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Central auditory disorders: toward a neuropsychology of auditory objects

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Abstract

Purpose of review—Analysis of the auditory environment, source identification and vocal communication all require efficient brain mechanisms for disambiguating, representing and understanding complex natural sounds as ‘auditory objects’. Failure of these mechanisms leads to a diverse spectrum of clinical deficits. Here we review current evidence concerning the phenomenology, mechanisms and brain substrates of auditory agnosias and related disorders of auditory object processing.

Recent findings—Analysis of lesions causing auditory object deficits has revealed certain broad anatomical correlations: deficient parsing of the auditory scene is associated with lesions involving the parieto-temporal junction, while selective disorders of sound recognition occur with more anterior temporal lobe or extra-temporal damage. Distributed neural networks have been increasingly implicated in the pathogenesis of such disorders as developmental dyslexia, congenital amusia and tinnitus. Auditory category deficits may arise from defective interaction of spectrotemporal encoding and executive and mnemonic processes. Dedicated brain mechanisms are likely to process specialised sound objects such as voices and melodies.

Summary—Emerging empirical evidence suggests a clinically relevant, hierarchical and fractionated neuropsychological model of auditory object processing that provides a framework for understanding auditory agnosias and makes specific predictions to direct future work.

Keywords

auditory object; auditory agnosia; neuropsychology

Deficits of auditory cognition are less familiar and less well understood than their visual equivalents. The objects of auditory cognition are natural sounds, but ‘auditory object’ is a problematic concept[1]. An auditory object might be defined neuropsychologically as a collection of acoustic data bound in a common perceptual representation and disambiguated from the auditory scene. This definition suggests the importance of perceptual regularities whilst allowing that ‘top-down’ processes may forge associations between acoustic properties and current behavioural goals may give prominence to particular objects within the same acoustic data (e.g., in the spoken word “dog”, relevant sound objects could include the speech token ‘dog’, the speaker’s voice, emotional state, accent, etc). Even this general definition raises certain difficulties. Most everyday sounds have a complex, time-varying frequency structure (see ‘A brief acoustic primer’, Supplementary Material; available using

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website <http://journals.lww.com/co-neurology/pages/default.aspx>), and temporal object boundaries are often difficult to determine. Furthermore, sounds, unlike visual objects, are 'transparent' when superimposed; and auditory objects are associated with diverse physical entities, including both discrete sources (e.g., a barking dog) and acoustic events (e.g., a gust of wind, a spoken phoneme). These various auditory object properties and categories have potentially separable neural representations and associated clinical deficits.

The literature on central auditory disorders illustrates these difficulties. Terms such as 'cortical (or 'cerebral') deafness' and 'auditory agnosia' (see Table 1) are widely used, but remain rather loosely defined and demarcated from one another, and progress in defining a useful taxonomy has so far been limited. This is partly attributable to difficulties extrapolating between symptom-led single-case studies and lesion-led group studies in patient populations that may or may not be representative (such as temporal lobectomy series), lack of uniformity of test materials across studies, and the rarity of strategically located brain lesions.

Here we review recent progress in characterising central auditory disorders, focusing on disorders of auditory object processing: the auditory agnosias. From an auditory neuroscience perspective, we are here concerned chiefly with the effects of damage affecting object processing in the putative auditory ventral ('what') pathway[2]; however, auditory object processing entails important interactions with dorsal 'where' and 'how' pathways, particularly in the parsing of natural auditory scenes. Our approach is based on a simple operational classification of four fundamental stages likely to be involved in processing auditory objects: parsing of objects in the auditory scene; encoding of auditory properties (at the sub-object level); representation of the perceptual structures of whole objects; and recognition of objects. Key terms are summarised in Table 1. Recent studies of central auditory disorders are summarised in Table 2.

