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Non-auditory processing in the central auditory pathway

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Abstract

Multisensory responses have been observed throughout the central auditory pathway, yet the origin, function and perceptual consequences of cross-modal integration remain unresolved. Recent studies have applied modern neuroanatomical and functional perturbation techniques to dissect the circuits that might enable multisensory information to sculpt the processing of sound. These highlight in particular the role that subcortical pathways might play relaying multisensory information to and between sensory cortical fields. We also examine the consequences of integrating non-auditory information into auditory processing, identifying key areas where this may be critical for successful listening and potential roles for visual information in augmenting auditory scene analysis, and for non-auditory information in facilitating coordinate frame transformations.

35 Multisensory responses in early sensory cortex are ubiquitous. Visual responses have been observed
36 in normal hearing primate [1,2], carnivore [3] and rodent [4-7] auditory cortex. Similarly,
37 somatosensory responses are observed in the auditory cortex of primates [8-11], ferrets [12] and
38 rodents [13]. While auditory deprivation can radically increase the prevalence of cross-sensory
39 responses [14], here we focus on those that exist in the normal hearing brain. We first review recent
40 studies that have addressed the origin of crossmodal signals in the auditory pathway. In the second
41 half of the review we discuss the potential purposes that multisensory processing might serve for
42 listening.

43

44 [Anatomical routes through which multisensory information is conveyed to Auditory Cortex](#)

45

46 Anatomical investigations identify potential substrates for multisensory responses in auditory
47 cortex. Direct connections between sensory cortices provide one potential route through which
48 crossmodal information can access auditory cortex. There are direct connections from visual cortex
49 and auditory cortex in primates [15-17,18 ,19], carnivores [3,20 ,21] and rodents [22,23].

50 Somatosensory cortex also directly innervates auditory cortex [17,24-27]. Across species and studies,
51 it is apparent that connections between primary areas, though present, are sparse and that there
52 are specific projections between higher areas. For example, in the ferret distinct regions of visual
53 cortex innervate anterior versus posterior secondary auditory cortical fields [3].

54

55 In addition to cortical crossmodal inputs to auditory cortex, multiple nuclei within the auditory
56 thalamus integrate cross-modal information and may then relay this to non-primary auditory cortex
57 [28,29 ,30 ,31,32]. The proportion of the input that such non-lemniscal areas provide accounts for
58 only a few percent of the total thalamic input to primary areas, but to 30% or more in non-core
59 auditory fields (e.g. [28 ,29]).

60

61 While both cortical and thalamic routes offer the potential for multisensory information to access
62 auditory cortex, it is likely that multisensory information influences the encoding of sound even
63 earlier in the central auditory pathway. The inferior colliculus (IC) comprises a central division (ICCN)
64 that relays auditory information to the ventral division of the MGB and on to auditory cortex, and
65 'shell' nuclei (ICX, encompassing the external nuclei, dorsal and lateral cortex, the brachium of the IC
66 and the pericentral nucleus, [33]). The ICX receives significant ascending auditory inputs from the
67 dorsal cochlear nucleus (DCN) and ICCN and descending auditory inputs from auditory cortex.
68 Additionally the ICX receives significant somatosensory information from the cortical [34] and

