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Research paper

There's more to auditory cortex than meets the ear

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Abstract

The auditory cortex is typically defined as that portion of the cortex containing neurons that respond to sound. This definition is adequate in a narrow context, but does not take into account sufficiently the subtleties associated with more complex behaviors and cognitive processes. Thus, it is easy to demonstrate that cortical regions essentially unrelated to sound processing may nevertheless be activated by an auditory stimulus; conversely, it is possible to demonstrate responses within classical auditory cortical regions in the complete absence of sound. We give several examples that indicate that responses in auditory cortex cannot be predicted based solely on knowledge of stimulus features. Rather, factors such as memory, attention, and mental imagery can be shown to play a major role in modulating or producing neural responses within auditory cortex. We argue that the interactions between classically defined auditory regions and other sensory, motor, and cognitive systems underlie many behaviors of interest; and that a more complete understanding of these processes will emerge from a consideration of the distributed nature of auditory cortical function.

Keywords: Functional neuroimaging

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1. Introduction

The auditory cortex is traditionally defined based either on anatomical criteria, as the cortex which receives input from the medial geniculate, or physiologically as the cortex containing neurons responsive to acoustic stimulation (Brugge and Reale, 1985). Such definitions have proven very useful in helping to delineate the different fields of auditory cortex and their response properties. They have also served to provide an overview of the distribution of auditory cortex in the brain, for example using metabolic methods (Poremba et al., 2003). However, such definitions have their limits, and these become more obvious as soon as one enters the realm of complex behaviors, particularly those involving human cognitive processes. The need for a more wide-ranging conception of auditory cortex is evident for example in the broadened definition offered by Hackett and Kaas (2004), who distinguish between more classical view of auditory cortex, vs what they term auditory-related cortex, which are those regions receiving second-order projections from auditory cortices proper, and which may be involved in auditory functions, though not exclusively so.

Discussions about definitions are rarely of great interest to non-lexicographers; but the issue of interest here is not so much the definition per se, but rather how to view the complex interactions across multiple brain sites that characterize higher-order auditory processes. To the extent that definitions might restrict one's ideas, it is useful to review them. To take a somewhat frivolous example, if I say to you "wiggle your left toe" and I measure brain activity in some way while you do so, I will likely see increased neural responses coming from the the precentral gyrus within the medial wall of the right hemisphere. Strictly speaking, this would qualify as auditory cortex according to one of the above definitions, since a neuronal response is elicited specifically to an acoustical event. Conversely, functional responses can be elicited within cortical areas directly connected to the medial geniculate nucleus in the absence of any sound at all, and in this contribution I shall give examples of this sort of effect. The principal point here is not

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necessarily that we need to abandon classical definitions, but rather that in addition to these ways of thinking, we also need to consider more broadly how the auditory cortex works within a highly distributed system.

The conventional experimental approach, evident both in neurophysiological and neuroimaging research, has not usually taken into account many of the issues raised in this discussion. A typical study might try to characterize the response of the auditory cortex by endeavouring to describe its input–output function, for example. That is, a certain stimulus parameter would be manipulated, and the resulting neural response (e.g., firing rate, or hemodynamic signal) would be noted, with the aim being to define the function that allows one to predict how the stimulus features are mapped onto the response. This approach has served the field very well in many respects. But in this paper I will argue that the field is now at the point where it can take the next step, and start to consider some of the factors that are important in understanding more complex interactions that are not modelled in the more traditional approach.

These influences can be classified, broadly speaking, into several categories, depending on their source as: past, present, and future. Influences that arise from interactions between an organism and its past environment would be one class. These influences could be described as being related to memory, training, or associations. Influences that arise from interactions between an organism and its current state are another; these would include such factors as attention, context, and general state of arousal or consciousness, as well as factors in the immediately present environment, such as multimodal influences due to the presence of stimuli in several modalities. Sensory feedback that is received based on ongoing actions might also fit within this category. Finally there are influences that we may categorize as related to future interactions between an organism and its environment. Such influences are necessarily cognitive in nature since they involve representations, rather than physical conditions. They are no less real for that, however, and include such powerful influences as expectations, intentions, and plans. I also include the concept of imagery within this last category only because via imagery one may produce perceptual representations of events that have not occurred, and as such can be thought of as representing future possibilities.

