

# Multisensory contributions to low-level, 'unisensory' processing

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Neurobiologists have traditionally assumed that multisensory integration is a higher order process that occurs after sensory signals have undergone extensive processing through a hierarchy of unisensory subcortical and cortical regions. Recent findings, however, question this assumption. Studies in humans, nonhuman primates and other species demonstrate multisensory convergence in low level cortical structures that were generally believed to be unisensory in function. In addition to enriching current models of multisensory processing and perceptual functions, these new findings require a revision in our thinking about unisensory processing in low level cortical areas.

## Addresses

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## Introduction

Recent studies in both monkey and human subjects have provided evidence for multisensory convergence at low-level, putatively unisensory, stages of the sensory cortical pathways [1–10,11\*]. For example, somatosensory responses can be observed in auditory belt cortical regions (i.e. at the second level of auditory processing [4]), and eye position input modulates auditory responses even at the primary cortical (A1) level [12,13]. Parallel findings have emerged in carnivores [12–14]. Most dramatically, two laboratories [15,16] have shown anatomical interconnections between low-level visual and low-level auditory areas, which include the primary cortices (V1 and A1), and two others have shown that eye position can affect the gain of auditory responses in A1 [17,18]. Recent reviews [9,19,20] have highlighted the fact that low-level (early) multisensory convergence is paradoxical from a hierarch-

ical sensory perspective, and its functions are not yet clear.

This review focuses on low-level multisensory convergence in the primate auditory system. First, we review the neurophysiological evidence in this area. Second, we discuss the potential anatomical sources of non-auditory input, and the types of projections used (i.e. feedforward, feedback, lateral). Finally, we consider the functional implications of early multisensory integration in the context of the hierarchical model of auditory processing. To avoid confusion, we will use the term 'low-level' to refer to the anatomical stage at which a multisensory process is observed, reserving the term 'early' for reference to the time domain.

## Visual and somatosensory responses in auditory cortex

Studies using event related potentials (ERPs) in humans have demonstrated short latency audio–visual [3,7] and audio–somatosensory [21,22] interactions, and have raised the possibility that these interactions occur in auditory cortices of the superior temporal plane. Localization of multisensory interactions within the superior temporal plane is independently supported by findings from other brain imaging techniques that have better anatomical resolution, including magnetoencephalography (MEG) [1,23,24] and functional magnetic resonance imaging (fMRI) [11\*,25].

Intracranial recordings in several macaque species directly confirm multisensory convergence in auditory cortex [4,5,8,26], showing somatosensory and visual inputs in regions posterior to A1. The initial report of non-auditory inputs [4] used multi-electrode recordings in awake monkeys to show that somatosensory responses triggered by electrical stimulation of the median nerve have approximately the same latency as co-located auditory responses, and have a similar, although not identical, feedforward laminar profile. That is, the response begins in Lamina 4 and is followed by responses in the supra- and infragranular laminae [27]. The laminar profile of these inputs contrasts strongly with that of nearby visual inputs [5,27]. These inputs have a feedback profile, in that, activity begins outside of Lamina 4, typically in the supragranular laminae, and then spreads to Lamina 4 [27]. In addition, a study [8] used microelectrode recordings in anesthetized monkeys to confirm that convergence occurs at the single neuron level [12,13], and showed that, although cutaneous, proprioceptive and vibratory inputs are present, the dominant specific type of input is a cutaneous representation biased toward the skin surfaces of the head and neck.

Corresponding studies of specific visual properties have not yet been conducted, although other studies (e.g. [11<sup>\*</sup>,25]) predict strong motion sensitivity.

These results fit into a complex of earlier findings on somatosensory inputs into the region of posterior auditory cortex in macaque monkeys. Leinonen *et al.* [28] reported auditory–somatosensory co-representation in Area Tpt, the parabelt region occupying the posterior most portion of the superior temporal plane in macaque monkeys. Also in macaques, Robinson and Burton [29] described a body map in a medial retro insular (RI) region of the superior temporal plane, in a location just medial to the caudo-medial (CM) belt region of auditory cortex; our ongoing studies (P Lakatos and CE Schroeder, unpublished) show that RI receives auditory inputs. Subsequently, Krubitzer *et al.* [30] suggested the existence of one or more body surface maps in a region they referred to as ventral somatosensory area (VS), which adjoins the medial edge (foot representation) of parietal operculum areas S2 and PV and extends out over the surface of the posterior superior temporal plane. A portion of VS probably corresponds with the RI of Robinson and Burton [31]. In any case, in macaques, the somatosensory region extending over the caudal superior temporal plane apparently corresponds to Areas CM, MM and RI and possibly also to the caudo-lateral (CL) belt area, in addition to Area Tpt.

