

Auditory attention — focusing the searchlight on sound

Jonathan B Fritz, Mounya Elhilali, Stephen V David
and Shihab A Shamma

Some fifty years after the first physiological studies of auditory attention, the field is now ripening, with exciting recent insights into the psychophysics, psychology, and neural basis of auditory attention. Current research seeks to unravel the complex interactions of pre-attentive and attentive processing of the acoustic scene, the role of auditory attention in mediating receptive-field plasticity in both auditory spatial and auditory feature processing, the contrasts and parallels between auditory and visual attention pathways and mechanisms, the interplay of bottom-up and top-down attentional mechanisms, the influential role of attention, goals, and expectations in shaping auditory processing, and the orchestration of diverse attentional effects at multiple levels from the cochlea to the cortex.

Addresses

Centre for Auditory and Acoustic Research, Institute for Systems Research, University of Maryland, College Park, MD 20742, USA

Corresponding author: Fritz, Jonathan B (ripple@isr.umd.edu)

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Introduction and overview

Auditory attention allows us to rapidly and precisely direct our acoustic searchlight toward sounds of interest in our acoustic environment. Attention can be top-down (voluntary or task-dependent) or bottom-up (sound-based salience). At the interface of perception and action, top-down attention leads to enhanced information processing, behavioral sensitivity, and shortened response latencies. Top-down attention is a selection process that focuses cortical processing resources on the most relevant sensory information in order to maintain goal-directed behavior in the presence of multiple, competing distractions and comprises several distinct behavioral and neural processes operating at multiple levels [1,2,3,4,5]. Bottom-up ‘pop-out’ attention also plays an important role in ‘reading’ the acoustic scene and selectively gating incoming salient signals [6].

This review seeks to provide a roadmap to current insights and outstanding questions in the neurobiology

of auditory attention. Although of great interest, we will say little about the psychophysics of selective auditory attention in extracting salient ‘signals’ from a complex and noisy acoustic ‘background’, as this topic has recently been reviewed elsewhere [7]. Since tremendous insights have been gathered on the mechanisms and effects of attention in other modalities, particularly visual attention [8,9], we shall discuss some of the emerging parallels (and differences) between visual and auditory attention. We shall focus on recent advances that reveal different ways in which the neural representation of sound is influenced by task-specific demands, expectations, and the focus of attention [10,11,12,13,14,15].

Since the pioneering work of Hubel, Galambos and colleagues [16], it has been known that the responses of neurons in auditory cortex can be strongly modulated by attention. Other neurophysiological studies confirmed these effects of auditory attention, and subsequent human studies showed that event-related potential (ERP) responses, including early responses (the P20–P50 — a mere 20–50 ms after stimulus onset) and the N1 waveform (~100 ms latency) could be influenced by attention [17,18]. Since these early single-unit and ERP studies, there has been a gathering interest in the neurobiology of auditory attention, using a variety of approaches and techniques, including psychoacoustic, behavioral, neurophysiological (in single-unit, multi-unit, local field potential (LFP) and whole brain EEG studies), MEG (magnetoencephalography), and functional neuroimaging (PET and fMRI), all of which have added considerably to our insights into the nature of auditory attention.

One important methodological caveat and conceptual caution is that while many human and animal studies infer the presence of auditory attention (or its absence) from a combination of task design, subject behavioral performance, and the ensuing neural effects — attention itself can be flickering and elusive. It is notoriously difficult to precisely measure its highly variable selectivity, intensity, and duration. The lack of a commonly accepted, quantifiable measure of attention bedevils cross-study comparisons. Although the magnitude of attentional modulation of neuronal activity may scale with increasing task difficulty [19,20], this correlation can be confounded with the effects of task design and subject behavioral strategy [20]. In studies of human auditory attention, typical controls are to direct the subject to view a silent video or read a book and to ignore auditory input, but it is quite possible that the subject could sneak an occasional ‘listen’ or auditory peek. These

Glossary

A1: Primary auditory cortex.

ACC: Anterior cingulate cortex — medial prefrontal structure likely to be important in control of attention.

ASA: Auditory scene analysis — decomposition of complex mixture of incoming sounds into individual sound sources and sound streams.

ERP: Event-related brain potentials (averaged EEG segments time-locked to stimulus-onset).

FBD: Foreground–background decomposition — separation of foreground sound stream of interest from background acoustic scene.

MMN: Mismatch negativity — a negative waveform in the deviant ERP response that occurs about 150–200 ms after stimulus onset, evoked by an ‘oddball’ stimulus in a sound sequence in which rare sounds (‘deviants’) ‘pop-out’ in contrast to the repeated ‘standard’ sound. MMN is based on largely pre-attentive mechanisms, but can be influenced by attention.

N1 (also known as the N100): First negative wave in ERP, occurring ~100 ms after sound onset, followed by the N2 wave, occurring ~200 ms after sound onset (later N2b is associated with auditory attention).

P2 and P3 (also known as the P200 and P300): ERP positive waves following the N1, occurring ~180 ms and ~300 ms after sound onset (like N2b, later P3b is also associated with auditory attention).

PFC: Prefrontal cortex — important component of frontal–parietal attentional network and likely to play a major role in setting goals and expectations, allocating and directing attentional resources, monitoring ongoing events in a short-term memory buffer. PFC is also a source of top-down projections that can dynamically shape sensory cortex in accord with changing task demands.

SSA: Stimulus-specific adaptation — in probabilistic settings, in which one stimulus is common and another is rare, responses to common sounds adapt more strongly than responses to rare sounds. SSA, measured at a cellular level in auditory cortex, precedes and may induce the neural activity giving rise to MMN.

SNR: Signal-to-noise ratio — in a physical acoustics sense, the ratio of the target signal amplitude in comparison to background noise (clutter) amplitude.

STRF: Spectrotemporal receptive field — a characterization of both the spectral and temporal tuning properties of an auditory neuron, usually measured with reverse correlation or related regression techniques.

difficulties present real challenges for experimentalists studying auditory attention in both humans and animals.

Relationship between pre-attentive and attentive processes in auditory scene analysis

In order to focus auditory attention on specific acoustic objects of interest in the real world, we typically make use of a combination of auditory spatial cues and auditory feature cues to solve the pattern recognition problem of foreground–background decomposition (FBD). This is illustrated by one of the best known examples of auditory attention, the ‘cocktail party effect’, in which we can attend and selectively eavesdrop on different speakers in a crowded room brimming with multiple conversations. Cherry [21] speculated on possible cues to its solution, including location, lip-reading, mean pitch differences, different speaking speeds, male/female speaking voices, and distinctive accents. Beyond the cocktail party example, sound sources may differ in a variety of acoustic

dimensions (such as location or trajectory, instantaneous fundamental frequency, harmonicity, intensity, duration, rhythm, or the patterns of energy envelope modulation in different frequency bands) that facilitate grouping. Whatever the combination of cues, or the exact mechanisms involved in deciphering them [22], we accomplish this remarkable feat of selective attention to a single stream on a daily basis in varied acoustic environments with multiple sound sources. In order to do this, listeners must develop great proficiency at auditory scene analysis (or ASA), the process of segregating and grouping sounds from the mixture of sources that typify our acoustic environment to form representations of relevant auditory streams or objects [23–25]. This process of selectively directing attention to a single auditory stream in a complex, multisource auditory scene with different auditory elements vying and jostling for attention, may actually shape our perceptual organization of the elements in the scene [26]. Another familiar variation of the cocktail party effect occurs in the musical version when a listener focuses on the ‘voice’ of a single musical instrument playing in an ensemble [27]. Many animals are also extraordinarily adept at ASA, and there are numerous ethological parallels to the cocktail party, such as emperor penguins identifying the display call of their mate or offspring in the midst of a raucous cacophony of colony babble [28], or vampire bats identifying characteristic individual human snoring and breathing sounds [29] in polyphonic jungle soundscapes.

