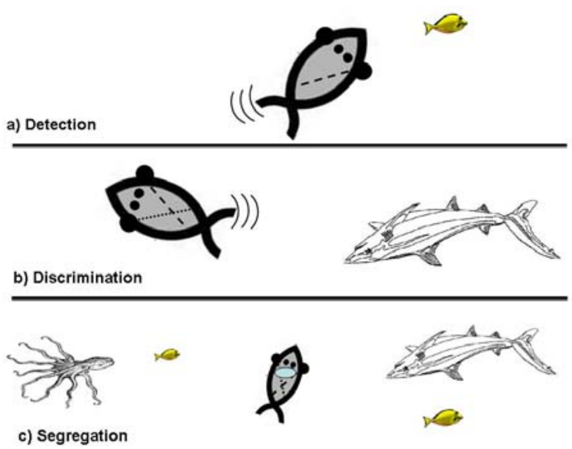

Figure 1. Three potential stages in the evolution of an auditory system: Detection (Figure 1a), Discrimination (Figure 1b), and Segregation (Figure 1c). In detection (Figure 1a), a sound coming from one side of the fish is received by an auditory receptor on the same side and triggers a fin to move on the opposite side of the fish propelling it toward the sound source (prey). But the fish would need to discriminate (Figure 1b) between prey and predator, perhaps by sensing a difference in the sound of prey versus predator and stimulating a fin on the same side of the fish where a predator produced a sound and as a result the fish is propelled away from the predator. However, in the real world prey and predator and other sound sources exist together and the fish must use a neural computer (a "brain') to segregate the various sound sources.

probably not have survived very long, as an animal would need to move away from a predator that produced a sound rather than toward it. This would require an auditory system that could discriminate the sound of a predator from that of prey and move an animal toward the prey and away from the predator. As long as only prey or predator existed at one time, a simple system such as shown in Figure 1b might have worked. But in the real world both prey and predator often exist together along with many other objects producing sound waves. Thus, the auditory system must be able to segregate the acoustic information in the complex sound field so that it can determine what sources produced the sounds that it received (Figure 1c). Based on this knowledge animals could take appropriate actions (e.g., consume prey, avoid predators, mate, etc.) required for survival.

Thus, at the most elemental level an auditory system that could detect, discriminate, and segregate would allow an animal to adequately cope with a complex environment. But even at this simple level the challenge facing the auditory system is daunting. The sound wave an animal receives from a vibrating object is a change in acoustic pressure over time. A sound pressure wave has no dimensions of space, location, distance, shape, or size. That is, the sound wave itself contains no information about the vibrating object's location, size, or shape. It appears that almost all animals evolved peripheral auditory receptors that code for the acoustic attributes of the sound pressure wave, rather than about the vibrating objects producing the sound wave. Thus, the only way the nervous system could determine what sources produced sound is for it to compute information about location, size, and shape from an analysis of the neural peripheral code of the acoustic properties of sound.

3. THE EVOLUTION OF AN AUDITORY NEURAL COMPUTER

Consider a case of localizing the source of a sound in the horizontal, left-right plane (azimuth). The pressure wave traveling from a source off to one side of a listener interacts with the head of the listener such that the sound reaches one ear before the other and the sound at the far ear is less intense than at the near ear due to the head sound shadow. It is assumed that the auditory system (in mammals most likely within the olivary complex of the brainstem) computes the interaural differences in arrival time and level and these computed values determine the azimuthal location of a sound source. That is, the auditory system computes interaural differences produced by the fact that two ears reside on opposite sides of the head. Some sort of computation is required in order to provide information about the location of a sound source, since sound itself has no dimension of space. It is almost certainly the case that all other physical aspects of the source of sound (3) also have to be neurally computed.

Thus, the ability to segregate sounds sources in complex acoustic environments probably required the evolution of a sophisticated neural computer. As that computer was evolving it is perhaps not surprising that organisms "learned" to use sound for communication. Patterson and colleagues (3) suggest that a primitive animal may have noted that making an object resonate produced a sound that stood out from the background of turbulence (wind or water motion) that was probably a major sound in its environment. Large sources have lower resonance than smaller sources, so an animal might have learned to use the spectral differences in the resonances to infer the size of the resonant object. If the animal itself produced the resonance, then the spectrum of this resonance could inform another animal about the sender's size. Repetition of the resonance could also be used to communicate additional information. Again, a neural computer is required to use this acoustic information for effective communication.