In what follows I have selected a particular example from each of these three general categories: memory, attention, and imagery. The aim is not at all to give a review of each of these domains as they pertain to the question at hand, but merely to illustrate with a few examples how these various factors can play a role in determining the nature of auditory cortical responses, and by so doing to broaden our perspectives.

2. Memory/learning

The influence of prior events, particularly training or exposure to certain conditions, on current function is one way to think of memory-related effects. For many years there has been considerable research aimed at understanding how auditory cortical responses can change as a function of learning or early environmental exposure to certain stimuli. Despite the interest generated by these studies of cortical plasticity, a more general consideration of memory-related processes has not always been prominent in accounts of auditory cortical function. That is to say, the typical neurophysiological or neuroimaging study of responses in auditory cortex does not take into account the subjects' prior history. The assumption would seem to be that such responses are relatively basic, and hence fairly immutable. But because of the distributed nature of cortical functional mechanisms – our theme in this paper – we argue that an organism's previous history can strongly influence cortical responses even at early stages of processing. This idea has been strongly endorsed for example, by Fritz et al. (2003), who described short-term plastic changes in spectro-temporal neural response profiles that depend specifically on both the very recent history of stimulation and on behavioral contingencies.

Longer-term contingencies are also relevant, as shown for example in an elegant neuroimaging study by Molchan et al. (1994), who studied auditory cortical activity as a function of associative learning. They used a simple conditioning task in which a tone stimulus was paired with an unconditioned stimulus (air puff) that results in an eye blink. Participants were scanned in a control condition in which tones and air puffs were presented in a random temporal relationship, and during a conditioning phase in which the tone was paired with the air puff. The number of tones per scan was identical in all cases, but comparison of the paired condition to the control indicated significantly increased cerebral blood flow in primary auditory cortex bilaterally (together with decreases in learning-related areas, including cerebellum and neostriatum). This finding suggests that auditory cortex activity reflects the shift in contingencies during the different phases of conditioning, a conclusion supported by electrophysiological (Gonzalez-Lima and Scheich, 1986) and MEG (Alho et al., 1993) evidence. Thus, auditory cortical activity is a function not only of the physical properties of a stimulus, but is also related to its associative value, that is, in some sense, the meaning that the stimulus may hold for the organism.

As a more cognitive example of how meaning can affect the response of auditory cortex, consider studies of the processing of speech syllables. One interesting approach is to use sine-wave speech (Remez et al., 1981) which can be perceived as speech or not depending on one's familiarity with the stimulus and/or one's expectation that they contain speech information. Several recent fMRI studies exploit sine-wave speech by comparing how these sounds are perceived before and after training sessions which resulted in a subject being able to hear speech content (Dehaene-Lambertz et al., 2005; Liebenthal et al., 2003; Möttönen et al., 2006). All of the studies concur that the cortex within the left superior temporal region showed altered responses as a function of training, although the Liebenthal study showed decreases post training whereas the others showed increased activity. The directionality of the response is of less relevance here than the fact that a modulation was observed as a function of prior experience. In the Möttönen study the enhanced response was seen only in those subjects who were able to learn to identify the stimuli as speech, making the link between perception and brain activity even more explicit. Regardless of the details, these findings clearly demonstrate that identical physical sounds are processed differently when they are perceived as speech – that is, when they have a certain meaning – than when they are not, and that this difference is evident in the pattern of neural response within auditory cortex.