Some have argued that an auditory stream can be formed completely without attention [30], but once formed it can become an object of attention. Others have presented experimental evidence in favor of a role for attention in the formation of auditory streams [31]. The controversy about the contribution of attention to ASA and stream formation has led to considerable experimentation on this fundamental question, which continues to be the focus of intensive research. Overall, the extraction of signal from noise and the separation of foreground from background is likely to be a multi-stage process that draws on bottom-up gestalt grouping primitives, on auditory memory (our prior knowledge or expectations of the auditory ‘players’ in the acoustic scene), on attention, as well as other forms of top-down control (Elhilali *et al.*, unpublished data) [32,33].

A crucial and ubiquitous survival skill in the toolkit of animal hearing is the ability to detect the presence of novel or ‘deviant’ sounds amidst the familiar hum of background environmental noise. There is evidence that the brain has evolved a fairly sophisticated novelty detection system that includes an automatic, pre-attentive component that assists in parsing the acoustic scene into streams and analyzes stability and novelty, even for task-irrelevant streams [34–37]. In this system, repetitive stimuli are generally ignored and deviant or ‘oddball’

stimuli ‘pop-out’. Oddball detection has been particularly well studied in the auditory system, but is likely to share a common neural network with deviance detection in other modalities [38,39].

The acoustic change-detection system comprises an interconnected set of elements, including ‘adaptive’ neurons, with generalized stimulus adaptation responses, and also more specialized acoustic ‘novelty’ detection neurons that encode stimulus deviation from the pattern of preceding stimuli. ‘Novelty’ signals have been studied primarily at a cortical level, but may occur as early as inferior colliculus [40], suggesting the possibility that subcortical pathways for change detection may play a role in directing attention to novel sounds. However, an alternative explanation [41] is that the ‘novelty’ responses in the inferior colliculus arise from top-down cortical projections. Two EEG signatures for change detection have been described in the human brain: first, the attenuation of an early (~100 ms) N1 response with repeated stimulation and secondly, the evocation of a later (~100–200 ms) mismatch negativity (MMN) response when a novel stimulus occurs after a repetitive sequence of acoustic ‘standard’ stimuli [42]. Although the N1 wave may represent change-detection processes distinct from MMN [43], the main focus of change-detection studies has been on MMN. As mentioned, MMN is evoked in response to any infrequent, discriminable acoustic change in the stimulus stream and can be elicited by deviations in stimulus frequency, intensity, duration or spatial location, or by irregularities in spectrotemporal sequences (over periods as long as 20 s), or in other patterns of complex sounds including speech [44,45] and music [46,47]. MMN has been shown to be sensitive to changes in global acoustic context. Since MMN to elementary acoustic events can be evoked in sleep or under anesthesia, or when attention is diverted to other modalities, these novelty responses are believed to be largely pre-attentive. This deviancy detection system continuously monitors the auditory environment, tracks changes, and dynamically updates its representation of the acoustic scene [44] and is likely to be composed of parallel sensory (refractory-response-based) and cognitive (memory-comparison-based) components [48]. The source of MMN may shift depending upon the auditory areas analyzing the deviant acoustic change. The underlying basis of MMN is thought to be that incoming sounds are compared with the current neural representation of regularities in the acoustic scene and ‘oddball’ sounds that do not match the representation elicit MMN. Once the novel sounds are identified by the automatic detection system, they activate an attentional ‘interrupt’ involving frontal activation. These ‘flagged’ novel sounds can then be analyzed further to see whether they may merit attention and behavioral response (the pre-attentive salient filters may also automatically enhance responses to stimuli that have instinctive or learned biological importance). Although MMN can be elicited independent of attentional state, under certain

conditions it can also be modulated by attention [18,30,49–53] and hence may be thought of as ‘semi-automatic’. Top-down control may trump involuntary attention switching to task-irrelevant distractor sounds through attentional modulation by the prefrontal cortex of the deviance detection system in the auditory cortex [54]. In target detection, the ‘pre-attentive’ MMN can also occur in conjunction with other later ERP components associated with focused attention (the N2b (~200–300 ms after stimulus onset) and the P3b (~300–350 ms after stimulus onset), which may be generated by activity in the anterior cingulate and prefrontal cortices [55]. The presence or absence of these late ERP components can be used to ascertain whether or not subjects actually attended to sounds detected by their pre-attentive deviance detection system. There is also a ‘cognitive’ component of the MMN as shown by its sensitivity to linguistic change. Recent studies have reported a left-lateralized ‘phonological MMN’ for native phonetic features. MMN has been reported to reflect categorical perception of consonants and vowels, and MMN response characteristics are influenced by the lexical status and grammaticality of a word string, and even the semantic meaning of words used as deviant stimuli [45]. A pre-attentive ‘cognitive’ ERP, similar to MMN, can be elicited by violations of musical harmony or syntax [56]. Thus, MMN can be evoked by changes in a series of highly complex acoustic stimuli, and by cognitive rules, as well as by low-level acoustic changes in tone-pip frequency or intensity.

Considerable effort has been directed to discovering the neural basis of this fast, pre-attentive, ‘bottom-up’ novelty detection system in the human brain, and there is debate as to whether the dominant locus of MMN cortical generation in auditory cortex might vary as a function of changing acoustic features. A recent study [57[•]], combining EEG and fMRI, suggests that at least three cortical regions are involved in MMN, including primary auditory cortex, cortical areas in the planum temporale and neighboring posterior superior temporal gyrus, and ventrolateral prefrontal cortex. The authors conjecture that these regions may comprise a functional hierarchical network, with corresponding initial detection of acoustic change in A1 (or below), further feature analysis of the identified change in higher auditory areas, and attentional gating in prefrontal cortex if the acoustic change is deemed sufficiently novel or salient [57[•]]. Although the MMN has been attributed to a comparison of incoming sounds with a sensory memory ‘trace’ of previous repetitive acoustic features, questions remain about the relative contributions of the temporal and frontal lobe generators [58], and a recent combined MEG and fMRI neuroimaging study [59] suggests instead that the MMN is generated as a result of differential stimulus-specific adaptation of two distinct auditory cortical N1 sources. Recent promising animal studies have emphasized the importance of stimulus-specific adaptation (SSA) in A1 as a possible neuronal mechanism underlying this

initial stage of ‘oddball’ detection [60[•],61]. In these studies, SSA was not observed at the thalamic level [60[•]]. As few neurophysiological studies of SSA have been performed in higher auditory areas [41,62], it remains to be seen whether single-unit studies of SSA can help pinpoint the source of MMN generation. Although detailed mechanisms are still unknown, MMN generation, but not early stimulus onset responses, is suppressed by blockade of NMDA receptors [63]. Although promising, further studies of the molecular and cellular basis of MMN must await further development of a good animal model system, ideally one in which simultaneous event-related potentials (with results comparable to human MMN) and single-unit recordings can be conducted simultaneously [41].

The common behavioral design of many human MMN studies consists of subjects listening passively to a stream of auditory stimuli in the oddball paradigm — with no measure of the behavioral effects of the deviant acoustic stimulus in the stream. Without such a measure, it is not possible to distinguish between automatic neural responses arising from acoustic variability and responses related to ‘attentional capture’. In fact, the network activated during involuntary auditory stimulus-driven ‘attentional capture’ [64] is neuroanatomically similar to the dorsal fronto-temporal spatial attention network [65,66] activated during voluntary focus of auditory attention and may be complementary to the ventral ‘MMN’ network composed of bilateral superior temporal gyri and inferior frontal gyri, which automatically responds to acoustic variability independent of task salience or auditory attention.