Object parsing: auditory scene analysis

'Auditory scene analysis' comprises two fundamental operations in the early cortical processing of auditory objects: grouping of temporally spaced sounds into a single object (e.g. tones into a melody) and segregation of behaviourally relevant sound objects from the auditory background (e.g., one's name heard at a cocktail party). Efficient auditory scene analysis might be based on stored perceptual 'templates': 'bottom-up' (perceptual) and 'top-down' (attentional, executive, mnemonic, semantic) mechanisms[3,4] might interact recursively, leading to an initial template match, and the output of the matching algorithm would then be used to construct a more complete object representation[1,5,6]. Auditory scene analysis depends on attentional mechanisms: the process is impaired with unilateral neglect[7], may be object-based rather than primarily spatially-based[8], and may be largely independent of specific auditory object properties[9]. While auditory neglect has been most frequently described with large infarcts involving the posterior right hemisphere, detailed neuropsychological investigations are few. However, clinical observation suggests that deficits of auditory scene analysis may occur relatively commonly and early in the course of neurodegenerative diseases involving temporo-parietal areas, including Alzheimer's disease. In line with normal functional imaging evidence ([3,10,11]; Table 2), electrophysiological studies of preclinical familial Alzheimer's[12], subjects at high risk for schizophrenia[13] and established Parkinson's disease[14,15] have implicated a distributed neural network encompassing auditory cortex, temporo-parietal junctional regions and subcortical auditory pathways in aspects of auditory scene analysis.

Disorders of auditory property encoding: sub-object level deficits

Auditory objects possess generic properties such as pitch, modulation and timbre, and encoding of such properties is likely to involve brain mechanisms prior to formation of whole-object-level representations.

Tone deafness

Congenital amusia ('tone deafness') has recently been characterised as a developmental disorder of pitch interval analysis (in particular, pitch direction changes and key violations) and working memory for pitch information. However, the psychoacoustic locus continues to be pinpointed[16,17]. A spectrum of auditory deficits has been reported[18,19,20], suggesting that this is not a music-specific disorder. Anatomically, it is underpinned by structural and functional disruption of a dorsally-directed cortical network involved in transforming dynamic pitch information[21,22,23]. There appears to be a genetic predisposition[16]. Evidence concerning the network basis of the deficit in congenital amusia is complemented by evidence for impaired tone memory in patients undergoing temporal lobectomies that encroach on more posterior cortices adjacent to lateral Heschl's gyrus[24], a key site for perceptual encoding of pitch information[25,26].

Developmental dyslexia

The brain basis of developmental dyslexia remains highly contentious, however a generic deficit of rapid spectrotemporal processing not restricted to verbal material has been described[27]. Emerging evidence in this population illustrates the role of corticosubcortical[28,29] and cortico-cortical[30] interactions and spectrotemporal integration[31] in auditory object encoding, both during early stages of auditory scene analysis and subsequent (including cross-modal) processing. A deficit of auditory temporal integration has recently been described in another developmental disorder, autism[68]. However, relations between developmental dyslexia, autism and the rather poorly defined 'central auditory processing disorder'[69] remain to be established.

Dystimbria

Selectively impaired timbre perception or 'dystimbria' has been described following focal infarction of the right posterior superior temporal lobe[32,33]. Lesion-led studies in patients undergoing anterior temporal lobectomy have affirmed the preeminence of the right temporal lobe for processing both spectral and temporal dimensions of timbre[34]. A defect of spectral shape encoding has been reported in progressive nonfluent aphasia[35], a focal degeneration of peri-Sylvian cortices.

Tinnitus

We classify tinnitus as a disorder of auditory object property encoding, resulting from abnormal autonomous cerebral activity. Recent neuroimaging evidence has implicated a distributed network of auditory, limbic and prefrontal areas in tinnitus pathogenesis, with reduced grey matter in primary auditory cortex[36], inferior colliculus and hippocampus[37], abnormal activation of prefrontal cortex, cingulate and caudate[38] and abnormal coupling within resting-state networks[70,71,72]. The extent to which these changes are primary, secondary or compensatory remains unresolved.

