J Am Acad Audiol 29:533–547 (2018)

A Review of Auditory Prediction and Its Potential Role in Tinnitus Perception

DOI: 10.3766/jaaa.17025

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Abstract

Background: The precise mechanisms underlying tinnitus perception and distress are still not fully understood. A recent proposition is that auditory prediction errors and related memory representations may play a role in driving tinnitus perception. It is of interest to further explore this.

Purpose: To obtain a comprehensive narrative synthesis of current research in relation to auditory prediction and its potential role in tinnitus perception and severity.

Research Design: A narrative review methodological framework was followed.

Data Collection and Analysis: The key words Prediction Auditory, Memory Prediction Auditory, Tinnitus AND Memory, Tinnitus AND Prediction in Article Title, Abstract, and Keywords were extensively searched on four databases: PubMed, Scopus, SpringerLink, and PsychINFO. All study types were selected from 2000–2016 (end of 2016) and had the following exclusion criteria applied: minimum age of participants <18, nonhuman participants, and article not available in English. Reference lists of articles were reviewed to identify any further relevant studies. Articles were short listed based on title relevance.

Study Sample: After reading the abstracts and with consensus made between coauthors, a total of 114 studies were selected for charting data.

Results: The hierarchical predictive coding model based on the Bayesian brain hypothesis, attentional modulation and top-down feedback serves as the fundamental framework in current literature for how auditory prediction may occur. Predictions are integral to speech and music processing, as well as in sequential processing and identification of auditory objects during auditory streaming. Although deviant responses are observable from middle latency time ranges, the mismatch negativity (MMN) waveform is the most commonly studied electrophysiological index of auditory irregularity detection. However, limitations may apply when interpreting findings because of the debatable origin of the MMN and its restricted ability to model real-life, more complex auditory phenomenon. Cortical oscillatory band activity may act as neurophysiological substrates for auditory prediction. Tinnitus has been modeled as an auditory object which may demonstrate incomplete processing during auditory scene analysis resulting in tinnitus salience and therefore difficulty in habituation. Within the electrophysiological domain, there is currently mixed evidence regarding oscillatory band changes in tinnitus.

Conclusions: There are theoretical proposals for a relationship between prediction error and tinnitus but few published empirical studies.

Key Words: auditory prediction, memory, models, neural mechanisms, perceptual organization, scene perception, sensory plasticity/adaptation

Abbreviations: AC = auditory cortex; ASA = auditory scene analysis; EEG = Electroencephalography; ERP = event-related potentials; MEG = Magnetoencephalography; MLR = middle latency responses; MMN = mismatch negativity

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INTRODUCTION

Tinnitus is the perception of sound in the absence of sound in the environment (Henry et al, 2005; Moller, 2006, p. 254; Kaltenbach, 2011; De Ridder et al, 2014c). The precise mechanisms giving rise to tinnitus perception and distress are still not fully known, although it is now understood to be generated predominantly as a result of peripheral lesions in the auditory system triggering cortical neuroplasticity changes or inadequate noise reduction in central processing pathways (Rauschecker et al, 2010; Kaltenbach, 2011; Vanneste et al, 2013; De Ridder et al, 2014b). It is important to note that tinnitus is not a disease in itself but a presenting symptom in various underlying diseases and pathologies (Vernon and Schleuning, 1978; Vernon and Meikle, 2000; Lockwood et al, 2002; Chan, 2009; Holmes and Padgham, 2011). If a cause is discernible, it is most likely to be noise-induced hearing loss.