The automatic component of the change-detection system may rely upon a concatenated set of basic habituation mechanisms and what Bregman referred to as a ‘bottom-up’ or ‘primitive’ grouping [23]. Automatic pre-attentive ASA is certainly not the only route to acoustic scene segregation — for example, attention may play an important role by limiting the processing of unattended input in favor of attended streams of input [37]. In addition, Bregman suggested a set of top-down grouping processes that he termed ‘schema-driven’ mechanisms on the basis of acquired expectations from prior experience or knowledge. Recent results also suggest the presence of at least two cortical mechanisms of streaming — an automatic ‘pre-attentive’ segregation of sounds and a streaming mechanism that builds up over a period of up to several seconds that can either be pre-attentive or modulated by attention [24,30,31,34,67–69]. Additional areas may be recruited, such as the intra-parietal sulcus [70], which was differentially activated depending upon whether subjects heard either one or two streams (this same area is activated in visual scene segregation and may be involved in supramodal scene analysis). The process of auditory scene analysis sets the stage for further attentional selection and seamlessly interacts with the auditory attention system

[36,48,71]. The existence of this capacity for automatic pre-attentive scene analysis can free up attentional resources to ‘fine-tune’ segmentation of a complex acoustic scene [31], or focus on individual streams and extract meaning from the attended stream [30]. Thus, even a simplified explanation of the cocktail party effect must include an understanding of the interplay between ASA, and our abilities to selectively direct spatial attention to specific sound sources within the acoustic scene and to direct featural attention by focusing on distinctive acoustic vocal features (such as fundamental frequency, timbre, accent, intonation) in order to identify individual speaker voices, all interwoven with top-down disambiguation processes, that assist in the retrieval of lexical information in noisy speech conditions [72] and help parse phonetic input in accord with the semantic line of the conversation.

Auditory spatial attention

Depending upon whether an auditory task requires attending to a spatial location, or to an auditory feature or object, there may be differential activation of the auditory ‘what’ and ‘where’ pathways [73–75]. Attentional mechanisms can modulate neural activity encoding the spatial location and/or the acoustic attributes of the selected targets and the early sensory representation of attended stimuli [2[•]]. For simplicity, we shall distinguish between auditory spatial and non-spatial featural attention in the present and subsequent sections, although as our discussion of the cocktail party problem illustrates, we are usually confronted in the real world with acoustic challenges that require a combination of both.

Spatial attention is supramodal — in the sense that cross-modal (visual or tactile) spatial cues can enhance the auditory ERP for acoustic stimuli presented in the same location [76]. A series of recent neuroimaging papers has emphasized the presence of a shared frontoparietal neural network for both visual and auditory spatial attention [65,66,77]. Impairment of this network, which includes medial frontal cortex and frontal eye fields, cingulate and posterior parietal cortex and anterior insula, can lead to combined visual and auditory neglect [78–80]. In the overlapping auditory and visual spatial attention network, the PFC plays important roles in tracking task goals and biasing sensory cortices toward task-relevant stimuli, the ACC is critical for executive attentional control, the FEF contributes to attentional orienting, and posterior parietal cortex in the human superior parietal lobule (and homologous monkey LIP) also shows enhanced responses to salient stimuli [81,82].

Top-down modulation of spatial attention in the visual system appears to work at multiple cortical and thalamic processing levels to achieve different functional goals [4]. The latency of attentional effects can be variable depending upon the task — a recent study [83] of top-down

feedback underlying visual spatial attention demonstrated relatively long-latency (~150–250 ms) attentional effects in V1, occurring well after the initial stimulus-driven response (~60–90 ms). A recent study has shown that microstimulation of the FEF (frontal eye fields) at levels too small to elicit eye movements leads to increased behavioral sensitivity for visual motion or stimulus change at that location and other attention-like enhancement of V4 responses [84]. Although these results suggest that a tight coupling can exist between planned eye movements and predictive attentional gain increases in the primate visual system, however other recent work has shown that the oculomotor system can be decoupled from the attention system. There is evidence that FEF is a component of a spatial attention system independent of eye movements [82,85,86] and plays a role in covert spatial attention (without eye movements). Nevertheless, given the presence of increased FEF activity preceding aurally guided saccades [87], one might predict selective gain increases in auditory cortical activity following FEF microstimulation.

In fact, evidence for top-down modulation of spatial attention in the auditory system has recently been obtained in studies of the barn owl [88]. The barn owl is a superb animal model for auditory attention since it has developed neural mechanisms for exquisitely focused spatial auditory attention in order to optimize sensory processing by using an ‘auditory searchlight’ directed toward its prey. Microstimulation of the fore-brain gaze control field in the barn owl (analogous to the frontal eye fields in primates) sharpened the spatial selectivity and enhanced the responsiveness of matched space-specific neurons in the topographic map of auditory space in the deep layers of the midbrain tectum. By contrast, responses of neurons with preferred sound receptive fields outside the stimulated arcopallial gaze field (AGF) location suppressed responses. Moreover, since the AGF controls both visual and auditory gaze, this suggests multimodal integration and shared mechanisms for visual and auditory attention (Winkowsky and Knudsen, unpublished data) [89]. In a natural context, such top-down attentional signals in the owl could spotlight a spatial location and by sharpening auditory as well as visual tuning, it could enhance precision of spatial localization for sounds and visual stimuli emanating from this point in space. As mentioned, these results are especially intriguing because the pathways for top-down modulation of auditory and visual attention in the owl are so closely parallel those described for descending modulation of visual attention in the primate from the frontal eye fields to the superior colliculus [84]. These results also suggest that the strategy that the brain uses to direct the spatial attentional spotlight is common to both sensory modalities, and the pattern of top-down modulation may be highly conserved across species [5].

Auditory feature and object attention — extracting signals from background

A variety of complex, shifting acoustic soundscapes present enormous challenges for acoustic scene analysis and for attentional focus on auditory features or objects such as environmental soundscapes (such as a morning chorus of birds), polyphonic music and speech. Top-down attention can selectively focus on a limited range of an acoustic feature dimensions [7], or can even focus on the expected (or recalled) features of an auditory target [15]. Although bottom-up salience certainly plays a vital role, voluntary auditory attention is the key to highlighting foreground over background and switching attentional focus to different features, objects, or streams of interest within the acoustic scene [10,11,13,27,34,90,91].

In an ongoing set of animal studies on auditory attention, selective spectral attention in single tone and multi-tone detection and two-tone discrimination tasks has been shown to rapidly reshape neuronal receptive fields in primary auditory cortex to enhance responsiveness at the target frequency and suppress responsiveness at adjacent spectral frequencies [10,11,12,92,93]. Similar spectral receptive-field effects were observed when the task was to detect a target tone signal in the midst of a noisy background [94]. By contrast, a distinctive set of temporal changes in cortical spectrotemporal receptive fields was found [95] when the animals engaged in temporal tasks (such as silent gap detection, duration discrimination, or click rate discrimination). These results suggest that top-down signals can adjust attentional filters precisely and rapidly to dynamically reshape receptive fields in the primary auditory cortex in accord with salient target features and task demands [12]. Recordings from the orbital prefrontal cortex of the behaving ferret [96] have shown rapid onset (75–150 ms latency) phasic and sustained target responses, independent of the acoustic characteristics or identity of the target stimulus. These prefrontal target responses were often behaviorally gated, developed rapidly and may contribute to target recognition during task performance. Future experiments will investigate whether such prefrontal activity plays a role in top-down influence over primary sensory filter properties.