Tinnitus exemplifies a much broader spectrum of hallucinatory auditory phenomena, likely associated with different levels of auditory object processing. While these phenomena have diverse phenomenology and clinical associations[73], certain common themes have emerged. These include phenomenological and anatomical overlap with brain mechanisms sustaining normal auditory imagery[39,74] and altered structure and function of auditory

and limbic networks that process real sounds[75,76,77,78,79,80,81,82]. These pathophysiological findings suggest possible therapeutic strategies, such as transcranial magnetic stimulation to modulate network function in tinnitus[83] and acetylcholinesterase inhibitors to reduce musical hallucinations[84].

Disorders of auditory object perception: apperceptive agnosias

The brain must process sensory data corresponding to particular auditory objects under widely varying conditions (e.g. the same phoneme spoken by different voices[25]; see also Supplementary Material, sound examples 9 and 10). In vision, the process of ‘object invariance’ enables different views of the same object to be associated with the same stored representation via brain mechanisms that compute abstract sets of relations between perceptual characteristics. Stored auditory object ‘templates’ might have formal and neural similarities with such visual structural representations[1,3,40]; however, this notion has yet to be widely tested experimentally. Sounds within a perceptual category (e.g. speech sounds, music) tend to share spectrotemporal characteristics, suggesting a possible basis for perceptually-based agnosias restricted to sounds that have similar representations at whole-object level.

Word deafness

Spoken words exemplify a highly characteristic and salient category of auditory objects, and so-called ‘pure word deafness’ is the best documented example of a perceptually-based, selective auditory agnosia. Although a core perceptual deficit of auditory temporal resolution has been proposed to underpin impaired discrimination of speech sounds, the deficit may extend to impaired processing of rapid spectrotemporal variations in non-verbal sounds[41], suggesting a generic ‘pre-phonemic’ impairment of dynamic spectrotemporal analysis. This would accord with emerging psychoacoustic evidence that accurate speech encoding does not depend simply on spectral or temporal mechanisms but rather higher-order joint spectrotemporal modulations[85]. Word deafness typically follows bilateral (or left-sided) damage involving early auditory areas implicated in sublexical processing[42]. The syndrome may develop during the recovery phase of a generalised auditory agnosia or with neurodegenerative diseases affecting posterior peri-Sylvian cortices[35,43], and the mechanism is likely to vary among cases in this spectrum.

Environmental sound agnosia

Environmental sounds collectively span a broad range of spectrotemporal characteristics, but specific abnormalities of spectrotemporal analysis might give rise to more selective deficits. For example, one patient with environmental sound agnosia but not word deafness[44] showed a selective impairment for sounds with spectrotemporal structures dissimilar to words, thus mirroring the deficit of word deafness. This deficit might align with impaired perception of speech prosody or musical melodies, which also require tracking of changes over time windows generally longer than those pertinent to single words. Whilst selective deficits of environmental sound perception (without involvement of other sound categories) are rare, they have been described in association with right hemisphere damage[45,46]. Impaired discrimination of musical instrument sounds has been documented in semantic dementia, in association with asymmetric (predominantly left-sided) focal atrophy of the anterior temporal lobe[47], while deficient short term memory for environmental sounds has been demonstrated in patients undergoing left or right anterior temporal lobectomy[24]. However, ‘apperceptive’ agnosias for environmental sounds are often difficult to distinguish from earlier perceptual as well as higher-level semantic deficits.

The neural mechanisms that represent auditory object categories are of considerable interest though poorly understood. Patients with progressive aphasia due to neurodegenerative pathologies show impaired categorisation of animal calls under conditions of varying spectrotemporal structure and familiarity ([35]; see Supplementary Material, sound examples 11 and 12); however, performance in patients with progressive nonfluent aphasia (but not semantic dementia) is influenced by familiarity (semantic information). Such evidence suggests that sound categorisation may occur at the interface of perceptual and semantic processing. This is corroborated by emerging functional neuroimaging evidence in healthy subjects ([6,48,49,50,86]; Table 2).