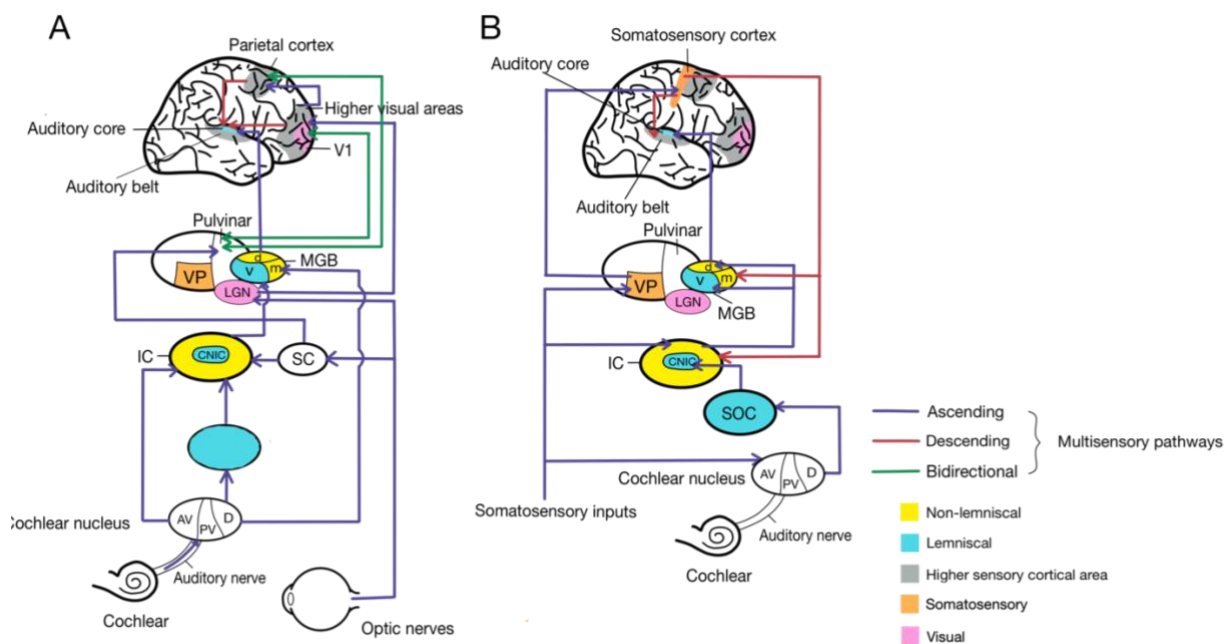
69 subcortical regions [35] and visual inputs from the retinal ganglion [36], Superior Colliculus (SC) [37]
 70 and primary visual cortex (V1) [34]. The potential for somatosensory integration in auditory
 71 processing occurs at the earliest possible stages with vestibular and somatosensory information
 72 targeting the DCN [38-40] and IC [41] (for a comprehensive review of somatosensory-auditory
 73 integration see: [42]).

74

75 One recent study has elegantly demonstrated the extent to which non-auditory information may be
 76 integrated into the early stages of auditory processing [43]. By placing retrograde tracer in the IC of
 77 rats and anterograde tracers in a series of cortical brain regions, Olthof et al (2019) determined that
 78 the central nucleus of the IC is innervated by visual, somatosensory, motor and prefrontal cortical
 79 areas. Thus the non-auditory responses observed in auditory cortex may be inherited from much
 80 earlier processing stages.

81

82 Revealing an anatomical connection provides information about which brain regions may relay
 83 multisensory information that shapes neural responses to sound within the central auditory
 84 pathway (Figure 1). Studying the innervation patterns in detail may be enlightening adding evidence
 85 in favour of a particular input source. For example, in the mouse, anterograde tracing studies with
 86 viral vectors demonstrate that visual cortical inputs terminate in the deep layers of mouse AC [23]
 87 which mirrors the observation that visual responses are found almost exclusively in layers 5 and 6
 88 [5]. Nonetheless, such approaches remain correlational and do not yield causal evidence that a given
 89 pathway contributes to multisensory integration.



90
 91 **Figure 1 Integrating non-auditory inputs with auditory processing**

92 A Visual inputs to the central auditory processing pathway. B Somatosensory inputs (including trigeminal,
93 dorsal column and spinothalamic pathways) into the central auditory pathway.
94 Cochlear nucleus: AV anteroventral; PV posteriorventral; D dorsal. SOC: superior olivary complex, IC: inferior
95 colliculus; ICCN IC central nucleus; SC: superior colliculus, VP: ventral posterior nucleus, LGN: lateral geniculate
96 nucleus; MGB: medial geniculate body (dorsal, ventral, medial).

97

98 [Manipulating activity to identify neural circuits that integrate auditory and non-auditory information](#)

99

100 One way to test whether an anatomically defined pathway plays a functional role in multisensory
101 processing in an auditory area is to modulate activity in that pathway. Slice work has demonstrated
102 that cortico-cortical (secondary visual to primary auditory) connections can modulate auditory
103 processing in mouse auditory cortex [44]. In vivo, stimulating activity in visual cortex using
104 optogenetics has been shown to alter the gain of IC responses to noise in rats [23], and silencing a
105 specific higher visual cortical field in the ferret abolishes visual-stimulus-elicited effects on sound
106 processing in auditory cortex [45]. However, disentangling whether such effects occur directly (that
107 is, monosynaptically) or via an indirect effect is tricky; observing an effect in an auditory area after
108 manipulating activity within a visual area only indicates that the candidate input field is part of a
109 brain network that is involved in conveying visual information to auditory cortex [46]. To identify a
110 monosynaptic rather than network level effect requires a pathway specific approach. Fortunately
111 with the development of increasingly sophisticated genetic methods [47,48] such causal
112 perturbations are now possible (albeit restricted for the most part to work in mice).

