Short-term plasticity in auditory cognition

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Converging lines of evidence suggest that auditory system short-term plasticity can enable several perceptual and cognitive functions that have been previously considered as relatively distinct phenomena. Here we review recent findings suggesting that auditory stimulation, auditory selective attention and cross-modal effects of visual stimulation each cause transient excitatory and (surround) inhibitory modulations in the auditory cortex. These modulations might adaptively tune hierarchically organized sound feature maps of the auditory cortex (e.g. tonotopy), thus filtering relevant sounds during rapidly changing environmental and task demands. This could support auditory sensory memory, pre-attentive detection of sound novelty, enhanced perception during selective attention, influence of visual processing on auditory perception and longer-term plastic changes associated with perceptual learning.

Introduction
Making sense of our everyday acoustic environments is a highly complex task. The brain must convert the stream of acoustic energy into features and objects, seamlessly combine auditory and visual information, and prioritize processing of relevant stimuli while maintaining capability to react quickly to unexpected events. The brain must also memorize the immediate past, predict what is going to happen next and learn to categorize new features and objects. For instance, in a crowded cocktail party, one can selectively attend to a given conversation despite interference from multiple overlapping conversations, especially when seeing the lip movements of the speaker. Yet background noise and other conversations are automatically analyzed to some extent, as evidenced by attention being drawn to unexpected (i.e. unpredictable) events, such as one’s name being brought up in a background conversation. Further, the brain quickly adjusts to an unfamiliar accent of a new conversation partner, with such perceptual learning effects persisting over long periods of time, even up to a lifetime.

How is the brain able to do all this? Hierarchical organization of parallel sound feature processing provides a partial explanation. Neurons are responsive to increasingly complex sound features when progressing from the primary to the surrounding secondary auditory-cortex areas [1]. There are parallel auditory-cortex processing streams specialized in speech perception and delineation of identity and spatial loci of perceptual objects [2,3]. These streams have their origins already in subcortical structures [4] and ultimately extend to prefrontal areas [2]. This hierarchical organization of

Glossary

Short-term plasticity and auditory cognition terminology

Center-excitation surround inhibition: Enhancement of neural sensitivity to some features within a given feature dimension with simultaneous decrease of neural sensitivity to adjacent features. Excitation of a part of a tonotopically organized cortex with simultaneous inhibition of the adjacent parts is a classic example of center-excitation surround inhibition.

Features and objects: Features refer to elementary building blocks of perceptual objects. For instance, red color is a feature of an apple, and descending/ascending sound sweeps are the basic constituents of speech. Perceptual object refers to an abstract higher-order representation that is also in most instances inherently multisensory. For instance, the smell or sight of an apple, or the sounds of someone eating an apple, each activate the same object representation.

Feed-forward and feedback: Connections targeting cortical layer IV are referred to as feed-forward (or driving) connections. Feedback connections refer to connections to layers above and below layer IV, and are predominantly modulatory in nature.

Parallel sound feature processing: It appears that the brain processes certain aspects of the auditory environment in parallel. There is empirical evidence indicating that the locations of auditory objects ("where") are processed in parallel with processing of the identity of those objects ("what").

Short-term plasticity: Short-term plasticity refers to any bottom-up and top-down inputs that transiently modulate the responsivity of the target neuron to a subsequent stimulus and thus also change the oscillatory properties of the local neuronal population.

Sine-wave speech (SWS): SWS stimuli typically consist of three sine waves tracking the lowest formants of speech sounds. They are heard as non-speech when perceivers do not know that the sounds are modified speech sounds, thus offering a powerful tool to study neural basis of speech processing.

Spectrotemporal receptive fields (STRF): Auditory-system neurons are more sensitive to certain sound features than others. The STRF of a given neuron determines to which frequency-modulated (FM) (i.e. sound sweep) features it is most sensitive. FM sounds typically elicit more robust responses in auditory-cortex neurons than tones of a fixed frequency.