A recent study from our own lab also explored the phenomenon of neural response modulation in auditory cortex in the context of speech learning (Golestani and Zatorre, 2004). Specifically, we examined the nature and extent of changes in hemodynamic response to speech sounds before and after training to discriminate a phonetic contrast not found in the subjects' native language. Listeners performed a discrimination task in which they heard a pair of syllables and made a same-different judgment; a noise burst acoustically matched to the speech syllables served as a control sound. Among the more salient findings, we observed that several speech-related zones, including a region within the left superior temporal gyrus, responded to a greater degree after training than before training (Fig. 1); since the stimulus itself had not changed, it was clearly the effect of the training that caused the change in neural activation. Of interest is that the region of auditory cortex recruited after training for the foreign speech sound overlaps with the response obtained to native speech sounds; hence, the training engaged cortical regions sensitive to speech contrasts which the listener is able to perceive. Prior to training this region would only respond to native speech contrasts, whereas after training foreign speech contrasts engage the same region. More generally, these results indicate that experience with sounds, and not only the physical cues, influences patterns of auditory cortex activity, a conclusion which is also consistent with cross-language studies using various methodologies. For example, the size of the mismatch negativity response, presumably originating from left auditory cortex, is affected by a listener's knowledge of vowel categories in their language (Näätänen et al., 1997). Kraus et al. (1995) also showed that behavioral training of two slightly different native speech stimuli in adults results in a significant change in the duration and magnitude of the mismatch negativity.

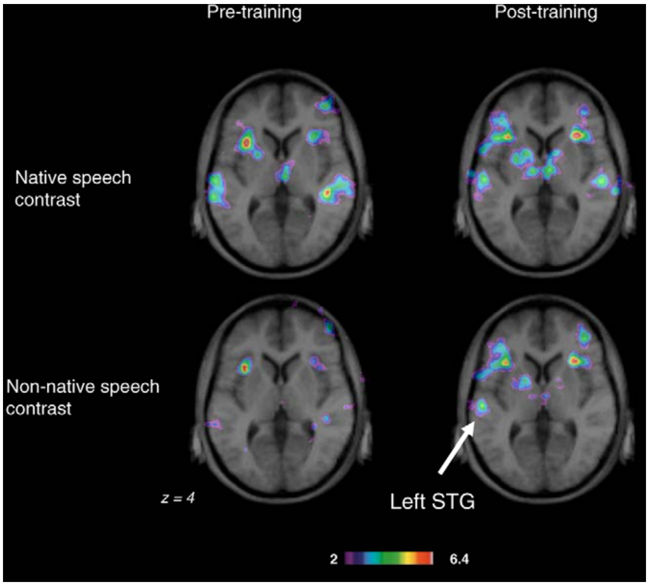

Fig. 1. Horizontal sections illustrating fMRI activity changes associated with learning a novel speech contrast. Top: control condition (no change). Bottom: novel speech sound; note area of activity after training in left auditory cortex (arrow). (Golestani and Zatorre, 2004).

These findings and many others raise interesting and so far largely unanswered questions regarding the nature of the changes that are observed under conditions of learning. There is little reason to believe that the mechanisms involved are similar in the various situations in which learning or experience seems to modulate auditory cortical response, and therefore it is likely that many distinct effects are operating. For instance, short-term adaptations to the local history of the sensory environment are unlikely to depend on the same synaptic mechanisms that would likely underlie long-term learning. Yet auditory cortex responses are altered in both cases. What one would like to know is the source of these alterations; does input from other cortical regions control the changes? If so how would this work? Or do the changes reflect modification of intrinsic responses which are handled by local circuitry? Perhaps both types of mechanisms play a role depending on the nature of the change, and this may be a profitable hypothesis to exploit in future research.

3. Attention

It has been well-known for many years that electrophysiological responses are subject to alteration as a function of attentional state, as in the classic demonstration by Hillyard et al. (1973) that evoked responses are larger to attended than to unattended stimuli. More recently this phenomenon has been linked directly to the region of primary auditory cortex (Woldorff et al., 1993), both on grounds of signal localization, as well as on the basis of the timing, since the modulation can be observed as early as 20 ms after the onset of the stimuli. The reason for bringing up attentional effects in this discussion is because they also serve to highlight the importance of considering the auditory cortex in terms of its position in a distributed system, rather than in isolation.