113

114 The pulvinar provides a potential subcortical route through which visual information can access
115 auditory cortex. The pulvinar is innervated both by the SC and both early and higher visual cortical
116 areas [49]. A recent study demonstrated that manipulating activity in the mouse homologue of the
117 pulvinar (the lateral posterior nucleus, LP) modulated activity in auditory cortex [41]. Stimulating LP
118 increased responsivity and broadened frequency tuning in auditory cortex (additively), while
119 inhibiting LP had the opposite effect, narrowing tuning curves. The effect of pulvinar stimulation was
120 replicated using a looming visual stimulus. Silencing the SC, which is known to be robustly driven by
121 looming stimuli, prevented any crossmodal effects being observed in AC [41]. Thus, a salient visual
122 stimulus was able to boost the representation of sound in auditory cortex via a SC-pulvinar-auditory
123 cortex pathway (Fig. 1A).

124

125 Another recent study provided evidence that subcortical regions could also be critical for the
126 transfer of multisensory information between sensory cortical fields [50]. Lohse et al., observed that
127 whisker stimulation decreased the gain of auditory cortical responses to sound. However, while

128 dependent on somatosensory cortical activity, these effects were not mediated by direct
129 connections from somatosensory to auditory cortex but instead involved a circuit from
130 somatosensory cortex to the shell of the IC, which in turn inhibited responses in the MGBv and
131 MGBd; the cortical multisensory effects were inherited from those observed in these thalamic
132 regions [50] (Fig 1B). A parallel pathway from the somatosensory cortex targeted the non-lemniscal
133 thalamus directly, where somatosensory information enhanced responses to sound, even though
134 this information was not relayed to primary auditory cortex.

135

136 [What role does multisensory integration play in auditory processing?](#)

137

138 While multisensory responses have been reported in the auditory pathway of anaesthetised and
139 passively listening animals, studies of multisensory integration during active sensation or perceptual
140 decision-making have mostly been restricted to the role of higher brain areas such as parietal cortex
141 (e.g. [51]). A few studies have examined the role of thalamic and frontal areas in multisensory tasks
142 that require switching attention between (rather than integrating across) sensory modalities [52,53].
143 One notable exception was a study that investigated auditory – somatosensory integration in
144 auditory cortex of macaques [54]. Animals were trained to discriminate the rate of two consecutive
145 stimuli which could either be auditory and/or somatosensory. While tactile-only trials elicited
146 activity in auditory cortex, there was no evidence for multisensory interactions or any link between
147 these tactile responses and task performance. This study suggests that crossmodal inputs to early
148 sensory cortex do not play a significant role in shaping perception. However, since multisensory
149 stimuli provided no additional benefit over unisensory stimuli, such a conclusion may be premature
150 [54]. To address this question, neural responses should ideally be examined in animals engaged in a
151 task where a robust multisensory benefit could be observed.

152

153 What, then, are the circumstances in which non-auditory information might benefit sound
154 perception? Here we highlight two broad areas in which multisensory processing may be
155 advantageous for successful listening: firstly, in organising sound mixtures into auditory scenes, and
156 secondly supporting spatial processing.

157

158 [Visual stimuli can alter how auditory cortex processes sound mixtures](#)

159

160 Auditory scene analysis is the process by which sound mixtures that arrive at the ear are organised
161 into sources, and is a key challenge for the auditory brain [55]. For human listeners, effective
162 auditory scene analysis mechanisms are critical for understanding speech in the presence of