Most studies of attentional effects in visual cortex have emphasized modulatory changes in background firing rate and contrast gain control, and hence an additive or multiplicative enhancement of feature tuning curves [97]. However, there is recent evidence in V4 for modulatory effects of attention, leading to shifts in neuronal tuning, and hence in the neural representation of stimuli [98,99]. These results in visual cortex, and parallel findings in the auditory cortex, are consistent with a matched filter model, in which neurons shift their tuning properties toward attended features in order to increase processing efficiency (David *et al.*, unpublished data) [10,11,12].

Human behavioral studies have shown a dissociation between a pre-attentive, low-level sound segregation process and an attention-dependent process that can be called into play in forming perceptual objects and streams. The perception of streaming can take up to several seconds to build up, and this attention-dependent streaming mechanism can be reset by an attentional shift [31]. There is a similar build-up at the neural level, measured by modulations in ERP in auditory temporal cortex [69] and in a recent MEG study [34].

Considerable work on the neural basis of attention to speech has recently been reviewed [100], focusing on neuroimaging studies of the attentional selection of foreground speech, differing by location or speaker identity from concurrent background speech. Selective attention to the human voice (compared with a silent reading condition) enhanced brain activity bilaterally in the superior temporal sulcus, higher auditory cortex, inferior frontal cortex, though not in the prefrontal cortex [101]. This was not the case for a selective-attention working memory task where subjects were asked to attend to either voice identity or location [102]. In this study, attention to voice location evoked greater activation in the dorsal prefrontal cortex, whereas relatively greater activation for voice identity was observed in the ventral prefrontal cortex. As might be expected, task conditions could also change the pattern of brain activation for attention to speech — for example, the left hemisphere temporal areas were dominant during speech comprehension tasks, whereas right hemisphere temporal areas were activated preferentially during attention to prosody [100]. If subjects were presented with the same set of speech stimuli but were asked to attend to specific linguistic stimulus categories in different task conditions, striking differences were observed in the pattern of activation with temporal lobe auditory areas [103]. Moreover, our greater familiarity with speech than with other acoustic stimuli may cause differential effects in otherwise similar task conditions. For example, although the PFC is activated in listening tasks that require selective attention to location, pitch cues, or even attentional listening to dichotic CV syllables [104], PFC was not activated during selective attention to the human voice [101]. ERP recordings showed a very different pattern of activity when listeners either were asked to identify concurrent vowels, or were asked whether one or two auditory objects were present using mistuned harmonic information [25]. Given the paramount importance of speech to our daily lives, research on both pre-attentive and attentional processing of speech is valuable — to study speech comprehension and auditory selective attention to speech as an information channel in the presence of background noise (which may help to develop improved automatic speech recognition systems) and also to understand the process of attention to the vocal features that reveal speaker vocal identity and vocal prosodic qualities that color speech (such as mood, emotional inflection, and nuance).

Research has also begun to explore the neural basis of auditory attention to music, which presents a complex challenge similar to that presented by selective auditory attention to speech [56]. As an example of future directions, a recent study [105] has shown that attention can enhance ERPs elicited by deviations in harmonic context.

Auditory attention in time

Precisely focused temporal expectancies, such as musical expectancies, are likely to be very important in auditory processing since many auditory patterns unfold in time. A recent ERP study has shown that auditory attention can be temporally directed to focus on events that are projected to occur at a particular future point in time [106]. In another study, subjects engaged in an auditory task could avoid involuntary attentional capture by distracting acoustic stimuli, by foreknowledge of when the task-irrelevant acoustic changes would occur [107]. Performance improved for subjects who were cued when to listen for an acoustic target [108]. A combination of temporal and spatial cues was particularly effective [106,108]. Temporal foreknowledge of acoustic events can lead not only to enhancement of cortical responses but also to their suppression, particularly when the sounds are self-triggered [109]. Recent research has also begun to explore other aspects of timing in auditory attention, such as the role of attention in auditory temporal discrimination [110] and in event segmentation in music [111].

General principles are likely to apply to both auditory and visual attention selectively directed to different points in the dimension of time [8]. There is evidence that the neural basis for temporal expectancies and temporal discrimination is supramodal [112–114] and involves a network including prefrontal cortex, basal ganglia, and cerebellum. Top-down modulation of neural responsiveness during temporal attention, can be precise and influence timing in primary and higher order visual cortex [115,116]. There is abundant experimental evidence for unimodal and crossmodal temporal attentional effects for auditory as well as for somatosensory and visual tasks.

Attentive imagery in silence and hallucinations

In auditory induction (such as the familiar psychoacoustic phenomena of FM completion or phonemic restoration) the auditory system fills in occluded information, as when missing foreground sound segments are perceptually restored in the presence of background sound [23,117,118]. Although it might seem at first glance like a reasonable candidate for top-down effects, there is considerable evidence for pre-attentive mechanisms in auditory induction [118], though this may be influenced by attention in phonemic restoration [119]. However, there can be remarkably strong effects of top-down attention on auditory processing in active listening, as observed in studies that have shown that human auditory cortex is activated in silence, in the complete absence of any

real-world acoustic stimulation, when there is simply an inner expectation of sound [66,120,121], during the short, quiet interlude of musical transitions [111], or when subjects are imagining auditory stimuli [122], or when they are prompted by silent visual stimuli that are usually accompanied by sound [123,124]. In a recent neuroimaging study of auditory attention [125[•]] subjects were asked to indicate when they heard a noise burst following a silent period of variable duration. In addition to activation of frontal cortical areas implicated in attentional control, imaging also revealed increased activity in auditory cortex contralateral to where the sound was expected to occur while the subjects listened in silence (as well as enhanced responses to the stimulus itself). In another recent neuroimaging study [126] subjects also listened to musical passages in which silent gaps had been introduced. If the subjects were familiar with the music, they heard ‘the music in their mind’ throughout the silence, although this was not the case with unfamiliar music. This is an extraordinary display of the importance of attentive expectation in shaping cortical responses. Activation of auditory cortex was greater during the silent gaps inserted in familiar songs than during silence in unknown songs, showing the continuous interaction of attention and memory during active, expectant listening. Auditory cortical activation has also been reported during silent lip-reading [123,127[•],128] or during observation of silent piano playing [124]. There are parallel findings in the visual system, indicating top-down attentional increases in cortical activity in V1 [129] and enhanced reward timing expectancies [116] even in the absence of a visual image. These compelling results suggest a general set of attentional mechanisms for top-down priming of sensory cortices. Modulatory effects of attentive expectation may be very similar to the top-down effects of perceptual decisions and can influence the earliest stages of cortical auditory processing. This is shown by an ERP study of a difficult acoustic target detection task [130] in which activation was highest for subjective perceptual decisions leading to target-present behavioral responses (even in cases of false alarms in which the subjects incorrectly believed that the target was present, in the physical absence of the target stimulus).

In order to differentiate between imaginary and real-world sound, the brain may rely on a validation system, dependent upon reciprocal interactions in a neural network including auditory cortex, frontal cortex, and anterior cingulate cortex (ACC). A recent imaging study [131] of speech-sensitive auditory cortex during silence found spontaneous, intermittent episodes of increased neural activity. In light of previous observations that the ACC is activated during auditory hallucinations, it may be that in the ‘default mode’ of the brain, endogenous activity within auditory regions is modulated by the ACC. Such spontaneous activity of the auditory cortex during silence may offer a neural substrate for the de-

velopment of auditory hallucinations in patients with acquired deafness or schizophrenia [9,131–133,134].