As evolution continued and the neural hardware and software became more sophisticated, animals could gain more and more information about sound sources and refine their sound communication abilities, so eventually speech as a form of communication developed in humans. Speech led to language and then probably to refined higher cognitive abilities. Such abilities include an esthetic appreciate of the objects in one's world, and, similarly, sound also developed an esthetic aspect in the form of music. Speech and music rely to a large extent on the auditory system's ability to compute the spectral content of resonances (the phonemes produced by the vocal tract and the timbre of different instruments) and the repetition of the resonances (voiced pitch provided by the vocal cords and musical pitch produced by an instrument).

A sound source is characterized by its physical properties (size, mass, tension, vibration modes, etc.) that allow it to vibrate and radiate a sound pressure waveform. These physical source properties determine the acoustic frequency, level, and timing attributes of the sound pressure wave traveling from the source to the receiving animal. Much is known about how these acoustic attributes are processed by the peripheral auditory system and the resulting sensations. However, a source's physical properties characterize the source better than the sound produced by the source's vibratory sound pressure wave. Few data describe the extent to which a source's physical properties directly affect the perception of sound sources (4). So far, these results suggest that auditory perception is more related to the attributes of the sound's pressure wave than to the physical properties of the source itself. So, the information that is apparently processed by the auditory system may be only indirectly related to the physical properties and description of the source. This reinforces the need for a neural computer to process the peripheral neural code of the sound-wave attributes so that detection, discrimination, segregation, and communication occur.

What do we know about the neural computer that allows sound to provide valuable information about our world? We know a lot about the auditory receptor mechanisms (outer, middle, and inner ears and the auditory nerve) that provide the neural code of the sound pressure wave that impinges on a listener, but far less about the neural computation of the information in this neural code responsible for auditory detection, discrimination, segregation, and communication. Since the auditory periphery appears to have been designed to provide a neural code for the sound pressure wave that travels from the source to the auditory system, auditory scientists have used stimuli that are best suited for exploring this neural code. The power of linear analysis and the Fourier transform have formed the basic acoustic approach used in most studies. Simple stimuli such as sinusoidal tones, brief clicks, and filtered noises are ideal for using this linear system's approach for investigating auditory processing. Thus, these stimuli have revealed many of the wonderful mysteries of the auditory peripheral operations and the impact those operations have for the basic sensations associated with the three variables of the sound pressure wave: frequency, level, and time. However, real sound sources rarely produce sinusoidal, click, or noise vibrations, especially as they are employed in the auditory laboratory. While the complex vibrations that characterize those produced by real sound sources can be mathematically formed from these simple stimuli, the perception of the sounds of actual sources cannot be explained adequately by similar mathematical manipulations formed from the sensations associated with simple stimuli. Thus, a direct study of the complex waveforms produced by actual sound sources appears necessary for a thorough understanding of auditory perception. The challenge for understanding the perception of complex sounds produced by actual sound sources is to develop the same predictability and generalizability acquired with simple stimuli and linear system analysis which led to an understanding of the auditory periphery and auditory sensations. That is, what stimulus manipulations, neural measurements, and perceptual procedures can reveal the operations of the neural computer that appears responsible for detection, discrimination, segregation, and communication? At the moment, auditory science has not developed techniques, models, or theories that provide powerful predictions or accurate generalizations regarding auditory processing of the complex sounds generated by most real sounds sources, especially in complex multisource acoustic environments. It appears that such advances will be required to achieve a thorough understanding of auditory processing of the complex sounds of the everyday world.

4. NEURAL COMPUTATION AND EXPERIENCE

To what extent does the neural computer require input from other neural processes, including experience, for it to effectively compute information about sound sources? It could be that the organism acquires experience from its genetic inheritance or from its present interactions with the world. At one extreme, it might be argued that the neural computer is entirely an auditory computer operating solely on the neural information provided by the auditory peripheral code. This bottom-up approach can be contrasted with a top-down view that argues that the auditory computer requires input from other neural processes for it to detect, discriminate, and segregate sound sources. For instance, it appears obvious that at a cocktail party one must attend to a friend talking so as to not be distracted by other sounds at the party. But are the sound sources at the party first segregated by the auditory system before attentional mechanisms are employed? Or do these attentional mechanisms themselves inform the auditory system so that it can segregate the sound sources (5)?

Sound is a temporal event, so that the perception of sound we experience at one instant depends entirely on the sound we previously experienced. That is, the neural code for sound must be constantly stored in and retrieved from some form of memory. How does auditory memory influence auditory computations? Or is this even the case? Does auditory memory interact with auditory attention in ways that inform the auditory computer as it processes the neural code (6)?