Stimulus-specific adaptation (SSA): Sound feature-specific suppression caused by a preceding auditory stimulus. For instance, a 1 kHz sound transiently suppresses (after initially exciting) auditory-cortex neurons that are sensitive to sounds of similar frequency. SSA has also been referred to in the literature as post-stimulus inhibition, response saturation, paired-stimulus inhibition, paired-pulse inhibition, adaptation, habituation, forward masking and refractoriness. Lateral inhibition could be the primary neurophysiological mechanism underlying auditory-cortex SSA.
parallel processing streams offers a highly attractive explanation as to how, for instance, perception of complex auditory scenes is accomplished by the brain. However, it cannot alone explain how auditory sensory memory, involuntary and selective attention, audiovisual perception, and perceptual learning come about. Here we review converging evidence from recent studies suggesting that short-term plasticity within the hierarchically organized parallel auditory processing system has the right properties to support these cognitive functions.

With short-term plasticity, we refer to any feed-forward (bottom-up) and feedback (top-down) inputs, both excitatory and inhibitory, that transiently (from tens of milliseconds to minutes) modulate the responsiveness of the target neurons to a subsequent stimulus (for a summary diagram of short-term plasticity in the auditory system, see Figure 1). Short-term plasticity also changes local neuronal population oscillatory properties [5] that, via cortico-cortical and corticofugal [6] connectivity, influence processing in other cortical and subcortical structures (for a recent review on the relevance of oscillatory activity in perception and cognition, see Ref. [7]). Indeed, auditory system short-term plasticity should be understood as modulations within a given level of processing hierarchy. These then stimulus-specifically influence processing at both higher and lower levels of the auditory pathways, possibly even as low as at the level of outer hair cells [8], which mechanically modulate sound processing in the cochlea [9].

### Short-term plasticity driven by bottom-up inputs: tuning by stimulus-specific adaptation

Within the auditory cortex, individual neurons are receptive to auditory stimuli with particular physical features. These neurons can be suppressed for several seconds after their initial excitatory response to an auditory stimulus. Here we call this important phenomenon stimulus-specific adaptation (SSA) [10,11]. Lateral (or surround) inhibition could be the primary neurophysiological mechanism underlying the SSA [12-14]. This offers a potential explanation of how bottom-up and top-down inputs interact in the auditory cortex (see Figure 1). Sometimes, post-stimulus facilitation is also seen in instances when the stimulus widely differs from the preceding stimulus [11]. This might be a result of SSA reducing the tonic inhibition exerted by the adapted population on its neighbors [15].

Recent studies of the auditory cortex suggest that SSA underlies auditory sensory memory [10,16]. Auditory sensory memory is an accurate memory representation of the auditory environment. Often referred to as echoic memory, it lasts for several seconds, and is vital for speech comprehension and working memory tasks where relevant auditory information needs to be accessed over a period of a few seconds. Auditory sensory memory representations also form a sensory-level prediction of the immediate future, thus allowing determination of stimulus novelty.

Single-neuron recordings in cats have shown that primary auditory-cortex neurons exhibit SSA timescales varying from hundreds of milliseconds up to tens of seconds [17]. Such a range of adaptation time constants is useful for supporting representations of auditory objects that typically have their features distributed over time [18]. Indeed, it is feasible to assume that auditory-cortex neural populations selective to sound frequency [19], pitch [20], intensity [21], periodicity [22], location [3] and speech-specific features [3,23,24], together with variability in adaptation time constants [17], could form the basis for auditory sensory memory representations. The notion that the auditory cortex supports auditory sensory memory is backed up by transcranial magnetic stimulation results showing that disruption of auditory-cortex activity specifically impairs short-term memory [25].

Neurophysiological recordings and non-invasive neuroimaging results suggest that SSA underlies the so-called mismatch negativity response (MMN), which is an event-related potential (ERP) component thought to reflect auditory sensory memory function [10,12,16]. Specifically, a computational model suggested that SSA (specifically lateral inhibition) within a tonotopically organized neuronal population delays and weakens responses to stimuli that slightly differ in frequency from the preceding sounds, thus giving rise to the characteristic MMN response [12]. Subsequent single-neuron recordings from cat primary auditory cortex supported this model. Robust responses and hyperacuity to rare sounds differing in sound frequency (both hallmarks of MMN) were explained by SSA of A1 neurons [10].