Consider, as a salient example, the modulations of auditory cortical response that can occur depending on competing inputs coming from other modalities. These interactions indicate that in order to account fully for the response of an auditory cortical neuron to an auditory stimulus, one may need to know what other stimuli are impinging on the nervous system, and how they are being attended to. There are a wide variety of effects that have been described in the literature, and once again in this discussion we can only briefly and superficially mention some of them. One of the more consistently reported interactions involving auditory cortex is that it often shows decreases in activity (relative to a no-stimulus baseline) in the presence of a visual stimulus (Laurienti et al., 2002; Zatorre et al., 1999). This result has been interpreted as an attentional effect, in that the presence of a visual stimulus may result in suppression of ongoing background processing of auditory signals. However, the phenomenon of suppression is not always observed; indeed, in some studies presentation of an auditory signal recruits some visual cortical areas, rather than inhibiting them (e.g. Zatorre et al., 1994), a phenomenon which may also be related to imagery (see below) or to associative learning (see above).

Several studies have specifically examined how auditory cortical response to a particular auditory stimulus may change depending on how attention is distributed to other ongoing sensory events. Many of these studies do report modulations in the expected direction, such that attention away from an auditory event is accompanied by decreased auditory cortex activity and vice-versa (Petkov et al., 2004; Shomstein and Yantis, 2004; Woodruff et al., 1996) although it is not a consistent finding across studies (Downar et al., 2001; Shulman et al., 1997), perhaps due to a relative lack of control over behavioral state.

In two recent fMRI studies from our own lab (Johnson and Zatorre, 2005, 2006) we explored this phenomenon using a paradigm that allowed us to measure and control the degree of attentional engagement via a behavioral index, a feature generally lacking in prior studies. Subjects were exposed to ongoing stimuli in visual and auditory modalities (geometric shapes and melodies, respectively) either separately, or they were exposed to both simultaneously. In each condition they were instructed to attend either to one or the other input in separate blocks of trials. Post-presentation recognition memory tests ensured compliance with these instructions, and demonstrated the expected enhancement of the attended over the unattended information, hence validating the procedure. Hemodynamic response during unimodal conditions showed interactions in the predicted direction: greater response was seen in secondary auditory cortical areas while attending to an auditory stimulus, as compared to simple listening to the same stimulus with no task (Fig. 2). A symmetrical complementary effect was seen for unimodal visual presentation. This phenomenon confirms the well-known effects of attention on unimodal sensory processing reported in other studies (e.g. Laurienti et al., 2002), and suggests that even under unimodal conditions, the auditory and visual systems do not operate in isolation. Of greater interest for our present discussion are the interactions when two competing stimuli are present, one in each modality. Under these conditions, modulations were once again seen, such that an enhancement in auditory cortex was accompanied by a decrease in visual cortex during the auditory attentional task, and vice-versa during the visual attentional task. Furthermore, functional connectivity analyses revealed that increases in auditory regions are directly correlated with decreases in visual regions and vice-versa (Johnson and Zatorre, 2006). Thus, these studies reveal that interactions between sensory cortices seems to underlie one's ability to attend to one sensory channel over another, most likely by enhancing the desired input and suppressing the response to the irrelevant input, leading in turn to influences on encoding of the information and subsequent ability to recognize it.