### Anatomical mechanisms of multisensory convergence in auditory cortex

In considering possible sources of somatosensory input to posterior auditory cortex, it is important to recognize that the anatomical inputs mediating electrically-evoked, median nerve responses [4,32] and those mediating cutaneous, proprioceptive and vibratory inputs [8] might not be of uniform type. In fact, we think that the electrically-evoked, median nerve responses might be mediated by subcortical inputs from nonspecific, extralemniscal systems, whereas the cutaneous, proprioceptive and vibratory are likely to reflect more specific lemniscal inputs, conveyed through somatosensory cortical circuits. As elaborated below, the known connectivity patterns of the posterior auditory cortices provide several routes, both cortical and subcortical, by which somatosensory and visual inputs can converge in auditory cortex.

#### Cortical sources

Given the involvement of RI, and its close association with CM, a wide range of areas are potential cortical sources of somatosensory input, including Areas 3b, 1, 2, 5 and S2 and/or PV (reviewed by Burton and Sinclair [33]). Also, the input could originate in the somato-recipient zones of several multisensory regions including those in the intraparietal sulcus, superior temporal polysensory area (STP) and prefrontal cortex (Pfc) [34–36]. These areas, in addition to anterior cingulate (AS) cortex, are emerging as possible sources in our ongoing tracer studies (Hackett

TA, *et al.* unpublished; Smiley J, *et al.* unpublished). Given the heterogeneity of the connections of caudal auditory cortex with this widespread network of areas, use of the full range of feedforward, feedback and lateral connection types appears likely. The visual inputs to audiovisual interactions that are believed to occur in auditory cortex [3,5,7,25], similar to the somatosensory inputs discussed above, could be mediated by well-documented feedback projections from the STP [35,37], intraparietal sulcus [34] and Pfc [36,38]. Also, recent findings from two laboratories [16,39] indicate projections from auditory regions including A1 and posterior auditory association areas to Areas V1 and V2. According to Rockland and Ojima [16], the projections are sparse and focused in the uppermost layers, but those to V2 are much more dense and extend through both the upper and the lower layers of the cortex. The basic laminar profiles of these projections fit into the feedback or lateral categories of projections (KS Rockland, pers comm). If these projections follow the usual cortical pattern [40], then a reverse projection, that is, one from visual to auditory cortex, is predicted. Ongoing tract tracing studies confirm this prediction, that is, they outline a clear projection to the caudal superior temporal plane from V2 (TA Hackett, J Smiley, G Karmos, I Ulbert, CE Schroeder, unpublished). Our earlier findings on functional manifestations of visual–auditory convergence in auditory cortex (above) outline a physiological response pattern that conforms to the bilaminar profile expected for a feedback input [5]. It is possible that in contrast to cortical somatosensory inputs, cortical visual inputs might be confined to the 'feedback' and 'lateral' connection patterns.

#### Subcortical sources?

Potential subcortical sources of somatosensory and visual input to auditory cortex (reviewed by Schroeder *et al.* [27]) include several thalamic structures. These include the posterior (PO), postero-medial (PM), limitans (LIM) and supragenulate (SG) nuclei of the thalamus, in addition to the magnocellular (MGm) and anterior dorsal (AD) divisions of the medial geniculate nucleus. There is also an input from a population of neurons in the ventral posterior complex (VP), which is the main thalamic relay for the somatosensory system. An extensive ongoing analysis of potential subcortical sources of non-auditory inputs to auditory cortex (Hackett TA, *et al.* unpublished) suggests that, based on the pattern of multisensory innervation of these thalamic nuclei, there might be a weighting of functions as follows. MGm is mainly auditory with some somatosensory inputs, SG and LIM mainly involve visual processing, with some representation of auditory and vestibular signals, and PO is somatosensory and auditory, with minor visual input. An important common factor in these non-auditory inputs to auditory cortex is that the neurons of origin appear to fall mostly within the non-specific or koniocellular thalamocortical system. In this context, 'specific' pertains to two things, the spatial extent of the peripheral receptive field and that of the

target zone in cortex. In the case of visual and somatosensory systems, peripheral receptive fields that cover a large portion of the receptor surface are less sensitive to fine spatial detail. In the case of auditory system, a larger receptive field corresponds to a greater area of the basilar membrane, and a reduced frequency specificity. And in all cases orderly targeting of small, circumscribed cortical domains increases the precision (specificity) of the first order cortical representation. Jones [41,42] refers to the specific and nonspecific systems as the 'core' and 'matrix' components of the thalamocortical projection. The core system is the one most often considered in connection to the thalamocortical relay of sensory inputs. It carries spatially specific information through a circumscribed subcortical route, which projects to the middle layers (lower 3 and 4) of a primary sensory region of cortex. In the case of the auditory system, it is the pathway that courses through the central nucleus of the inferior colliculus and through the ventral division of the medial geniculate body (MGv) to terminate in Layer 4 and lower Layer 3 of A1 and R(Rt). The matrix system carries diffuse sensory input through a diverse network of subcortical pathways projecting to widespread cortical regions, and synapsing primarily in the uppermost cortical layers [25,40,43]. Although matrix inputs do target cortices appropriate for the sensory modality from which they originate, because of their less-specific cortical projection patterns, they clearly also project across sensory modalities, thus forming a potential substrate for multisensory interactions in low level cortical areas.