Combined functional magnetic resonance imaging (fMRI), electroencephalography (EEG) and magnetoencephalography (MEG) data in humans further extended this model. Differential SSA within anterior and posterior auditory-cortex areas was observed to give rise to MMN following changes in sound frequency [16]. Specifically, there are two electromagnetic auditory-cortex sources that partly overlap in time: an early posterior and a late anterior source. The amplitude of the posterior source was rapidly suppressed with decreasing difference in sound frequency between the standard and deviant sounds. Suppression of the posterior source amplitude was suggested to explain reduced behavioral distraction caused by novel sounds on visual task performance. The amplitude of the anterior source was less affected. This finding suggested that neurons generating the anterior source are more narrowly tuned on sound frequency than the neurons underlying the posterior source. The anterior response was also robustly increased in latency as a function of decreasing standard-deviant difference. The adapted anterior source might thus correspond to the “classic” temporally delayed and slightly anteriorly generated MMN response to small changes in sound frequency [16]. Subsequent studies have suggested that the differential SSA in anterior and posterior cortices likely reflects specialization of the underlying neural populations to processing of object identity and spatial location of auditory stimuli, respectively [3].

The validity of the SSA model of MMN has been questioned by findings of MMN responses to abstract patterns (see Ref. [26]). However, it seems that the MMN to abstract patterns is generated by different cortical sources than MMN to sound frequency change [27]. Thus, the existence of the abstract/pattern MMN may not be used as a strong argument against the validity of the SSA model of MMN to sound frequency change.
Traditionally, the auditory system has been thought to be dedicated to bottom-up processing of auditory stimulus features. However, the majority of input connections to both primary and secondary auditory cortical areas are top-down inputs from other cortical areas (see Ref. [28]), and robust task-related auditory-cortex short-term plasticity has been observed in recent studies. We will review these findings next.
Short-term plasticity driven by top-down inputs: receptive field changes

Enhancement of auditory-cortex responses to attended versus non-attended stimuli has been consistently shown in human MEG [29] and fMRI studies [30], with more robust effects seen in the secondary than in the primary auditory cortex [30]. Rather than there being a single, unitary, selective-attention effect, the task of the subject seems to determine which parts of the auditory cortex are modulated by top-down inputs. Human anterior auditory cortex (the putative “what” processing pathway) exhibited enhanced selectivity to phonemes when subjects directed their attention to phonetic features in a recent fMRI/MEG study [3]. Conversely, selectivity of the posterior auditory cortex (the putative “where” processing pathway) to spatial location of auditory stimuli was enhanced when subjects directed their attention to stimulus locations. These attention effects were prominent already at relatively early latencies (~100 ms from stimulus onset [3]) (see Figure 2). Changes in tonotopic maps [31] and increased auditory-cortex selectivity for sound frequency [15] have been further observed at comparable latencies when subjects selectively attend to sound frequency cues. Enhanced sound frequency selectivity correlated with improvements in frequency discrimination task performance [15]. Thus, focusing attention to a given acoustic feature seems to enhance neuronal selectivity to that feature in the particular part of the auditory cortex that is specialized in processing it.

Recent studies in awake, behaving ferrets have further clarified the neurophysiological basis of selective attention. Spectrotemporal receptive fields (STRF) of A1 neurons were transiently modulated to encompass the frequency of the target tone [32] (see Figure 3). This happened only when the animals attended to a sound frequency that was sufficiently close to the excitatory center of the neuron’s receptive field. This effect seemed to be caused by top-down center excitation, spanning approximately one octave around the target frequency, and surround inhibition [32]. Subsequent studies have investigated STRF changes that occur when the animals attend to temporal sound features (detection of gaps in stimulation and discrimination of click rates) and when the target is a multiple-tone sound [33,34]. Results from these studies suggest that the STRF changes constitute “task-specific signatures” of facilitation and suppression. Further, a given neuron could differentially change its STRF in different task conditions. It was suggested that the STRF changes enhance figure/ground separation by filtering out the background while simultaneously enhancing the target [34]. In terms of cognitive models of attention, these findings favor “early-selection/gating” [29] over “late-selection” [35,36] models. In other words, attentional memory traces against which incoming stimuli are matched during selective-attention performance seem to be represented in the same auditory-cortex neuronal populations that represent auditory sensory memory.