Effects of auditory attention on receptive-field plasticity

The adaptive functions of the cerebral cortex rely upon flexibility and plasticity of information processing networks. Since the topic of plasticity of auditory cortical processing has been recently reviewed [135], we will focus in this section on the evidence that attention may play a decisive role in triggering auditory plasticity, particularly in the adult brain [12,136]. Parallel studies have shown that attention can initiate plasticity in other sensory cortices, as well as in motor cortex [137]. Unlike experience-induced plasticity in juvenile animals, where experience alone can induce plasticity by mere exposure during the sensitive period, adult animals must generally attend to an acoustic cue for plasticity to be induced for the attended auditory feature [12,135,136]. A recent animal study [138[•]] showed that two very different forms of auditory cortical global plasticity arose during perceptual learning over a period of weeks when rats were trained, and presumably attended, to different features (frequency or intensity) of the same acoustic stimulus set. In another study of global plasticity in A1, rats were trained on an operant auditory conditioning task. In a cleverly designed parametric set of task conditions, rats were variably motivated to respond to the conditioned stimulus, and a range of performance levels was obtained corresponding to behavioral importance of the CS [139[•]]. Subsequent A1 mapping showed a CS-specific expanded representation whose area was directly correlated with performance level, showing that behaviorally important, and presumably attended, sounds gain relative representational area.

A complementary set of experimental studies, designed to explore local neuronal plasticity over a much shorter timescale (a period of minutes) for animals trained on multiple tasks, indicates that shifting the selective attentional focus to different acoustic dimensions or features may be instrumental in dynamically shifting acoustic spectral filter properties of A1 neurons and swiftly changing from one cortical state to another [10[•],11[•]]. These results suggest that rapid auditory task-related plasticity is an ongoing process that occurs as the animal switches between different tasks and changes its focus to new, salient acoustic cues and goals. These changes are persistent and widespread — as many as two-third of cortical neurons in A1 showed such frequency-selective enhancement during, as well as following, tone detection or tone discrimination task performance [10[•],140]. This suggests that adaptive changes in receptive fields and frequency response profiles of A1 neurons that shift cortical states or filter properties depending upon the behavioral demands of the ongoing task demands can be attentionally gated. In this view, attention is the key trigger that initiates a

cascade of events leading to the dynamic receptive field changes to enhance figure/ground separation, by using a contrast matched filter to filter out the background, while simultaneously enhancing the salient acoustic target in the foreground [12]. A recent set of studies examined attentional modulation for auditory features in a frequency-independent task [141,142*,143] and demonstrated a long-term increase in the proportion of neurons preferring downward contours in A1 of monkeys trained on a frequency-independent tone contour task (in which reward was associated with downward contours). Preliminary evidence from our current studies of A1 activity during a similar frequency-independent contour task indicates that changes in preferred directional contour also occur dynamically, at short-term as well as long-term time frames [144].

Three relevant sets of animal studies also emphasize the importance of auditory spatial attention in relation to plasticity. The optic tectum (OT) of the barn owl contains matched topographic maps of auditory and visual space. Barn owls raised during a crucial developmental period with horizontally displacing prisms rapidly acquire a new auditory space map in the OT that restores alignment with the prismatically displaced visual map. Although juvenile owls readily acquire these new aligned maps of auditory space as a result of experience, this plasticity is severely reduced in adults. Similar age dependencies have been shown for plasticity of the auditory space map in the superior colliculus in ferrets [145]. In previous studies in owls, the plasticity of the space map was tested in owls that were fed dead mice. However, when adult owls were given the opportunity to hunt live prey for a short period each day, drawing on their extraordinary nocturnal hunting skills, and powers of attentive listening, their auditory maps showed greatly increased adaptive plasticity. This increased adaptive map plasticity correlated with behavioral improvements in the owls' hunting prowess [146*]. There are multiple factors in the hunting condition that may have contributed to the increase in map plasticity, including increased arousal, and what is likely to be the key, greater auditory and visual attention to a highly salient bimodal source (movements of the live mice prey provided the owl with correlated auditory and visual information) that could enhance crossmodal integration and thus help calibrate the auditory and visual space maps. Additional recent experimental evidence also shows that training can induce enhanced plasticity of auditory localization in the adult mammalian brain [147*]. Adult ferrets rapidly relearned to localize sounds following reversible occlusion of one ear, but only if they performed an auditory localization task that used these cues, not if they performed a comparable visual localization task. In both examples, auditory attention appears to be essential to elicit adult plasticity. The third study is a preliminary investigation of behaviorally driven plasticity in the spatial sensitivity of neurons in the dorsal zone of the cat primary auditory

cortex [148]. The spatial tuning curves of dorsal zone neurons were sharpened when the animals performed a sound localization task, compared with the same neurons when the animal was either engaged in a simple sound detection task, or listened passively to the stimuli. Thus, selective attention to a spatial task can lead to rapid spatial receptive-field plasticity results from selective attention to the spatial task.

In addition to the evidence from animal studies, attention-driven plasticity has also been shown to occur in the human auditory cortex for spectral, temporal, complex spectrotemporal, and spatial processing [32,110,149–152]. For example, in a study of the neural basis of rapid perceptual learning, listeners were trained to segregate concurrent double-vowel stimuli [33]. In parallel with improved performance, there were rapid changes in ERP amplitude within the first hour of training, consistent with top-down modulation. By contrast, no changes in ERP amplitude were observed in the absence of attention to the double-vowel stimuli (this was shown in a separate group of participants, given the same acoustic exposure, but instructed to ignore the double-vowel stimuli and attend visually to a muted movie of their choice). The presence of dynamic plasticity in cortical representation of acoustic space has been suggested by studies of the ventriloquism after effect [153] and supported by subsequent research showing that spatial auditory attention can also drive auditory spatial plasticity [152]. Attention to target frequency in a discrimination task rapidly changed the tonotopic map in primary auditory cortex, expanding the distance between the two discriminant tone pair frequencies [152]. In all of the studies described in this section, attention appears to have fast and also slow, lingering plastic effects — raising twin questions: specifically, what determines the duration of the persistent plasticity triggered by attention, and more generally, what is the nature of the neural trace that attention leaves in its wake?

Intermodal and crossmodal interactions between auditory and visual attention

There are many similarities between attention in the auditory and visual modalities, where a two-component framework for attentional selection (top-down and bottom-up) has also emerged from psychophysical, behavioral, and neurobiological studies. Two sets of mechanisms are thought to operate in parallel in both modalities: using either bottom-up, automatic, image-based saliency cues or top-down, attentional, task-dependent cues. Another fundamental similarity is that attention can modulate both spatial and non-spatial feature processing in both modalities. Moreover, in addition to these similarities, there is now mounting neuroimaging evidence for visual modulation of activity in many auditory cortical fields [154] and a growing realization that all cortex is multisensory [155] that was presaged by earlier

work, such as a pioneering neurophysiological study of auditory and visual responses in auditory cortex of monkeys performing a modal selective-attention task [156].