Not all patients with peripheral lesions experience tinnitus, however, and it is also now generally recognized that tinnitus perception and the level of tinnitus distress experienced by an individual are not identical (Meikle et al, 1984; Stouffer and Tyler, 1990; Stouffer et al, 1991; Hiller and Goebel, 2006, 2007). Hiller and Goebel (2007) conducted a large-scale study of 4958 participants with tinnitus and found only a moderate correlation of 0.45 between subjective ratings of loudness and annoyance. Tinnitus distress may be dependent on higher-order decision making processes. Some 15–20% of those in the population with tinnitus experience disruption to quality of life (Heller, 2003; Hoffmann and Reed, 2004), manifesting as impaired concentration, problems with hearing, irritation and annoyance, anxiety, depression, disruption of everyday activities, and disturbed sleep (Davis and El Refaie, 2000; Heller, 2003; Malouff et al, 2011). The complexity of influences on tinnitus distress also extends to influences from an individual's culture, beliefs, and work and social environments (Searchfield, 2014).

Self-perceived tinnitus magnitude (a combination of loudness, severity, and tinnitus awareness) has been hypothesized to be the result of interplay between spontaneous and driven higher-order auditory activity, personality, emotion, attention, and memory (Searchfield et al, 2012; Searchfield, 2014; Durai et al, 2015). To a certain extent, tinnitus may be processed in a similar manner to external sound by the hearing system, undergoing feature extraction, schema formation, and auditory object formation (Searchfield et al, 2012; Searchfield, 2014). The auditory cortex (AC) carries out significantly complex processing (Skipper, 2014). Top-down feedback connections exist from the AC to all levels through the auditory pathway, in addition to several multisensory projections. Prediction of future auditory events, which relies on existing memory representations and uses cognitive space, also occurs within this framework (Näätänen et al, 2001; Baldeweg, 2006). The evolutionary advantage of prediction is to reduce environmental uncertainty and ensure that sensory processing is economical (Bendixen et al, 2009; Bendixen, 2014), and regularities or patterns in incoming sound allow the system to identify objects in complex auditory scenes (Winkler et al, 2009). Both temporal (concerning "when" or onset of a stimulus) and formal regularities ("what" or physical features of stimulus) can be used to determine future events (Schwartze et al, 2012; Hughes et al, 2013). Moreover, first-order formal regularities can be established (e.g., frequent repetition of a tone) as well as more complex, higher-order formal regularities (e.g., semantics of speech, music) (Hughes et al, 2012). The formation of higher-order formal regularities appears to be automatic to a certain extent and dependent on the repetition probability of events (Tavano et al, 2014). For external sound input, recent studies suggest that auditory prediction does not occur independently within unimodal sensory areas but also integrates input from other regions such as the visual and motor systems (Desantis et al, 2014).

A new proposition is that dysfunctional prediction processing may also give rise to the phenomenon of tinnitus. According to De Ridder et al (De Ridder et al, 2014b; De Ridder et al, 2015b), deafferentation at the peripheral auditory level results in missing input reaching the cortex for certain frequencies which generates a topographically restricted prediction error. Subsequent central plasticity processes focus on and attempt to compensate for this error, ultimately giving rise to the sensation of tinnitus. Such prediction errors are also consistent with models of tinnitus that suggest an important role for auditory scene analysis (ASA) in tinnitus (Searchfield et al, 2012; Searchfield, 2014) and can help explain tinnitus saliency and bridge the gap between peripheral lesions and central compensatory processes. The nature of literature in relation to predictive coding system in the auditory system is extensive; current knowledge is spread over several domains of psychoacoustics, neuroimaging/electrophysiology and neuroscience, higher semantic speech and music, and multisensory networks to name a few. To assess the feasibility of the prediction error hypothesis in tinnitus generation and perception, it is of interest to obtain comprehensive narrative syntheses of published information specifically in relation to tinnitus, prediction, and auditory memory.

Better understanding of the nature and extent of auditory prediction and memory influences on tinnitus can significantly contribute to the current literature regarding underlying mechanisms, which currently does not focus on these factors.