We rarely use only one sensory modality to process information about the world around us, even when the information is redundant. One sense can complement another, as when a source behind us produces a sound that alerts us to turn around to look at it. Thus, it is probably wise to consider the role other sensory information plays in the processing performed by any one sense modality. Thus, the neural computer is likely aided in auditory detection, discrimination, and segregation by other sensory system inputs. However, little is known about such multisensory interactions in sound processing.

There appears to be little current agreement on the extent to which the computations required for the perception of complex sounds depend on experience, attention, memory, and information from other sensory systems. And there is very little information - perceptual or neural data or theories - on how such inputs would assist processing the acoustic information received from the complex acoustic, real-world environment. An understanding of complex sound processing is likely to remain limited until auditory science develops a better understanding of experience, memory, attention, and multisensory processing.

So far, this discussion has been about processing sound for basic biological functioning (e.g., detecting prey), but humans use sound in other ways as well (and other non-human animals may make similar use of sound). One might describe these uses as: 1) Communication (sending and receiving an informative message, e.g., speech), 2) Awareness (what sound sources exist? e.g., rustling leaves), 3) Utility (what information does the source provide?, e.g., a siren signaling danger), and 4) Esthetics (emotional aspects derived from sound, e.g., music). Note, for most of these functions exact knowledge of the physical properties of the sound source may not be required. And, such detailed source information may not always be required for basic biological functioning (e.g., avoiding a predator). For survival an animal may need only to be aware of a loud sound, not the size of the source or even its location. For instance, a preying mantis appears to avoids bats with the initiation of a dive reflex whenever the mantis' auditory receptor receives a high-frequency sound in the spectral range of a bat's echolocating signal (7). The mantis dives to avoid the bat that is almost always above it, even though the mantis probably has no neural hardware to compute the actual location of the bat.

Thus, the neural computer may not have to extract detailed information about the physical properties of sound sources to detect, discriminate, segregate, or, in some cases communicate. What is needed is enough information indicating that different sound sources exist. Details about the physical properties (e.g., size and shape) of these sources may be necessary only in particular circumstances and may not be a prerequisite for the neural computer to process the sources in the first place. These details probably come from experience that enables us to label the source based on our past experience with the sound it produces (e.g., a particular squealing sound is that from of car tire). While the ability to identify a source with a label is probably not a necessary and sufficient condition for a sound source to be determined by the auditory system (i.e., that a source exists as in awareness), perhaps identification makes it easier for detection, discrimination, and segregation to occur. And perhaps the uses that we make of sound also inform the processes of detection, discrimination, and segregation.

Principles of the Gestalt school of perception (8) and those borrowed from ecological or Gibsonian psychology (9) have been suggested as ways in which one might better understand the relevance and importance of experience in sound source perception. These theoretical approaches have not been widely used in audition perhaps because they are usually qualitative rather than quantitative, have limited predictive power, are based largely on analogy to vision, and are often human-centric (they are not always generalizable to non-human animal auditory processing). However, the Gestalt and ecological approaches when applied to audition have produced strong evidence that processing the sources of sounds in many contexts depends on experience. And these "schools" have suggested useful aspects of the relationship between experience and the temporal-spectral structure of sound that could be used by the neural computer for detection, discrimination, segregation, and communication.

More recently it is has been suggested that experience "teaches" an organism about the statistical nature of the world (10). The statistical lessons could have been learned over many generations and transferred via genetic inheritance and/or learned by an animal during its own development. This statistical information may be used to decide which type of source or what property of a source is most likely to produce a particular sound-pressure wave, e.g., low frequencies are more likely to arise from large rather than small sources. Thus, the auditory system might have learned that a sound dominated by low frequencies is likely (but not always) produced by a large source. The neural computer could take advantage of the acoustical statistical relationships that exist in nature to detect, discriminate, segregate, and acoustically communicate.

Scholars of perception have noted that while vision depends on processing direct light from a source as well as light reflected from other objects, hearing is based almost entirely on processing sound that comes directly from a source. Reflected sound has previously been viewed as a "problem" the auditory system has to overcome to effectively process sound (e.g., an animal does not want to try to mate with a reflected sound). Evidence is mounting that reflections may provide valuable information about one's current acoustic environment and, as such, this information allows the auditory computer to more effectively process sound and its reflections (11). Evidence suggests that the auditory system gains knowledge of an acoustic environment over the first few seconds of experience in that environment. This experience allows the auditory system to more accurately process sound from sources, rather than being confused by sounds from sources and reflections (e.g., determine the source's location as in the "precedence effect," 12).

Thus, it appears that both short-term and long-term experience play crucial roles in detection, discrimination, segregation, and communication. How experience is used is poorly understood and how memory, attention, and information from other sensory systems interact with experience and auditory processing is even more poorly understood. Further advances in understanding how the complex sounds of our everyday world are processed by the nervous system will require a great deal more knowledge about the interactions among auditory processing, experience, memory, attention, and other sensory processing.