Agnosias for specialised sound object categories

The more specialised sound object categories of human voices and musical melodies are candidate targets for selective apperceptive deficits.

Voices constitute a behaviourally important category; like face recognition, voice recognition demands detailed perceptual analysis and fine-grained inter-item discrimination. While it is plausible a priori that voice processing should have dedicated brain mechanisms, phonagnosia has been documented much less frequently than prosopagnosia. The apparent rarity of selective ‘apperceptive’ phonagnosia (which might be predicted to affect voice identification under degraded listening conditions or discrimination of unfamiliar speakers[51]) suggests that perceptual analysis of voices depends on processes (such as spectral shape encoding) that are at least partly shared with animal vocalisations and other complex sounds. This is in line with both neuropsychological[33] and functional neuroimaging evidence[6,50,52].

Music contains distinct levels and categories of auditory objects[47]. Music has characteristic spectrotemporal properties, and most amusias are perceptually based, arising from specific deficits in processing perceptual components of music (e.g., melody versus rhythm[46]). Apperceptive agnosia for music has been described following stroke, particularly involving the right cerebral hemisphere[53,54,55], though this lateralisation may be partly attributable to selection bias[56].

Disorders of auditory object recognition: associative agnosias

As is the case for apperceptive agnosias, disorders of auditory object recognition (associative agnosias) are difficult to establish across the broad category of environmental sounds, but somewhat better defined for the more specialised object categories of voices and melodies.

Environmental sounds

Pure associative agnosia for environmental sounds appears rare, though nonverbal agnosia frequently accompanies aphasia[57]. Lesion-led work in stroke patients has shown that predominantly perceptual and predominantly semantic deficits of environmental sound processing may arise from homologous regions spanning peri-Sylvian and inferior parietal lobe regions in the right and left cerebral hemispheres, respectively[45,46,57]. However, it is often difficult to draw a clear distinction between apperceptive and primarily associative impairments (e.g.,[44]). Recent studies in neurodegenerative disease have suggested that aspects of associative sound knowledge (e.g. sound naming[58]; within-modality semantic matching[35]) may dissociate from analogous knowledge in other modalities (in particular, vision). Patients with corticobasal / progressive supranuclear palsy syndrome are deficient in naming sounds made by manipulable but not non-manipulable objects, and this deficit correlates with atrophy of left premotor cortex [59]. This suggests involvement of cross-

modal ‘action schemas’ or mirror neuron networks, as corroborated by functional imaging evidence in healthy subjects (e.g., [48,60]; see Table 2).

Voices

A double dissociation between voice discrimination (apperceptive) and recognition (associative) deficits has been described[51]; and predominantly associative phonagnosia with relatively-preserved voice discrimination (and sparing face and proper name recognition) has been documented following degenerative brain damage[61] and developmentally[62]. While functional imaging evidence in healthy subjects has underlined the key role of the superior temporal sulcus in voice-specific processing[63], anatomical correlates of phonagnosia have not been clarified.

Musical melodies

Musical melodies can acquire rich semantic associations and like words (but unlike most environmental sounds) retain meaning irrespective of their source. However, well-documented instances of pure associative agnosia for music are rare[53,54,55] and acquired amusias are often associated with other auditory or extra-musical cognitive deficits[56]. Patients with semantic dementia may show selective preservation of melody knowledge despite breakdown of other knowledge systems, including knowledge of other aspects of music such as instrument timbres and emotions[47,87]; while patients with Alzheimer’s disease show impaired knowledge of familiar melodies[64,65] and impaired episodic memory for unfamiliar melodies[88] but retained recognition of musical emotions[89]. Although the brain substrates for musical agnosias have not been elucidated, pure associative deficits have been linked with left-sided and apperceptive deficits with right-sided peri-Sylvian insults[53,54,55]. This topography would fit with the classical formulation of agnosia; however, information concerning the anatomical organisation of musical semantic memory remains limited ([66,67]; see Table 2).