### Functional implications of multisensory convergence in low-level cortical processing

Assuming that activity in auditory cortex generally corresponds to a perceptual experience of something heard, a probable function of a converging visual or somatosensory input would be to enhance auditory analysis of that stimulus. How does auditory processing gain from non-auditory input? We consider two leading possibilities.

The first possibility is that somatosensory and visual inputs, due to their greater spatial precision, might support auditory spatial localization. This is in line with the proposition by Rauschecker [44] that caudal auditory cortical regions are specialized for stimulus localization (see also Recanzone *et al.* [45]). Also consistent with this view, an earlier study by Leinonen *et al.* [28] reported spatial correspondence between auditory and somatosensory receptive fields of bimodal neurons in Tpt. Our studies of the more detailed properties of somatosensory inputs to caudal and medial auditory cortex indicate that the cutaneous receptive fields of the neurons there are biased toward the skin surfaces of the posterior head and neck [8]. We have speculated that this pattern of representation fits better with spatial localization than with object identification functions [8]. The potential link between the nature of the cutaneous response and audi-

tory spatial localization rests on the basic premise that cutaneous receptive fields on the posterior scalp and neck could aid in localizing nearby stimuli that produce air puffs and noises. The cutaneous representation that would predict object recognition functions is biased towards the glabrous skin surfaces of the hands, and possibly the lips. The large size of the cutaneous receptive fields [8] suggests that in contrast to the median nerve-evoked response [4], the relevant input arises from higher order cortical regions such as Areas 5, 7 and S2. Thus, similar to visual inputs to posterior auditory cortex [5], cutaneous inputs from the head and neck might be mediated by feedback projections. Given this, one would predict that for events generating sounds with simultaneous visual or somatosensory concomitants, the non-auditory portions of the response in auditory cortex would develop later than the auditory portions; this temporal dissociation would be similar to that for feedforward and feedback processes observed in V1 for 'contextual surround' [46] and visual selective attention [47] effects, both of which use feedback input and lag the initial feedforward sensory input. In any case, given that the requirements for integration [48] are met, a visual or somatosensory input could enhance the spatial accuracy of the behavioral response to the auditory input and perhaps even its perceptual salience, with the dominant subjective experience remaining auditory.

A second possibility is that visual and somatosensory inputs to auditory cortex could predictively 're-set' ongoing auditory cortical activity, thus enhancing the local response to subsequent auditory input. Across a wide range of real-world events, prominent non-auditory stimuli are generated before auditory stimulus onset because some visible or palpable action is required to produce a sound. For example, a hammer must move before it can strike a nail to generate a sound, and for most vocalizations lip and/or facial movements precede sounds. It is generally acknowledged that viewing the event that generates the auditory stimulus increases the subjective intensity of auditory sensation. Two neural components are required to explain this phenomenon on a mechanistic level: some sort of auditory response amplifier, and a means for the non-auditory input to trigger the amplifier at the relevant time point. Recent findings from Lakatos *et al.* [49\*\*] reveal three findings crucial to the amplifier mechanism. The key question is then, can the auditory response amplifier be triggered by non-auditory input? Preliminary findings [50] suggest that both visual and somatosensory inputs can cause phase resetting of ambient oscillatory activity in auditory cortex.

### Conclusions: low-level multisensory convergence and 'the sensory hierarchy'

Suborning of activity in unisensory cortex by input from another sensory modality is an intriguing phenomenon that presents a paradox for hierarchical models of sensory

system organization [33,51,52]. On the one hand, it appears that in multisensory processing, as in sensory contextual processing [53], and in attentional modulation of processing [54–57], that recruitment of low level sensory areas into the cognitive–perceptual process is partially attributable to feedback-dependent processes that occur relatively late in post-stimulus time. Thus, the evolving concept of the sensory processing hierarchy must encompass temporal and anatomical dimensions [47]. On the other hand, our most recent findings show that multisensory interactions can occur shortly after response onset, at the lowest cortical processing stages [4,5,10,27]. Moreover, recent findings in our laboratory [49••] and elsewhere [58] reinforce the notion that cortical processing *per se* represents a collaboration between new sensory input and ongoing cortical processes. At some point, our basic understanding of 'low level (uni)sensory processing' will have to incorporate these facts.

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