Controlling for selective attention is highly challenging especially in animal studies, and indeed there are many neurophysiological findings in the literature with few links to behavior or cognition. However, the receptive field
changes in ferret auditory cortex were noted to occur relatively quickly (i.e. within the 2.5 min required for measurement of the STRFs [32]). Furthermore, these STRF changes correlated with improved behavioral performance in the tasks, and in most cases persisted only for the duration of the relevant task performance [32,34]. Thus, it is highly likely that the observed effects were caused by selective attention.

Interestingly, the center-excitation surround-inhibition modulations seen in STRFs during tone-detection tasks are tantamount with spatial selective-attention effects observed in the visual system. Attention-driven inhibition of visual stimuli near the attended location was recently observed in both striate and extra-striate cortex, in addition to the well-documented facilitation at the attended location [37].

Taken together, these results suggest that top-down inputs tune the feature-specific neural populations of the auditory cortex similarly to bottom-up inputs [12–14]. The auditory cortex could then be understood as an interaction surface between the auditory environment and the goals of the organism. This could well explain the commonplace observation of it being easier to direct and maintain attentional focus right after the attended stimulus has occurred (i.e. when bottom-up and top-down inputs match; see Figure 1). For instance, after hearing the faint extra sound from the car engine, it is easy to “tune in” to inspect it in more detail. On the other hand, sometimes when listening intently, one can hear sounds that are not there, such as when “hearing” the faint sounds made by an imagined burglar in the middle of the night. Tentatively, such illusory percepts could be explained by mismatching top-down and bottom-up inputs in the auditory cortex (see Figure 1).

What then initially drives these selective-attention-related modulations in the auditory cortex? More robust enhancements in feature selectivity are seen at the level of the secondary than primary auditory cortex [3,30]. Thus, it may well be that primary auditory-cortex receptive field changes are driven by enhanced feature selectivity at the level of the secondary auditory cortex. Secondary auditory-cortex plasticity could in turn be driven by hierarchically higher prefrontal/parietal networks [2,38,39]. There are also longer-latency selective-attention-related ERP
responses called processing negativity and negative difference that have been interpreted to support the late-selection models of attention [35,36]. Tentatively, these ERP responses could correspond to the hierarchically higher-order representations in prefrontal/parietal cortical areas.

Notably, top-down inputs might reach levels even hierarchically lower than the auditory cortex. The auditory cortex exerts center excitation and surround inhibition on subcortical auditory nuclei [40]. These corticofugal connections could play an important role in selective attention. In a recent study, inactivation of ferret A1 by implantation of a sustained-release polymer containing GABA agonist muscimol hindered relearning of auditory localization upon occlusion of one ear. However, selective lesions of the descending cortico-collicular fibers fully prevented relearning [41].

Top-down modulation of the auditory cortex is not limited to selective-attention tasks. Sensitization in animal studies leads to an overall increase in gain and reduction in neuronal selectivity to stimulus features, as though the brain entered a “detection mode” (as opposed to the “discrimination mode” in selective-attention tasks) [42]. Posterior superior temporal sulcus (STS) exhibited enhanced hemodynamic activity when human subjects perceived sine-wave speech as speech versus non-speech noise [43] (i.e. when the subjects were in a speech-perception mode). Auditory-cortex neurons that only respond to sounds that are relevant in a motor task have been described in non-human primates [44]. Furthermore, there are findings suggesting that visual stimuli significantly modulate the auditory cortex and influence what we hear. We will review these findings next.

**Auditory short-term plasticity driven by cross-modal inputs**

Perception is inherently multisensory. For instance, speech perception is enhanced in noisy conditions when we see the speaker’s articulatory gestures. Further, mismatching auditory and visual stimuli can result in audiovisual illusions such as ventriloquism effects and a phonetic illusion called the McGurk effect (e.g. experimental subjects hearing /da/ when simultaneously presented with auditory /ba/ and visual /ga/).

There are direct anatomical connections to the auditory cortex from the visual cortex [45], heteromodal cortex [46] and prefrontal “mirror-neuron” system [47,48] that can support multisensory processing. Somatosensory inputs to the auditory cortex meet the criteria for feed-forward connections (targeting layer IV). It is possible that this is a result of somatosensation (e.g. vibration) being evolutionarily close to the auditory modality. By contrast, visual inputs seem to be mainly top-down feedback connections that target cortical layers above and below layer IV [49].