METHODS

Green et al (2006) narrative review methodological framework was selected for conducting this literature overview. This style is advantageous in presenting a broad perspective on the topic, bridging between scattered assortments of articles and enabling conclusions to be drawn based on the scope of current findings. The research questions of interest were as follows: (a) "How does the auditory system predict upcoming sounds?", (b) "How can auditory predictive processing be measured or indexed?", and (c) "Is there a relationship between auditory predictive processing and tinnitus perception?".

The key words Prediction Auditory, Memory Prediction Auditory, Tinnitus AND Memory, Tinnitus AND Prediction in Article Title, Abstract, and Keywords were extensively searched on four databases: PubMed, Scopus, SpringerLink and PsychINFO. All study types were selected from 2000 to 2016 and had the following exclusion criteria applied: minimum age of participants 18 or less, nonhuman participants, article not available in English. This resulted in 892 results; 186 articles were short listed based on title relevance. After reading the abstracts, 112 studies were chosen for charting data. Reference lists of articles were reviewed to identify any further relevant studies. This resulted in the inclusion of two other articles. The inclusion of articles was made by consensus between coauthors to provide information regarding predictive and/or memory processes directly related to tinnitus. Articles related to nonauditory predictive processing (including diminished auditory responses to self-actions) were not included. Articles pertaining to general discussions of the neural networks of tinnitus were not included as well as those discussing musical hallucinations. While these topics are of interest, they do not fall directly within the scope of the research questions addressed in this review. Each article was read in depth and notes taken on the underlying theories which influenced the study, the main findings, and how this relates to auditory prediction and memory (and tinnitus) by one coauthor. The literature was then organized thematically, according to common idea threads. This charting of data and thematic organization were checked by all coauthors and rearranged until final consensus was reached. The results section is divided into sections devoted to each common idea thread.

Twelve reviews/theoretical frameworks and 58 experimental studies examined general prediction and memory processes within the auditory system. Eleven reviews/theoretical frameworks and 33 experimental studies examined prediction and memory processes in relation to tinnitus. The selection of studies is illustrated in Figure 1.

RESULTS AND DISCUSSION

The results first discuss studies relating to general auditory prediction and memory. This then moves onto studies relating to prediction and memory and tinnitus. General auditory prediction studies are further divided into underlying mechanisms of prediction, supporting evidence of predictive processing especially in the speech and music domains, role of prediction in ASA, electrophysiological evidence of predictive processing in the cortex, the contributory role of attention in prediction, and the use of neural oscillatory bands to map auditory prediction. The narrative then moves on to examine studies which conceptualize tinnitus as an auditory object in auditory stream analysis and a discussion of the hypothesized prediction error which is thought to give rise to tinnitus generation and maintenance. Oscillatory band studies are reviewed as well as studies which suggest compromised working memory in the presence of tinnitus.

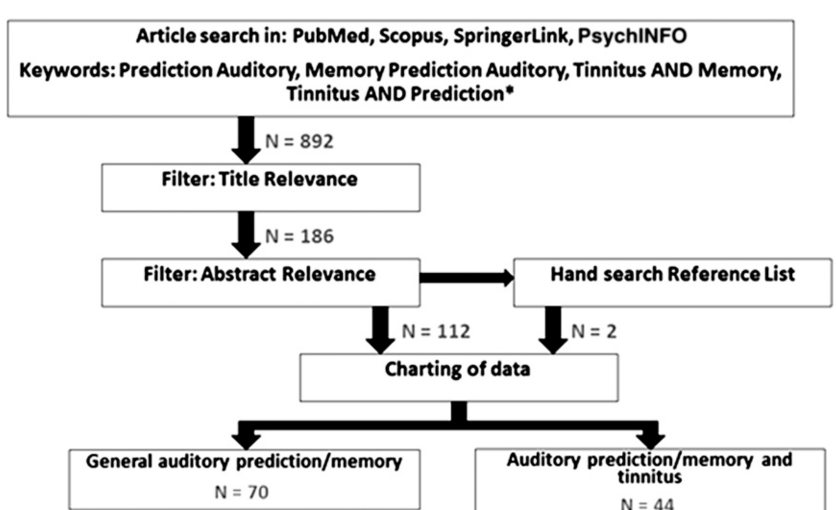

Figure 1. Flow diagram illustrating the number of articles included in each stage of the narrative review (Green et al, 2006) selection process. *Filters used for search: Date range [2000−2016], English only, human participants only, Age of participants [19+].