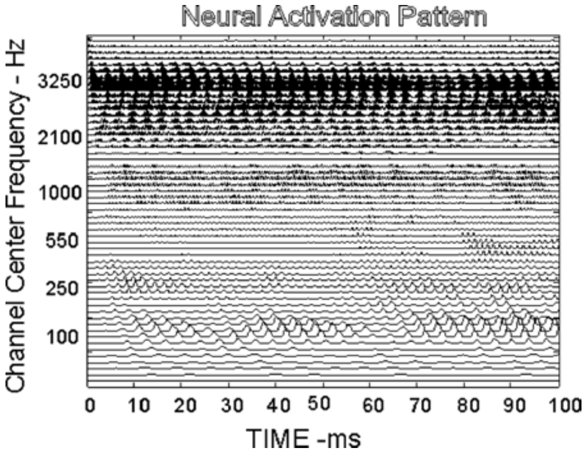

Figure 2. A simulation of the neural activity in the bundle of auditory nerves traveling to the brainstem and brain. Each horizontal trace depicts a neural histogram of an auditory neuron (or small group of neurons) tuned to a narrow frequency region indicated by the values on the ordinate. For this simulation (13) a 100 ms of the simulated neural response to a musical piece produced by a quartet of a trumpet, drum, bass, and piano is shown. The neural response pattern reflects the temporal-spectral structure of the complex sound pressure waveform produced by the quartet, but not a neural pattern that reflects the four instrumental sound sources. It is assumed that the auditory neural computer processes this coded information in order to neurally determine the four sound sources.

5. PARSING THE AUDITORY PERIPHERAL CODE

Experience, attention, memory, and other sensory information are all likely to provide input to the neural computer that is trying to detect, discriminate, or segregate sound source. But even then the peripheral neural code that forms the acoustic input to the neural computer is still devoid of direct evidence about sound sources themselves. Figure 2 represents a simulation of the temporal-spectral neural information that flows in the bundle of auditory nerves to the brainstem and brain. In this case the stimulus was 100 milliseconds of a piece of music generated by a quartet consisting of a trumpet, drum, bass, and piano. The display, based on the Auditory Image Model (13), simulates the histogram of neural responses of auditory nerve fibers tuned to narrow regions of the sound's spectrum. The model simulates the properties of the outer, middle, and inner ear along with neural transduction within the auditory nerve. The neural information traveling in the auditory nerve bundle somewhat faithfully represents the temporal-spectral structure of the physical sound-pressure waveform produced by the quartet. What is not directly present in this neural code is an indication that four instruments (sound sources) produced the neural pattern nor what the melody and beat may be. Somehow the neural computer must parse this peripheral neural pattern into subsets in which each neural subset represents each instrument. Thus, the peripheral neural code must contain information that is necessary and sufficient for such processing.

What type of information might exist in the peripheral neural code that would lead to these neural subsets? Several authors (1,8,14,15,16,17,18) have suggested a list of attributes of the sound pressure wave that are preserved in the peripheral code that could be used as a basis for sound source determination. Different sources have different spectra and many of these spectral differences are preserved in the peripheral code. The sound from different sources varies in the time of onset and offset, and sound sources produce other temporal modulations that are maintained in the neural code. Because the intensity profile of one source almost always differs from that of other sources, these level differences could aid the neural computer in determining sound sources. Many sources produce sounds with a harmonic structure or with other forms of temporal and spectral regularity that are preserved in the peripheral code. The neural code at one ear is different from that at the other ear, especially when sound sources are at different locations. These interaural differences could be exploited by the neural computer as a basis for sound source determination.

Clearly it is likely that the spectral-temporal information in one peripheral spectral channel could interfere with that in another spectral channel, and we know that such inference occurs when the information in the two channels does not overlap in time. That is, masking occurs. Masking usually means the ability to process one sound source or an acoustic aspect of that source (the target) is hindered when another sound (masker) exists at or near the same time as the target sound. Current considerations of masking differentiate between so-called "energetic masking" and "informational masking," where the total amount of masking is a sum of the two (19). Energetic masking is usually defined as that accounted for by neural overlap in the spectral-temporal peripheral pattern such as depicted in Figure 2. Informational masking is often defined as interference that cannot be accounted for based on energetic masking. Such additional (informational) masking has been shown to exist with there is uncertain variability in the stimulus context in which a target and masker are presented (e.g., the masker varies randomly from trial to trial) and when the masker and signal share a similar trait (e.g., both are speech). Both uncertainty and similarity appear to make it more difficult to attend to the target sound and segregate it from the masker. Thus, informational masking is probably a form of attention. The fact that interference occurs must be considered in determining how the neural computer uses the attributes of the peripheral neural code to form neural subsets that might aid in determining the originating sound sources.