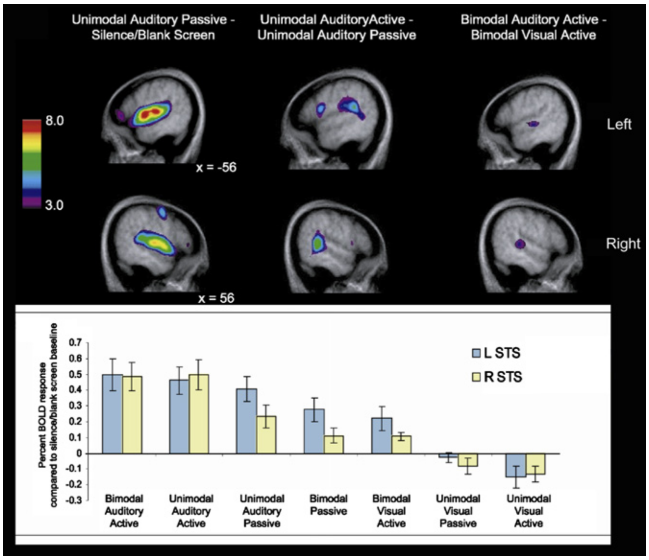

Fig. 2. Top 2 rows: left and right sagittal views of fMRI activity changes associated with each of three attentional conditions. Bottom: percent signal change in left and right superior temporal sulcus in each condition. (Johnson and Zatorre, 2005).

As a general conclusion from all these studies, it seems safe to say that one cannot consider sensory systems as isolated processors; instead, they exert mutual, reciprocal influences. Thus, to return to our theme of the distributed nature of auditory cortex function, findings from the attention literature support the conclusion that to achieve a more comprehensive understanding of how a neural response is elicited by a given acoustical input, one needs to consider not only the physical features of the input, but also what other stimuli may be impinging on the nervous system, and to what degree those other stimuli are the object of attention or not. This may not always be easy, or even feasible in certain experimental contexts, but it behooves the investigator to keep such phenomena in mind. Beyond the merely cautionary exercise, however, these findings raise additional issues which are also pertinent to understanding the nature of the functional properties of auditory cortex. One such question concerns understanding the pathways that mediate the interactions discussed in the previous paragraph. At present we know little of how sensory areas communicate with one another;

whether direct communication between them is necessary for the reciprocal effects observed; or whether top–down influences from heteromodal areas is required.

4. Imagery

The term mental imagery rarely enters the neurophysiologist's lexicon. But within cognitive neuroscience there is much interest and research on this topic, and it is pertinent to the theme of this paper in so far as one can show that imagery-related phenomena are relevant in understanding auditory cortical responses. In particular, regions of the auditory cortex, as classically defined either by anatomical or functional criteria, can be recruited in the absence of sound. It is this phenomenon that I wish to call attention to as further evidence of the need to consider a broader view of neural interactions in order to understand more fully the processes that auditory cortex is involved in.

A number of interrelated phenomena may be construed within the term auditory imagery, including working memory functions, such as might be involved in auditory rehearsal (Hickok et al., 2003), and cross-modal interactions, such as might be involved in silent lip-reading (Calvert et al., 1997). Expectancies can also play a role, as Voisin et al. (2006) have recently shown. In all these cases, auditory cortex activity occurs in the absence of a direct stimulus being present. For purposes of illustrating the phenomenon, however, perhaps its clearest instance occurs in the musical domain. There are various formal means to capture musical imagery effects and quantify them using methods from experimental psychology (Halpern, 1992), but phenomenologically, most people have a clear experience of being able to hear music in their mind – that is, in the absence of real sound. To understand the mediation of this phenomenon by auditory cortex, one can turn to Penfield's classic observations that electrical stimulation of the exposed surface of the superior temporal gyrus could result in the patient reporting illusory auditory percepts (Penfield and Perot, 1963). However, this effect is better termed a hallucination than imagery, because it was not consciously controlled by the listener, who believed the effect to be a real sound in the environment, and not an imagined sound.