Bayesian Prediction Processes and Neural Prediction Error Coding in the Auditory System

The Bayesian predictive coding model is a fundamental framework in existing literature, and all relevant studies into auditory prediction appear to hold this as basic premise (Winkler and Schröger, 2015; Obleser, 2016). The Bayesian brain hypothesis states that in situations of uncertainty, the brain relies on internal probabilistic models to optimize function (Friston, 2010). Incoming sensory input is combined with existing prior knowledge to generate predictions. At each level of the sensory processing hierarchy, only the prediction error, the difference between incoming sensory input and existing internal memory representation (involving both short-term memory storage as well as long-term representations), is passed onto the next level for processing. Redundant acoustic signals are canceled at multiple levels (inferior colliculus, thalamus, and cortex) (Ramaswami, 2014). The novelty of unpredictable sounds is given higher priority by the brain and allocated greater resources for processing. Based on this latest sensory input, internal memory representations are also updated, and these changes are passed via top-down projections to alter receptive field properties of low-level sensory units for future events.

The neural mechanisms for auditory prediction error coding, however, are still not comprehensively understood. Wacongne et al (2012) propose that differences between spiking excitatory thalamic input and spiking inhibitory predictive input can code violations, via inhibitory interneurons. Top-down feedback signals then readjust predictions via synaptic plasticity learning for future events. Ramaswami (2014) similarly suggest that familiar signals are canceled out by the presence of inhibitory (mirror) images which are neural memory representations of past sounds. Low-level sensory neurons have been observed to behave in a similar dynamic fashion to a perceptual Bayesian brain system: when two sensory neurons have overlapping input, the neuron which can provide an interpretation/explanation for the input will laterally inhibit the other from responding to the same input (Lochmann and Deneve, 2011). Rubin et al (2016) used computational modeling to examine an oddball sequence of two tones with varying probabilities. For most primary AC neurons, trial-by-trial response fluctuations were present correlating with the level of prediction error present, sometimes accounting for more than 50% of response variability. The memory representations had unexpectedly long durations (lasting for 10 or more stimuli) but were coarse, low-level representations; moreover, predictive power was inversely related to the complexity of the information recently presented. It is possible for neural models of mechanisms proposed to coexist.

Evidence for Auditory Predictive Processing

Some experimental studies directly assessing auditory prediction have been conducted (e.g., neuroimaging studies) and suggest that regions that are activated during prediction of a sound may closely resemble memory representations of sound within the AC. Nazimek et al (2013) found differential brain activity between expected and unexpected sounds, with the later evoking greater left temporal and insula activation. Precision of prediction error processing significantly correlated with neural activity levels in specialized auditory sensory areas used for making perceptual decisions in a study by Hesselmann et al (2010). Prediction-related activity and actual stimulus responses showed significantly overlapping and indistinguishable sources in the left superior temporal gyrus (SanMiguel et al, 2013). The activation of the neural representation of a stimulus when a stimulus is predicted closely resembles memory retrieval processes (Albright, 2012). In instances of redundant predictions, Pieszek et al (2013) observed that both predictions were processed by the system and compared against the other—when one of the regularities was violated, there was an additive error signal present representing the sum of the two prediction error signals. The degree of temporal prediction irregularities simultaneously present affected response times in a short-term memory scanning task; this effect was independent of the set size effect (Limongi and Silva, 2016).