Conclusion

Recent clinical studies, together with neuroimaging findings in the healthy brain, have underlined the difficulty of defining central auditory disorders in neuropsychological terms. At the same time, however, this emerging evidence does suggest a tentative hierarchical model of auditory object processing and its disorders, based on the interaction of spectrotemporal encoding mechanisms with ‘top-down’ processes in peri-Sylvian networks extending beyond primary auditory cortex. This model is outlined in Figure 1. Certain key empirical hypotheses follow from the model, summarised in Table 3.

In addition to sophisticated stimulus synthesis techniques designed to target particular aspects of spectrotemporal and auditory semantic processing, future progress in understanding these disorders will depend on a multimodal approach including neuroanatomical correlation with a range of structural and functional brain imaging techniques. Interpretation of the specificity of identified deficits requires parallel assessment of other sensory modalities (especially vision: e.g., [90]). Connectivity-based methods are likely to be particularly important in order to model auditory object processing and its breakdown in disease (particularly neurodegenerative pathologies) at the level of distributed neural networks; critical loci within such networks will continue to be identified within the traditional paradigm of the focal lesion study. Disambiguation of underlying neural mechanisms may require alternative imaging techniques (such as magnetoencephalography) that can track the time course of perceptual and semantic processing of sounds and sound categories.

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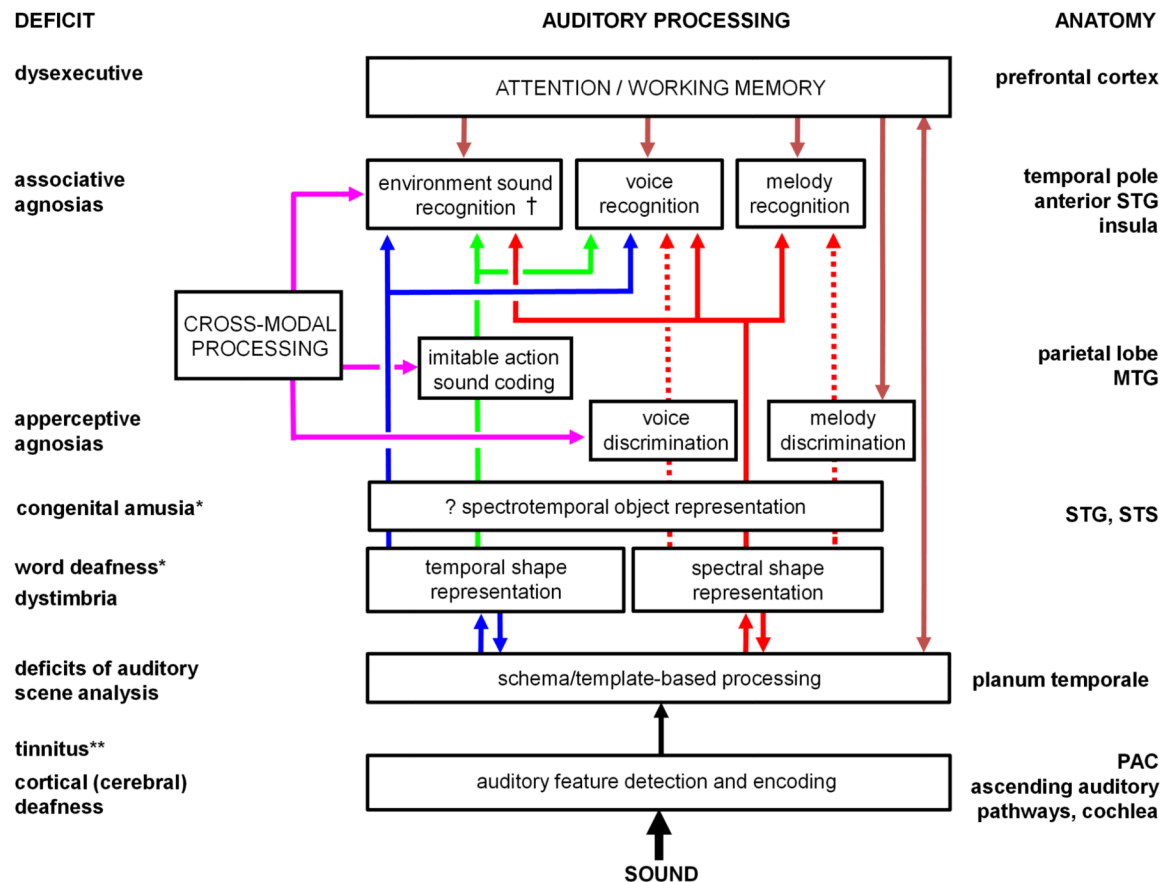