If the brain were to use common but limited attentional resources, then intermodal attention (attending to only one relevant sensory modality) might necessitate suppressing responses to the irrelevant sensory input. Several studies have examined how responses in auditory cortex to an acoustic stimulus are affected by other (attended or unattended) ongoing sensory events. In keeping with a limited resources model, a common finding is that when attention is drawn away from an auditory event (by the presence of a visual stimulus and particularly, by attending to a visual task (compared with a no-competitive-stimulus baseline)) then auditory cortex generally shows decreased activity in acoustic stimuli [157–160,161^{*}], but not always [162,163]. Conversely, many of these studies also find that attention to auditory stimuli enhances activity in auditory cortex. These basic results were confirmed and extended in studies [3^{*},164] that examined unimodal and bimodal task conditions. In the unimodal auditory task, there are generally greater responses, particularly in secondary auditory cortical areas when the subjects were actively, rather than passively, listening to the acoustic stimuli. In the bimodal case, enhanced responses in auditory cortex were seen during the auditory attention task and suppressed responses observed during the visual attention task. Analysis of the functional connectivity between auditory and visual cortical regions in visual and auditory tasks indicated a reciprocal inverse relationship — increases in auditory activation were directly correlated with decreases in visual activation (and vice versa). The ability to divide (and switch) attention between unrelated visual and auditory stimuli was decreased following transcranial magnetic stimulation that disrupted function of the dorsolateral PFC [165], thus emphasizing the importance of the PFC in allocating limited attention and working memory resources and in balancing simultaneous multiple attentional demands. A related neuroimaging study also used a bimodal behavioral paradigm [166] to create a conflict between an auditory or visual target, and a crossmodal distractor. As the distracting stimulus in the task-irrelevant sensory channel was increased, there was a compensatory increase in selective attention to the target in the relevant channel and a corresponding increase in activation in the relevant sensory cortex. Moreover, the larger this increase, the less behavioral interference was observed. The results of these studies suggest a form of top-down sensitivity control that regulates the flow of attended information by modulating the relative strengths of different sensory information channels.

There are multiple possible levels for intermodal effects on auditory processing and attention. It is truly remarkable that many of these attentional effects can be

observed not only at the cortical level but also at the auditory periphery. A recent study [167^{*}] confirmed earlier work suggesting that visual attention can modulate peripheral auditory responsiveness in the cochlea and in the cochlear nucleus. In cats, acoustic attention can enhance auditory responses in the dorsal cochlear nucleus. In contrast, visual attention to a mouse or olfactory attention to fish odors reduces auditory responses in the dorsal cochlear nucleus. In contrast, visual attention [168], and a visual discrimination task reduces auditory nerve responses to clicks [169,170]. In humans, evoked otoacoustic emissions can be modulated by auditory attention in a frequency-specific manner [171]. The massive auditory corticofugal system is ideally suited for attentional modulation and hence many of these early peripheral effects are likely to reflect top-down influences. For example, in mustached bats, cochlear hair cells can be modulated by activity in the auditory cortex [172].

Another intriguing set of results also bears on the potentially distracting effects of visual stimuli on auditory attention. In trace auditory fear conditioning there is a time gap between the end of the conditioned stimulus (such as a conditioning tone) and the start of the unconditioned stimulus (such as tailshock) in mice. Recent studies have shown that trace auditory fear conditioning requires attention in mice [173] and also in humans [174]. Supporting this attentional requirement, trace auditory fear conditioning is associated with increased activity in the anterior cingulate cortex (ACC) and is impaired by lesions of the ACC that may disrupt attention to the tone-shock contingency [173]. The key point is that trace auditory fear conditioning can be impaired by distracting visual stimuli, adding yet another twist to the story of manifold visual influences on auditory attention, auditory behavior, and auditory-driven brain activity.

Although our previous discussion has emphasized competition between sensory channels in the limited resources model, in relatively simple low-level task contexts (such as pitch discrimination or contrast discrimination) there may be no conflict over limited attentional resources since there are apparently sufficient separate attentional resources for both vision and audition [175]. There are clearly other cases where auditory and visual inputs both contribute to information processing. Such cooperative interactions lead to early multimodal integration [176] or to multisensory enhanced activation in primary and secondary auditory cortex, as in lipreading [123,127^{*},128], attention to complex audiovisual combination stimuli [177], source localization with bimodal cues [108,178], ventriloquism [179], or visual cueing in auditory scene analysis [180]. The neural representation of human walking in the temporal biological motion area is another example of higher level audiovisual integration — in which both visual and auditory inputs (sound of footsteps) activate the same area [181]. An early study

[156] showed that neuronal responses in auditory cortex (during a selective-attention task in which different auditory and visual cues were associated with a two-choice lever push) were stronger when visual and auditory cues were in agreement and were reduced when the bimodal cues were in conflict [156]. A recent physiological study [143] demonstrated enhanced spike activity in monkey auditory cortical neurons to task-related visual inputs (that signaled task onset), but only in an auditory behavior task-context, suggesting attentional gating of relevant visual input to auditory cortex. Such attentional or behavioral gating of task-relevant visual input was also observed in the inferior colliculus of monkeys trained to saccade to an acoustic target [182].

Neural networks of auditory attention

Auditory attention can be selectively directed to a rich variety of acoustic features including spatial location, auditory pitch, frequency or intensity, tone duration, timbre, FM direction or slope, speech versus nonspeech streams, and characteristics of individual voices. Given the multiplicity of acoustic dimensions to which we can attend and the richly interconnected auditory processing networks, there are likely to be multiple neural loci for auditory attention. In fact, the locations of the multiple loci of attentional influence on auditory information processing are flexible and are likely to be dependent upon the specific demands of the behavioral task being performed. This has also been suggested to be the case in the visual system [9,183]. Neuroimaging studies examining the common neural circuitry underlying the control of both visual and auditory attention have revealed a largely overlapping frontoparietal network [66]. Depending upon task, there may be a segregation of attentional effects along the what/where pathways, as suggested by a recent MEG/fMRI paper [2^{*}] that provides further evidence for the presence of dual-selective-attention effects on sound localization and identification.

Most functional imaging, EEG, MEG (but not physiological) studies find overall enhancement of auditory cortex activity by selective attention to sound [17,157,184–186]. However, one source of controversy has arisen over whether attentional effects are found predominantly in primary or secondary auditory cortex, or can be equal in magnitude throughout auditory cortex depending upon attentional demands. In the visual system, there is some evidence consistent with increased attentional effects at higher cortical processing areas compared with earlier cortical areas, but high levels of thalamic modulation [4] are inconsistent with an ‘attentional progressive hierarchy’, a concept that has recently been critiqued [9]. In any case, physiological studies of cortical plasticity induced by auditory attention have shown clear modulation of neuronal responses in primary auditory cortex [10^{*},11^{*}]. Although some human imaging studies have also shown attentional modulatory effects in A1 [157,184], as well as in other

primary and secondary auditory cortical regions, another study [160] has reported greater effects of auditory attention in higher auditory association areas, at least in an intermodal, dual task paradigm (comparing responses when one sensory modality is attended and the other is ignored). Since attentional effects are highly task-dependent, it may be premature to accept the attentional progressive hierarchy model in auditory cortex. As recent studies have shown, task-specificity of processing and attentional demands can differentially activate selective areas of prefrontal and auditory cortex during the performance of different auditory tasks. A preliminary study in the ferret [187] showed differential patterns of brain activation in prefrontal cortex and in primary and secondary auditory cortices using expression of the immediate early gene, *c-Fos*, while the animals were engaged in one of two listening tasks (sound localization or detection of tones embedded in a noise). The results of this animal study parallel findings of two recent human neuroimaging studies that also mapped differential activation in ‘what’ and ‘where’ tasks [2^{*},102]. The task-dependent shift in the distribution of attention leads to dynamic re-allocation of cortical resources depending upon task demands and underlines the flexibility in auditory processing.