A recent fMRI study showed increased hemodynamic responses in the primary auditory cortex when subjects were lipreading during continuous background fMRI scanner noise [50]. Tentatively, it is possible that the lipreading task tuned the auditory cortex to better filter speech-related acoustic features, thus resulting in differential auditory-cortex responses to the scanner noise. The activation of the primary auditory cortex also suggests that visual inputs influence auditory processing at a relatively early stage. Consistently with this, EEG [51,52] and MEG [53] recordings have shown suppressed auditory-cortex responses to audiovisual speech stimuli at relatively short latencies (~100 ms). Further, visual influence is not limited to speech stimuli but seems to be also caused by other types of stimuli with strong learned audiovisual associations. For instance, enhanced activations in the primary and secondary auditory (and heteromodal) cortex were noted during viewing of complex natural scenes in a macaque fMRI study [54].

Do these cross-modal inputs have anything in common with how other top-down and/or bottom-up inputs influence the auditory system? There currently is not a definite answer to this question. However, primary and secondary auditory cortex exhibited both inhibitory and excitation local field-potential modulations during viewing of species-specific vocalizations in the rhesus monkey (*Macaca mulatta*) [55]. With delayed voice onset there were increasingly more inhibitory modulations [55]. This suggests that cross-modal inputs initially cause excitation followed by post-stimulus inhibition. Visual stimuli also seem to modulate auditory EEG [51,52] and MEG [53] responses at latencies comparable to those of selective-attention effects.

Furthermore, it has been consistently reported that stimulus congruency matters [46,56,57]. As an example, the human auditory cortex was activated only by familiar congruent stimuli with strong learned associations in a recent fMRI study [58]. Further, human posterior lateral superior temporal gyrus responses to auditory speech stimuli were significantly more influenced by the addition of articulatory gestures than by meaningless facial gestures [59], and multisensory enhancement in macaque STS occurred only when the sound of an action matched the sight of the action [60]. Factors such as stimulus timing [55,61], the type of stimulus [62] and the type of task [63] seem to play a role in determining whether congruence causes response enhancement or suppression, and/or which cortical areas are involved.

The significance of audiovisual stimulus congruency suggests that the excitatory-inhibitory pattern caused by visual stimuli in the auditory cortex [55] is not a random or a general one, but might tune the auditory system to better detect the relevant auditory features of perceptual objects. Such tuning could well explain perceptual enhancements when auditory and visual stimuli match (e.g. seeing the lips of the speaker in the noisy cocktail party), as well as perceptual illusions when the auditory and visual stimuli mismatch (see Figure 1). For instance, the ventriloquism and McGurk effects could be explained by mismatching auditory and visual inputs to cortical spatiotopic and phonotopic maps, respectively.

**When short-term plasticity becomes long-term plasticity: perceptual learning**

There appears to be a relationship between the short-term modulations reviewed above and longer-term plasticity that supports perceptual learning. Perceptual learning refers to long-term (or even permanent) adjustment of perception to the relevant features of the environment. It is needed in a wealth of tasks, for instance, when...
learning to discriminate phonemes of a foreign language or sounds of musical instruments. The influence of visual stimuli on auditory processing reviewed above also depends on perceptual learning of particular auditory-visual associations during development.

MEG studies have shown that musical training enlarges auditory cortical representation of sound features that are relevant in music perception, for instance, the timbre of the instrument that the musician plays (see Ref. [64]). Changes in early ERP responses (presumed to originate from the auditory cortex) have also been reported when subjects learn to discriminate between phonetic stimuli [65,66]. Recently, it was observed that such auditory-cortex changes can occur very rapidly. The ability to discriminate phonemes improved as quickly as within 16 min of training, with concomitant changes evident in early (~120 ms) ERP responses [66].