Figure 1. A neuropsychological model of auditory object processing and disorders

This provisional and simplified hierarchical model of auditory object processing is based on emerging neuropsychological and neuroanatomical evidence. Representative deficits of complex sound processing are summarised on the left; cognitive operations proposed to underpin these deficits are schematised in the central diagram; and anatomical substrates for these operations are shown on the right. For schematic purposes, anatomical areas are shown in a discrete relation to particular cognitive operations, however it is likely that these 'nodal' areas cooperate as networks in mediating sequential processing stages. Arrows indicate the predominant direction of information flow between processing modules in the hierarchy; however, it is likely that information transfer between most of the processing modules shown is reciprocal. Arrows linking schema-based processing with spectral and temporal envelope representations and executive processes are shown as bi-directional to emphasise dynamic updating of on-line schemas by both incoming and stored information. Arrows are colour-coded according to the type of information transferred: black, basic acoustic features; blue, temporal properties; green, temporal properties relevant to encoding of imitable action sounds; red, spectral properties; magenta; cross-modal sensory processing; brown, 'executive' processes including attention and working memory. Solid arrows indicate 'obligatory' processes; dashed arrows indicate processes that may be engaged in some circumstances (typically, conditions of increased perceptual load). In addition to hierarchical processing within each cerebral hemisphere, levels of processing (e.g., apperceptive versus associative) are likely to be differentially distributed between the hemispheres.

Key: MTG, middle temporal gyrus; PAC, primary auditory cortex; STG, superior temporal gyrus; STS, superior temporal sulcus; *cognitive basis remains uncertain; **other auditory

hallucinoses syndromes arise at higher levels of the processing hierarchy; † the status of associative versus perceptual deficits remains unclear