In addition to auditory cortical areas, there are cortical association areas whose activity is influenced by auditory attention. Association areas in the supramodal frontoparietal attentional network [188] are also activated in auditory attention — such the left precentral gyrus and the right posterior parietal cortex [65,77,161^{*}]. A study of the neural dynamics of event segmentation in musical symphonies revealed a right-lateralized network, with peak cortical activation during the silent period between musical movements [111]. There were successive waves of activity in two distinct functional networks — first in a ventral frontotemporal network involved in the automatic detection of salient acoustic events, swiftly followed by activation of a dorsal frontoparietal network, which may direct attention to the acoustic event boundary and update the perceptual scene. This study illustrates the broad range of brain regions activated during auditory attention. Even a partial list of additional areas includes limbic cortex, anterior cingulate cortex, basal ganglia, thalamus (medial geniculate nucleus, pulvinar nucleus), superior colliculus, inferior colliculus, cerebellum, dorsal cochlear nucleus, and cochlea. Recruitment of additional brain areas may be dependent upon task conditions — for example, orbitofrontal cortex and hippocampal paralimbic belt areas are activated during auditory target detection tasks where the stimulus decision is based upon ambiguous sensory information [189]. On the basis of computational modeling [190], neuroimaging [191], physiological [192], and neuroanatomical evidence [193,194] the reticular nucleus of the thalamus may also be an important site of attentional modulation, but it has not yet been studied physiologically during auditory attention.

Thus, attentional effects in the auditory system can occur selectively and at multiple stages throughout auditory processing [195] and may even occur as early as the cochlear nucleus or even earlier, in the sensory transduction phase in the cochlea, as demonstrated by studies of crossmodal selective attention [167,168]. These peripheral attentional effects may be partly driven by local 'bottom-up' processes such as habituation, but may also be influenced by top-down effects mediated by the descending olivocochlear bundle projections. Given the range of neural loci where auditory attention is likely to modulate processing, there may very well be a variety of mechanisms in play, giving rise to the question of how these multiple mechanisms are coordinated, orchestrated, and enacted in concert. It is, of course, possible, that these multiple levels of attentional modulation operate relatively independently.

In fact, recent studies underline the point that attentional effects on auditory processing are likely to occur in a distributed and widespread pattern throughout the auditory cortex. Research on a 'deaf-hearing' neurological patient with extensive bilateral destruction of auditory cortices (including the primary auditory fields) demonstrated that the patient was still able to marshal sufficient auditory attention to perceive sound onsets and offsets. Conscious attentive perception of sound occurrence in this patient may have arisen from top-down projections from prefrontal cortex to the remaining non-primary auditory cortex or multimodal association cortex. Other insights into attention have arisen from neurological studies of two forms of auditory neglect: one an attentional deficit associated with basal ganglia lesions, and the other an auditory spatial deficit associated with parieto-prefrontal lesions [78,79].

At a global level, selective attention may channel information into specialized cortical modules localized in one hemisphere and hence lead to lateralized patterns of activation. There is considerable evidence for hemispheric specialization of the attentional system — for example, a study by Zatorre *et al.* [158] suggests that auditory attention to either spatial location or tonal frequency activates a common network of right hemisphere cortical regions (although one may argue that lateralized functional specialization arises first and that the hemispheric differences in attentional modulation are a consequence). Additional evidence for lateralization was provided by a recent ERP study [32] that observed plastic changes in event-related potentials during rapid perceptual learning that occurred in right auditory cortex and right anterior STG/inferior prefrontal cortex and were dependent upon auditory attention to the phonetic discrimination task. Clearly, attentional effects may be highly dependent on task paradigm. For example, differentially lateralized patterns of hemispheric activation were demonstrated in subjects attending to one of two

different features (duration or contour) of the same acoustic stimulus set [13].

A neuroimaging study [27] explored the neural basis of foreground-background decomposition, by comparing brain activation patterns when listeners performed a match-to-sample task for harmonic target tones (drawn from a stimulus set of tones with distinctive timbres from 15 different musical instruments) against a continuous FM (frequency modulated) background, to activity arising from the FM background-alone stimulation. They reported increased foreground-signal related activity in posterior regions of left auditory cortex, which was insensitive to masking influence of the background. Admittedly, one potential complication of foreground-background decomposition neuroimaging studies, even when using low-noise fMRI, is that the subjects are already engaged in distinguishing task-related foreground signals from background magnet noises (created by switching of magnetic gradients during imaging). However, notwithstanding these technical challenges, a subsequent neuroimaging study [91] of intentional stream segregation using timbre cues (comparing activation patterns in an alternating dual stream of ABAB sequences from two different musical instruments — trumpet and organ versus a single stream AAAA or BBBB from either instrument alone), also found enhanced left hemisphere activation in posterior areas of the auditory cortex, similar to the activation pattern described in earlier studies of foreground/background decomposition [27] and of selective tracking of individual melodic streams in polyphonic music [196]. This pattern of activation may be the result of the involvement of working memory as well as selective auditory attention in performing these tasks.

A recent MEG study explored the neural basis of the non-spatial aspects of attention in the cocktail party effect using a clever reversal of foreground and background attentional foci [34]. Subjects engaged in a set of complementary tasks that changed foreground and background using the same acoustic stimulus set, involving either listening for frequency change in a rhythmically repeating, constant-frequency target stream amidst a dense background texture of irregular, random-frequency notes ('target' task), or instead by listening for duration changes in the dense texture of changing notes and ignoring the rhythmic, constant-frequency stream ('masker' task). The subjects' behavior was correlated with their MEG neural responses indicating that auditory attention strongly modulated the relative neural representation of the target. Furthermore, the time course of the neural build-up of target representation correlated with the subjects' gradual perceptual learning and improvement in target detection.

These data suggest that one important mechanism for top-down attentional control is through enhancement of

coherent or synchronous neural activity in sensory cortex, a finding supported by recent results in the somatosensory [197] and the visual system [198–200]. In the auditory system, the early ‘transient’ gamma-band response in primary and secondary auditory cortex has also been shown to be related to top-down selective attention to auditory stimuli [72], which may be mediated by the dorsal anterior cingulate cortex [201,202].

Attention can influence neural activity not only through synchrony but also through an array of other mechanisms. Previous neurophysiological studies of visual attention have suggested that a possible biasing mechanism for top-down selective attention is an increase in baseline spiking activity in relevant sensory cortex [203]. Although such attentional increases have been observed in the visual cortex, they have not yet been demonstrated in auditory cortex. Preliminary data from A1 recordings in the behaving rat [204] indicate that there were no consistent changes in spontaneous activity during a two-tone frequency discrimination task. Surprisingly, evoked multi-unit and LFP responses were larger in the non-attending condition than in the attending condition. However, opposite results were obtained in recordings from the medial geniculate (auditory) thalamus, where an increase in spontaneous activity was observed during auditory task performance. At present, there is no compelling single-unit neurophysiological evidence for attention-related increased baseline firing rate in auditory cortex. On the contrary, all recent single-unit physiological studies indicate either a decrease in baseline firing in the attentive state or a lack of consistent gain changes during auditory attention [10^{*},11^{*},156,205] with one earlier exception [206]. One puzzle to be resolved in future research is how to reconcile these physiological findings from single-cell recordings in the auditory cortex that indicate an absence of gain changes during attention, with the results from many physiological studies in the visual system that show the opposite. Also, how can the single-unit data from auditory cortex be reconciled with neuroimaging data that suggest enhanced activity in auditory cortex during attention?

Other mechanisms of attention, observed in physiological studies of visual attention, are multiplicative modulation of neuronal responses and attentional increase in effective stimulus contrast (or contrast gain). Although both are perfectly plausible mechanisms in auditory attention, such systematic multiplicative changes in response gain or changes in stimulus contrast gain during attention without any change in receptive-field tuning have not yet been observed in the auditory system. These differences could be a matter of task design or data analysis, or simply reflect the paucity of physiological studies of auditory attention that have been conducted at a single-unit level.