In rats, robust task-specific topographic map changes were observed when identical sets of auditory stimuli were presented with only one feature, frequency or intensity, as task relevant [67] (see Figure 4). Primary and secondary auditory-cortex tonotopic maps exhibited enlargement of target sound frequency range when rats were trained to attend to frequency cues. Conversely, rats trained to

![Figure 4](https://example.com/figure4.png)

**Figure 4.** Task-specific enlargement of tonotopic and intensity maps in rat primary (AI) and secondary (SRAF) auditory cortex during identical stimulation conditions. (a) Task-specific reorganization of cortical tonotopy. Tonotopic maps from AI and SRAF were delineated using microelectrode mapping. The color of each polygon in the map represents the characteristic frequency of neurons in the middle cortical layers. Gray shaded polygons indicate recording sites with characteristic frequency values within the trained frequency range (5 kHz ± 0.375 octaves). Filled circles indicate unresponsive sites. Open circles represent sites not meeting the criteria for inclusion in AI or SRAF. During the frequency discrimination task, the representation of the trained sound frequency ranges was enlarged in AI and SRAF as compared with both the control and intensity recognition conditions. (b) Task-specific reorganization of cortical intensity maps in AI and SRAF. The color of each polygon indicates the best intensity level of the neurons. Empty polygons indicate recording sites where a best intensity level could not be determined. Blue shaded polygons indicate recording sites with best intensity level values in the trained intensity range (35 ± 5 dB SPL). During the intensity discrimination task, the representation of the trained range of intensities was enlarged as compared with both control and frequency recognition conditions. This effect seemed more prominent in SRAF than AI. Note that the intensity maps do not appear to be as orderly topographic as the sound frequency maps (adapted with permission from Ref. [67]).

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attend to intensity cues exhibited an increased proportion of non-monotonic intensity response profiles preferentially tuned to the target intensity range [67]. Attention to frequency cues appeared to produce equally strong effects in primary and secondary auditory-cortex areas, whereas intensity-training effects were pronounced in the secondary auditory cortex. Intensity maps were also not as clearly topographic as the tonotopic maps. Importantly, topographic map plasticity effects correlated with the degree of perceptual learning in the tasks [67].

Top-down influences seem to be specifically important in perceptual learning [66–68] (although see also Ref. [69]). Perceptual learning of phonetic stimuli and associated changes in ERP responses occurred only when human subjects attended the stimuli [66]. The ERP effects further seem to occur at latencies similar to the selective-attention effects. The importance of selective attention in perceptual learning is highlighted by a recent study showing improved auditory frequency discrimination following training with physically identical tones [68]. It is possible that this resulted from tuning of the low-level representation against which subsequent discrimination is performed.

Acetylcholine release from nucleus basalis (NB) onto the auditory cortex could explain why some selective attention-related auditory-cortex short-term plasticity effects persist [70]. Specifically, classical conditioning studies in rats [42] have demonstrated effects resembling the STRF changes observed in ferrets during selective attention [34]. These longer-term receptive field changes seem to depend on ascending acetylcholineergic neurotransmission from the NB [70]. Further, pairing of broad-spectrum noise with NB stimulation resulted in widening of receptive fields of rat auditory-cortex neurons, and this effect was reversed by subsequent pairing of NB stimulation with tones [71]. There are still, however, open questions. For instance, the serotonergic system has also been observed to play a role in consolidation of receptive field changes in the auditory cortex [72].

Concluding remarks

Converging lines of evidence suggest that short-term plasticity of the hierarchically organized parallel auditory system supports auditory sensory memory, sensory predictions, novelty detection, selective attention, audiovisual integration and perceptual learning (see Figure 1). However, there are several outstanding questions. For instance, although summation of short-term plasticity effects caused by bottom-up and top-down inputs on feature-specific auditory-cortex neural ensembles could explain a wealth of behavioral phenomena such as enhancement of selective attention when the target sound is presented more frequently (i.e. when top-down and bottom-up inputs match) and audiovisual illusions (i.e. when visual and auditory inputs mismatch), this has not been directly tested. Further questions also include: how does short-term plasticity relate to oscillatory phenomena at the local neuronal population and large-scale network level, and how does this relate to perception/cognition? What is the importance of subcortical short-term plasticity and its interactions with the auditory cortex in perception and cognition? What are the top-down mechanisms initiating auditory-cortex short-term plasticity, and why do some of the effects persist to enable perceptual learning? What is the role of the mirror-neuron system in cross-modal perception and perceptual learning? Rapid advances in functional neuroimaging techniques [3,73,74] are now making it possible to study these outstanding questions in detail.

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