Table 1

Terminology of central auditory disorders

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- **Amusia:** a selective deficit in perception of music not attributable to peripheral hearing impairment; both acquired and **congenital** forms are well described (see below and text).
 - **Apperceptive agnosia:** a deficit in processing perceptual **object representations**. In a strict neuropsychological sense, apperceptive agnosia manifests as impaired discrimination between perceptual objects or altered object identification under non-canonical perceptual conditions despite demonstrably intact early perceptual (sub-object) functions. Cognitively, this corresponds to a processing stage beyond the encoding of perceptual properties but prior to the attribution of meaning. The concept was developed and is best established for visual objects.
 - **Associative agnosia:** a deficit in associating perceptual **object representations** with meaning (semantic memory).
 - **Auditory agnosia:** a deficit of **auditory object** processing. Various taxonomies, including **apperceptive**, **associative** and category-specific forms have been proposed
 - **Auditory object:** a collection of acoustic data bound in a common perceptual **representation** and disambiguated from the auditory scene (e.g. the set of spectral and temporal acoustic properties and features that together constitute a cockerel's crow).
 - **Auditory scene analysis:** the collection of cognitive processes by which the auditory environment is parsed (resolved) into component **auditory objects**. There are at least two components: (i) grouping of temporally spaced sounds into single objects; and (ii) segregation of simultaneously present sounds into separate objects.
 - **Congenital amusia ('tone deafness'):** a deficit of auditory property encoding characterised by lifelong difficulty in perceiving the direction of pitch changes in music. The psychoacoustic basis of congenital amusia continues to be defined.
 - **Cortical (cerebral) deafness:** loss of perception of sound due to a cortical (or cerebral) lesion.
 - **Dystimbria:** a deficit of auditory property perception affecting the encoding of timbre, the acoustic property that allows sounds of identical pitch, duration and loudness to be distinguished (e.g., the sounds made by a piano and a violin playing the same note).
 - **Imagery:** in the neuropsychological sense, a persistent internalised sensory experience in the absence of direct external sensory input. Imagery is a normal phenomenon that should be distinguished from hallucinosis: an abnormal percept in the absence of external input that is experienced as external to self.
 - **Modulation:** instantaneous variation in the amplitude (amplitude modulation, AM) or frequency (frequency modulation, FM) of a sound. Modulation is an important attribute of many complex sounds that can be used both in early object parsing from the auditory background and in object identification.
 - **Object representation:** a set of properties and features bound together to encode a sensory object as a discrete perceptual entity. The term has most validity in the case of visual objects, for which specific deficits of 'structural [3-D] representation' – the **apperceptive agnosias** – have been defined; the status of such representations in non-visual sensory modalities remains to be established.
 - **Phonagnosia:** impaired perception or recognition of human voices; **apperceptive** and **associative** subtypes have been described.
 - **Semantic memory:** memory for facts, concepts and knowledge about sensory objects. The degree to which brain knowledge systems are modality-specific remains moot, however the neural representation of particular objects in semantic memory is likely to be affected both by modality-specific mechanisms linked to perceptual channels (compare the sound of thunder to the appearance of a sea anemone) and the direction and extent of cross-modal associations (face information is more likely to facilitate voice recognition than the converse).
 - **Tinnitus:** abnormal perception of (elementary) sound in the absence of an external source. Tinnitus exemplifies a much broader range of phenomena, the auditory hallucinosis, attributable to abnormal autonomous auditory cortical activity or excess auditory **imagery**.
 - **Word deafness ('pure' word deafness):** a selective deficit in the perception of words. Detailed psychoacoustic evaluation suggests that the syndrome is rarely confined to words and often has a pre-phonemic basis.
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Table 2

Summary of recent studies of central auditory disorders

Cognitive operation	Clinical syndrome	Process affected**	Lesion anatomy	Normal anatomy	Referenced studies***		
					Symptom-led	Lesion-led	Normal§
Auditory scene analysis	Object- and stream-based neglect	Segregation of sound sources	R > L PT, PL, PF ?subcortical	Lat HG, PT	[7,8,9]	[12,13,14,15]	[5,10,11]
	Congenital amusia	?dynamic pitch memory	Post TL, AF, R IFG	Lat HG / post TL, PL, PF, hippocampus	[16,17,18,19, 20,21,22,23]	[24]	[26]
Property encoding (sub-object processing)	Developmental dyslexia	?Dynamic spectrotemporal integration	PT, ant STG/STS, ant insula, subcortical	Ant insula	[27,28,29]	-	[30, 31]
	Dyslambria*	Spectral and temporal shape encoding, spectral 'templates'	R > L post sup / ant TL	PAC, PT, R > L STG / STS	[32,33]	[34,35]	[5,6,40]
	Tinnitus	Autonomous percept: elementary sound (?imagery)	IC, PAC, PF, limbic	Post STG, PL, PF, cingulate, basal ganglia, hippocampus [‡]	[36,37,38]	-	[39]
	Word deafness	Processing of rapid spectrotemporal transitions	PAC, PT, subcortical	PT, STS, PL	[41,43]	-	[42]
Object perception	Environmental sound agnosia: apperceptive	Perceptual coding of sound categories; short term memory of sounds	?R > L post TL, PL, ant TL	Lat HG, PT, post / mid / ant STG / STS	[53]	[24,35,45,46, 47]	[6,49,50]
	Phonagnosia: apperceptive	Voice perception	?R > L TL	PT, post / ant STS / STG	[32]	[51]	[25,52]
	Melody agnosia: apperceptive	Melody perception	R > L peri-Sylvian, ant STG, insula, FL	PT / STG, IFG ^{‡‡}	[47,53,55]	[46,54,56]	[66]
	Environmental sound agnosia: associative	Environmental sound recognition:	L > R peri-Sylvian, ant STG, PL		[44] †††	[24,35,45,46, 57,58,59]	
Object recognition	Environmental sound agnosia: associative	Animals		Mid STG, L PF			[60]
		Tools		Post MTG/STS; L IFG, PF, PL			[48]
		Human nonvocal		IFG / PF, PL			
		Animal nonvocal		Post insula			
		Mechanical		Ant STG, post MTG/STS, PHG			
		Environmental inanimate		PL			
	Phonagnosia: associative	Voice recognition	?R > L peri-Sylvian, PL	Post / ant STS, medial TL, fusiform gyrus	[61,62]	[51]	[63]
	Melody agnosia: associative	Melody recognition	?L > R peri-Sylvian, FL	R STS, L ant STG / IFG	[47,53,55]	[56,64,65]	[66,67,68]