However, as mentioned earlier, there is compelling evidence for an alternate mechanism in primary auditory

cortex in which attention plays a role in adaptively reshaping receptive fields, depending upon salient task cues and behavioral context [10^{*},11^{*},12]. Convergent evidence for matched filter changes in receptive-field tuning has come from studies in the visual system [98,99]. Task-dependent sharpening of auditory spatial receptive fields was also observed in primary auditory cortex [148] and also been described in visual cortex [206]. Such adaptive mechanisms enable neurons to rapidly multiplex in a task-dependent (or state-dependent) manner as has been shown in the visual system [9]. Thus selective attention could be based on short-term feature-specific plasticity of auditory cortical neurons, enhancing their selectivity for task-relevant information, rather than amplifying overall responses. It is an open challenge to determine the role that these various mechanisms may play in auditory attention.

Summary

Auditory attention involves a distributed network of auditory cortical and subcortical structures that are activated selectively in a task-specific manner during auditory processing, which also integrate with a generalized multisensory attentional network that includes parietal, frontal, and anterior cingulate cortical regions [74,207–210]. Recent research has revealed a richly interconnected network for auditory attention that assists in the computation of early auditory features and acoustic scene analysis, the identification and recognition of salient acoustic objects, enhancement of signal processing for the attended features or objects, priming of persistent plastic changes that may enhance future processing, and the planning of actions in response to incoming auditory information. Auditory attention is dynamic and flexible, modulates many levels of auditory processing from association cortex to cochlea, and may rely upon adaptive mechanisms that rapidly reshape receptive fields in accord with current task demands and behavioral context.

Many outstanding questions remain to be answered by future research. We still do not know the synaptic mechanisms and cellular architecture [211] underlying auditory attention, nor the manner in which attentional effects at multiple levels in the distributed attentional system are orchestrated and directed. How much of the acoustic novelty system can be explained by simple habituation mechanisms? How are learned ‘bottom-up’ salience filters formed? (for highly meaningful and over-learned stimuli such as one’s own name). Do attentional effects in the auditory system increase with task-difficulty as they do in the visual system? [19,20]. What are the differences and similarities between visual and auditory attention? What are the pathways for crossmodal and intermodal attention? What is the interaction between the neural systems for arousal, vigilance, and attention? [212]. What is the relationship between attention and its close companions — expectation, reward, short-term memory, and

plasticity? [5,136,213]. How does top-down auditory attention modulate acoustic scene analysis, interact with the 'pre-attentive' acoustic novelty detection system and also with bottom-up 'pop-out' auditory attention? This fascinating array of questions will keep neuroscientists interested in auditory attention quite busy for years to come.

Acknowledgement

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References and recommended reading

Some articles have been marked as worthy of special interest. All papers in this subjective category are recent (publication within the last five years) and relevant (results making an important contribution to the field of auditory attention).

- of special interest

1. Fan J, Posner M: **Human attentional networks**. *Psychiatr Prax* 2004, **31**(Suppl 2):S210-S214.

2. Ahveninen J, Jaaskelainen IP, Raij T, Bonmassar G, Devore S, Hamalainen M, Levanen S, Lin FH, Sams M, Shinn-Cunningham BG *et al.*: **Task-modulated 'what' and 'where' pathways in human auditory cortex**. *Proc Natl Acad Sci USA* 2006, **103**:14608-14613.

Human neuroimaging study of selective attention to auditory object identification and localization using dual approaches (fMRI and MEG). Subjects were asked to attend either to the phonetic content of sound pairs or to their location. The key finding was a double dissociation in response adaptation to sound pairs with phonetic versus spatial sound changes dependent upon attentive focus, and the demonstration of parallel 'what' and 'where' pathways for sound processing. Further, with the time resolution of MEG, it was possible to show that activation of these parallel pathways occurred as early as 70–150 ms from stimulus onset and that the 'where' pathway was activated ~30 ms earlier than the 'what' pathway. These results suggest that auditory selective attention effects are feature specific and also that they may arise from enhanced tuning of receptive fields of task-relevant neuronal populations.

3. Johnson JA, Zatorre RJ: **Neural substrates for dividing and focusing attention between simultaneous auditory and visual events**. *Neuroimage* 2006, **31**:1673-1681.

In order to map the neural basis of bimodal divided attention—attending to one sense while ignoring another—an fMRI study was conducted in which subjects simultaneously heard novel melodies and viewed geometric shapes, and in different conditions, were instructed to attend to only one sense (bimodal selective attention) or to both senses at the same time (bimodal divided attention). Bimodal selective attention lead to increased activity in relevant sensory cortices and simultaneous decrease in irrelevant sensory cortex. Thus top-down attentional effects modulate the interaction of sensory cortical areas by enhancing processing in one modality at the expense of the other. Subjects with the best performance during the selective-attention task showed the greatest enhancement of activity in relevant sensory cortices. However, unlike the selective-attention conditions, divided attention recruited heteromodal areas in dorso-lateral prefrontal cortex (DLPFC). These results suggest that selective attention was achieved by a different neural set of neural processes. Selective attention acted by modulation of sensory cortices, whereas bimodal attention recruited DLPFC.

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8. Nobre AC, Correa A, Coull JT: **Temporal effects of attention (review)**. *Curr Opin Neurobiol* 2007, (this issue).

9. Gilbert CD, Sigman M: **Brain states: top-down influences in sensory processing (review)**. *Neuron* 2007, **54**:677-696.

10. Fritz J, Shamma S, Elhilali M, Klein D: **Rapid task-related plasticity of spectrotemporal receptive fields in primary auditory cortex**. *Nat Neurosci* 2003, **6**:1216-1223.

This study developed an innovative approach that made it possible to simultaneously measure spectral-temporal receptive fields (STRFs) with task performance, providing multiple snapshots of the dynamically changing STRF during ongoing behavior. Ferrets were trained on a generalized tone detection task, in which they learned to detect tones of any frequency, in the context of background noisy stimuli. Attending to a specific target frequency during the detection task consistently induced localized facilitative changes in STRF shape, which were swift in onset (<2 min) and could persist for hours, and provide a form of sensory memory. The authors propose that such modulatory changes could enhance overall cortical responsiveness to the target tone and increase the likelihood of 'capturing' the attended target during the task.

11. Fritz JB, Elhilali M, Shamma SA: **Differential dynamic plasticity of A1 receptive fields during multiple spectral tasks**. *J Neurosci* 2005, **25**:7623-7635.

In this behavioral physiology study, ferrets were initially trained on generalized frequency-independent tasks—a single-tone detection task, and a two-tone discrimination task. While recording from the same neurons, spectral-temporal receptive fields (STRFs) were measured in A1 under resting (non-task conditions) and also while ferrets successively performed frequency discrimination or tone detection tasks. Both tasks enhanced STRFs at the target frequency. In the discrimination task, however, STRF suppression was observed at the reference frequency. STRF changes were rapid and frequency-selective for both task conditions. In successive tasks, neurons responded differentially to identical tones, depending upon whether the tone was a reference or target. These task-dependent differences in receptive-field plasticity reflect differences in the meaning attributed to identical stimuli according to the context in which they were presented.

12. Fritz JB, Elhilali M, David SV, Shamma SA: **Does attention play a role in dynamic receptive field adaptation to changing acoustic salience in A1? (Review)**. *Hear Res* 2007, **229**:186-203.

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A neuroimaging approach was used to test the prediction that differential attentional focus on the same stimulus set would differentially activate auditory cortex. Subjects were presented with the same set of frequency-modulated tone sweeps, which the subjects were asked to categorize, either in pitch direction (rising or falling), or in duration (short or long). When the task involved attention to pitch direction, there was greater activation in right posterior auditory cortex than passive stimulus exposure. By contrast, there was greater left posterior auditory cortex activation when the task involved attention to sweep duration. These results provide strong evidence that top-down influences can differentially shape responses in the two hemispheres, leading to lateralized patterns of activation, dependent upon task constraints and attentional focus.

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