163 background noise. Seeing a talker's face is well known to increase a listeners' ability to discriminate
164 speech in the presence of speech or competing noise, as lip movements convey phonetic
165 information [56]. However, independently of phonetic information, visual signals can also provide
166 information useful for separating an attended signal from other competing sounds. For example, a
167 temporally coherent visual stimulus can influence the performance of human listeners in an auditory
168 selective attention task, such that performance is enhanced when a visual stimulus is temporally
169 coherent with a target sound and impaired when the visual stimulus is temporally coherent with a
170 to-be-ignored sound [57]. A neural correlate of this effect is seen in single neurons in the auditory
171 cortex of passively listening ferrets. Specifically, the responses of neurons could be biased from
172 representing one sound in a mixture to another, simply by switching which sound source was
173 temporally coherent with the visual stimulus. This effect was not restricted to the encoding of the
174 sound's modulation envelope, that was shared with the luminance-varying visual stimulus, but
175 extended to enhancing the representation of brief timbre deviants which were independent of the
176 changes in visual luminance that linked the stimuli. Silencing visual cortex with cooling confirmed a
177 role for visual cortex in conveying visual information to auditory cortex (although as noted above,
178 caution must be used in interpreting these results as indicating a direct monosynaptic influence).
179 While this study did not record neural activity in the context of a task, it nonetheless provides
180 evidence that visual inputs into auditory cortex provide a mechanism through which multisensory
181 signals can augment auditory scene analysis. The observation that both binding and non-binding
182 features were enhanced by audiovisual temporal coherence is consistent with the idea that
183 crossmodal features are being linked to form a multisensory object [58]. One general role for the
184 early integration of multisensory information into (uni)sensory processing may be to facilitate the
185 linking of information across the senses.

186

187 [Non-auditory information can support coordinate frame transformations](#)

188

189 Linking information across the senses to create multisensory perception requires that the different
190 latencies, qualities and reference frames are unified across sensory modalities. Both perception and
191 action require that information is linked across coordinate frames. In species that make substantial
192 eye movements, the eyes and ears are not in fixed alignment; thus integrating eye and head centred
193 reference frames is especially challenging. In macaque auditory cortex [59] and IC, neural firing is
194 influenced by eye position [60] and spatial reference frames are neither fully head or eye centered
195 [60,61]. It is not yet known whether the source of eye position signals is corollary discharge from
196 oculomotor centres or proprioceptive feedback from the muscles that control eye position. In
197 anaesthetised ferrets, spatially and temporally congruent audiovisual stimuli improve spatial tuning of

198 auditory cortical neurons relative to sound alone [62]. However, in this study, as in almost all spatial
199 hearing paradigms, the position of the head remains static within the centre of a speaker ring,
200 ensuring a fixed relationship between sound source location relative to the head and within the
201 world. It is therefore impossible to resolve whether spatial tuning reflects head or world centred
202 frames. Recording in freely moving animals that take a variety of head positions relative to sound
203 source locations allows this ambiguity to be resolved. A recent study that took this approach
204 observed that auditory cortical neurons can either represent sound source location relative to the
205 head, or can encode a sound source's position in the world independently of head position [63].
206 Such representations are likely to be critical for disambiguating self and source motion, both of
207 which may elicit identical changes in sound localisation cues. While these world-centered
208 representation were observed in near dark, their establishment and maintenance may require visual
209 cues to the current environment, either directly or through head direction signals in the
210 hippocampal formation, which are anchored by visual cues when they are available [64]. Encoding of
211 sound source position in the world will also likely require head and eye direction information
212 provided by vestibular signals and efference copies or corollary discharge from the motor systems,
213 and positional information from navigation systems. Such inputs may be integrated into auditory
214 processing at very early stages: we have seen that eye position information is available within the IC
215 [60], and the cochlear nucleus shows both somatosensory and vestibular modulation [40].
216 Moreover, the DCN contains cells modulated by head direction, and these neurons contain
217 information that can be used to discriminate self from sound source rotation [65]. Future studies
218 should address the availability of head direction information in the central auditory pathway and
219 assess the role of visual and somatosensory information in anchoring world centered
220 representations.

221

222 Outlook

223

224 State-of-the-art genetic methods have allowed researchers to dissect out the circuits underlying
225 multisensory integration and highlight a critical role for subcortical pathways in information transfer.
226 However, identifying the plethora of possible routes that information may take will not alone
227 advance our understanding of the purpose served by integrating multisensory information early in
228 hearing. Such insights will require the use of circuit-based methods in combination with recording
229 neural activity in complex naturalistic situations. For example, allowing animals to move freely and
230 interact with stimuli while tracking head and eye movements will allow coordinate frame

231 ambiguities to be resolved. Moving beyond overly simplistic laboratory stimuli is also likely to be a
232 necessary step in understanding the function of multisensory processing in hearing and listening.

233

234

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236

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