* Patients may describe a 'mechanical' quality to natural sounds such as birdsong or have difficulty interpreting emotions from human voices (e.g. Griffiths et al., 2007);

** proposed locus of deficit based on available evidence;

*** recent and representative studies;

† environmental sound imagery task;

†† unfamiliar musical melodies over random notes;

††† basis of agnosia not fully resolved (see text);

§ [67] positron emission tomography, others fMRI

Key: AF, arcuate fasciculus; ant, anterior; FL, frontal lobe; IC, inferior colliculus; IFG, inferior frontal gyrus; PAC, primary auditory cortex; PF, prefrontal cortex; PHG, parahippocampal gyrus; PL, parietal lobe; post, posterior; PT, planum temporale; STG, superior temporal gyrus; STS, superior temporal sulcus; sup, superior; TL, temporal lobe

Table 3**Key empirical hypotheses concerning disorders of auditory object processing**

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- Deficits of auditory scene analysis (object grouping and segregation) occur with lesions involving the planum temporale and parieto-temporal junction
 - Disorders of auditory property perception at the sub-object level (e.g. dystimbra, tinnitus) are neuropsychologically as well as clinically heterogeneous, due to spectral, temporal and/or spectrotemporal processing deficits.
 - Hierarchically organised networks based on the postero-lateral temporal lobe encode spectrotemporal object 'templates' for object-specific analysis in auditory association cortices and their downstream connections.
 - There is no simple correspondence between deficits of broad auditory object categories (e.g., 'environmental sounds') and generic spectral and temporal analysis mechanisms: adequate characterisation of auditory agnosia requires sampling across the broad acoustic range of real world sounds, to specify the spectrotemporal ranges disrupted.
 - Within the category of environmental sounds, particular kinds of auditory objects are more or less susceptible to spectral, temporal, or spectrotemporal processing deficits, depending upon their acoustic and perceptual structures (e.g., vocalisations, as harmonically rich sounds, may be relatively more dependent on spectral shape encoding).
 - Pure associative agnosia for environmental sounds occurs infrequently: whereas voices and melodies engage category-specific computations, environmental sound processing may be more dependent upon generic spectral, temporal and spectrotemporal analysis, and the interaction of 'bottom-up' and 'top-down' processes.
 - Imitable action sounds are neuropsychologically dissociable from other sounds, based on interactions of auditory perceptual and sensori-motor processes in the dorsal auditory stream.
 - Within the relatively specialised sound categories of human voices and music, the relative preponderance of apperceptive and associative deficits depends on an interaction of perceptual and semantic mechanisms: when encountered as selective deficits, musical agnosia is more often apperceptive (due to the requirement for specific encoding of spectrotemporal features peculiar to music) while phonagnosia is more often associative (due to the close relation of the voice to other aspects of person knowledge).
 - Executive (attentional, working memory) and cross-modal effects operate at different stages of auditory object processing, and may show specific effects at particular stages (especially, during auditory scene analysis) or for particular categories of auditory objects.
-