Nonetheless, auditory cortex does seem to play a critical role in auditory imagery. To take an example, the most recent fMRI study from a series conducted in our lab investigated imagery for the timbre of a tone (Halpern et al., 2004). We asked listeners to make judgments about the similarity of the timbres of various musical instruments and to rate them using a numerical scale. This task was performed twice: as a perceptual and as an imagery task (e.g., in the real sound condition one might hear a clarinet followed by a violin, which would likely be rated as relatively dissimilar; in the imagery condition one would be cued visually to imagine the sound of a clarinet and violin, and would then make the same rating). The tasks had two functions: first, to control the subject's mental processes so they would be very similar in the two cases; second, to generate quantitative behavioral data to permit comparison across tasks and verification that imagery was taking place. The values from the ratings were entered into multidimensional scaling analyses which result in representations of the different target stimuli in a space, such that similar-sounding stimuli would be close together and dissimilar-sounding stimuli would be far apart. The multidimensional scaling solutions turned out to be very similar for perceptual and imagery conditions thus validating the task and giving us confidence that subjects were successfully able to imagine the sounds as desired. Examination of the functional imaging data revealed, as expected, activity in regions within the superior temporal gyrus during the imagery task, despite the fact that no acoustical stimulus was delivered; moreover, these areas overlapped with those recruited during the perceptual task in which real sound processing took place (Fig. 3).

In addition to this study, the important role of auditory cortex in imagery is clearly indicated by various other studies using a variety of techniques, including, magnetoencephalography (Schürmann et al., 2002), positron emission tomography (Halpern and Zatorre, 1999), and functional MRI (Kraemer et al., 2005); see Zatorre and Halpern (2005) for a review. These diverse studies converge on the finding that neural activity within regions of secondary auditory cortex can occur in the absence of sound, and that this activity likely mediates the phenomenological experience of imagining music. That the participation of auditory cortex is necessary, and not merely a correlate of the imagery experience, is further suggested by the report of deficits in an auditory imagery task following lesions of the right temporal neocortex (Zatorre and Halpern, 1993). It remains to be determined, however, precisely which subfields of auditory cortex may be involved in which aspects of the imagery phenomenon. In particular, the involvement of core auditory cortical areas in imagery has not yet been clearly shown.

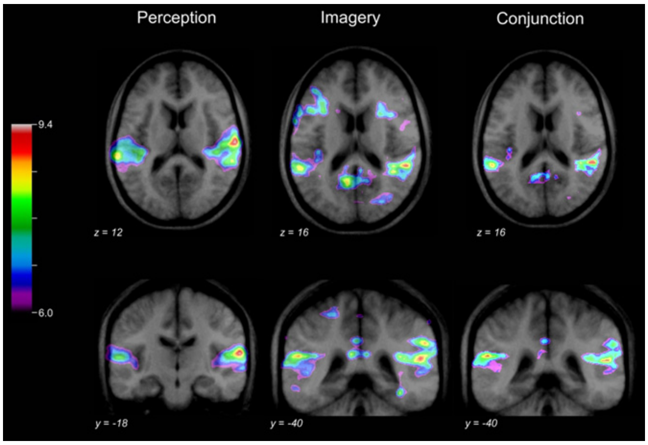

Fig. 3. Horizontal (top row) and coronal (bottom row) images of fMRI activity associated with perceiving tones (left) or imagining the same tones (middle). Areas of overlap in auditory regions are indicated by a conjunction of these two (right). (Halpern et al., 2004).

If auditory cortical activity underlies imagery, one must still answer the question of how it becomes active. The most likely explanation is that top–down mechanisms are involved in reactivating neural traces that are somehow encoded in sensory cortex. It is most likely that interactions between frontal cortical areas and auditory cortex are the way that imagery is instantiated, particularly involving retrieval mechanisms known to depend upon the ventrolateral frontal region (Petrides, 2005). In addition, feedback signals from auditory cortex are likely important in distinguishing between imagery and a real sound coming from the environment. Indeed, Griffiths (2000) proposed that a breakdown in this system might be responsible for the musical hallucinations suffered by some individuals with acquired deafness. Although these pathways and the interactions mediated by them are far from being understood at this time, the imagery phenomenon serves as a good way to remind ourselves that auditory cortical function is not only limited to inputs coming via the eighth nerve, but is also involved in more complex functions mediated via distributed networks. Further study of these phenomena therefore is likely to prove useful in gaining greater insight into these interactions.

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