Therefore, the neural computer uses attributes of the peripheral code to form neural subsets that allow for sound source determination. Its ability to do so can be affected by masking, and it appears highly likely that the neural computations require information from experience, memory, attention, and the other sensory systems. But how all of this information is processed, i.e., how the computer operates, is still largely unknown.

6. NEURAL IMAGING AND OTHER TECHNIQUES FOR STUDYING THE NEURAL COMPUTER

Until very recently, the study of the auditory system mostly relied on either behavioral methods or on data derived from anatomical and physiological measures obtained from non-human animals. With the advent of “brain imaging” technologies, a more direct investigation of the auditory system, especially the human auditory system, is possible. While the potential of brain imaging is substantial, the auditory system offers interesting challenges for using this technology. Some of these have been largely dealt with, such as providing headphone and sound generation systems that partially overcome the fact that some imaging instrumentation (e.g., fMRI) is very noisy making it difficult to present other sounds. Some challenges remain, such as the high temporal acuity of auditory processing as opposed to the current low temporal resolution of most imaging systems. Many current brain imaging techniques are functional in the sense that they can indicate which neural centers are likely participating in the processing of particular acoustic stimuli, and they can show how the gross neural activity in such centers is altered based on experience, memory, attention, or information from other sensory systems. Most brain imaging techniques are currently not functional in indicating how these centers themselves, or interacting with other centers process information. For instance, current evaluation of fMRI signals cannot differentiate between inhibitory and excitatory neural centers. Thus, if two neural centers are active during a stimulus presentation, it is not yet possible using fMRI alone to determine if both are providing excitatory outputs, inhibitory outputs, or if one center is providing input (excitatory or inhibitory) to the other center. Such inferences can be made based on knowledge of the active centers gleaned from other anatomical and electrophysiological (e.g., single unit recording) data. Thus at the moment, brain imaging technology by itself cannot describe how the auditory neural computer operates. These imaging techniques provide valuable pieces of the puzzle, but the puzzle is large and has many pieces. While brain imaging technologies are rapidly improving (e.g., new MRI techniques using powerful magnets may be able to directly measure neural currents rather than blood flow), it will likely take a multitechnique, multidisciplinary approach to unravel the mysteries of the neural computer that processes sound in our complex acoustic world.

7. BEHAVIORAL AND NEUROBIOLOGICAL BASES OF HUMAN COMPLEX-SOUND PERCEPTION

The many questions about “auditory scene analysis” as (8) has labeled the challenge facing the auditory system have been addressed in the literature, especially in the last decade or two (20). Data and theories exist about some aspects of the problems of detection, discrimination, segregation, and communication. But, no overall theory yet exists about how the auditory computer operates. This overview suggests that there are three aspects of the problem to consider: 1) The physical properties of the sound source and their relationship to the temporal-spectral attributes of the propagated sound pressure waveform, 2) The peripheral neural code for the temporal-spectral attributes of the sound pressure wave, and 3) The neural computations of the information available in the peripheral neural code with such computations aided by experience, memory, attention, and information from other sensory systems. Most is known about Part 1, a great deal about Part 2, and very little about Part 3, with Part 3 probably being the most challenging aspect of complex sound processing. Perception is the output of Part 3 which cannot exist without Parts 1 and 2. Thus, part 3 forms our view of the “acoustic reality” of any environment we may encounter.

The series of articles in this compilation of papers regarding the “Behavioral and Neurobiological Bases of Human Complex-Sound Perception” represents some of the recent issues involved with auditory detection, discrimination, segregation, and communication and provides some of what is known about these issues. Hopefully, this series will be both informative about current issues of complex-sound perception and will stimulate additional research on this exciting topic.

8. ACKNOWLEDGEMENTS

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Abbreviations: fMRI: Functional Magnetic Resonance Imaging

Key Words: Auditory Detection, Auditory Discrimination, Auditory Segregation, Communication, Auditory Periphery, Sound Sources, Auditory Sensation, Auditory Perception, Masking, Informational Masking, Energetic Masking, Speech, Music, Experience, Memory, Attention, Multisensory, Spectral Difference, Temporal Modulation, Sound Localization, Interaural Differences, Intensity Profile, Onsets, Offsets, Harmonicity, Auditory Scene Analysis, Functional Imaging, Review

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