The vast majority of evidence comes from the literature examining complex, higher-order auditory predictive processing in speech and music recognition (Koelsch, 2009; Abrams et al, 2011). Comprehension of speech in everyday life often relies on the ability to "fill in gaps" of missing information, using context or prior speech. Reduced AC processing is present in circumstances where top-down feedback from frontal regions and/or speech production regions can accurately pass down predictions regarding speech signals (Skipper, 2014). The active hypothesis-and-test model proposed by Skipper (2014) states that predictions about incoming speech sounds are generated by speech production regions (posterior, ventral, and frontal) of the brain using existing neural templates from past speech. The role of the AC is to confirm or deny these predictions—this "neural reuse" of speech production regions leads to more economical processing. In the absence of predictions, the AC processes the sounds completely. Lyu et al (2016) observed violations in spoken language comprehension expectations to elicit stronger activations of the left anterior superior temporal gyrus and the ventral inferior frontal gyrus, with top-down feedback from the left ventral inferior frontal gyrus to the anterior temporal regions potentially generating predictions. When speech is degraded, both intrinsic (e.g., the context of the speech) and extrinsic (e.g., other modality aids such as visual cues, accompanying facial movement) provide predictive cues for comprehension. Meaningful speech resulted in less auditory cortical activation compared with less meaningful sounds (Skipper, 2014). The level of intrinsic prediction cues provided in the intelligibility of sentences significantly correlated with the ability to behaviorally extract linguistic information (Peelle, 2013). Leonard et al (2016) conducted a study using direct cortical recordings. The left frontal cortex had preceding increased neural activity (thought to be the generation of predictions in language areas), followed by increased activity in the bilateral AC in real time with the missing speech. Ellermeier and Zimmer (2014) reviewed the psychoacoustic phenomenon of the irrelevant sound effect which describes the decrease in memory performance when listeners are exposed to irrelevant background sounds alongside acoustic stimuli. The irrelevant sound effect is largest for speech or speech-related background sound presence and may be more dependent on spectral cues in the data.

Music perception involves the collaboration of simple level predictions such as melody, beat, and harmony, overlaid by complex formal regularities that operate based on higher-order schema (Rohrmeier and Koelsch, 2012). Ohmae and Tanaka (2016) suggest that depending on rhythm speed, the brain may use either temporal grouping of discrete sounds or longer-term temporal prediction of upcoming stimuli to detect stimuli absence. Regions of the inferior frontolateral cortex which is involved in attention orientation (Levitin and Menon, 2003; Koelch et al, 2005; Bolger et al, 2014; Danielsen et al, 2014), ventrolateral prefrontal cortex (Koelch et al, 2005; Sridharan et al, 2008), and superior temporal gyrus (Koelch et al, 2005; Danielsen et al, 2014) play a role by implication in musical prediction and musical violation processing.

Prediction in ASA

At a higher-order level of processing, prediction is thought to play a role in ASA and in directing attention toward unusual sounds in the environment. ASA describes the process by which our auditory system analyses incoming sounds and separates it into distinct streams and auditory objects (e.g., water running, speech, and a car horn) (Bregman, 1990, Qiu and von der Heydt, 2005; Winkler et al, 2009; McLachlan and Wilson, 2010). Both "what" and "where" characteristics of sounds need to be identified, requiring complex integration of semantic, spatial processing, memory and attention. Winkler and Schröger (Winkler and Schröger, 2015) outline in their review and theoretical framework how ASA and auditory deviance detection often use common predictive inferences, following Bayesian principles.

Detecting regularities or patterns in incoming sound allows the system to identify objects in complex auditory scenes (Kiebel et al, 2009; Winkler et al, 2009). In experimental studies where two concurrent tones were administered and participants were asked to selectively attend to one tone, the presence of temporal regularities in the distractor tone enabled for easier stream segregation than if the distractor tone was irregular in nature (Andreou et al, 2011; Rimmele et al, 2012). If two tone sequences had temporal regularities present, there was also increased probability of hearing two sound streams (Bendixen et al, 2010, 2013; Szalárdy et al, 2014). New auditory input may be delivered as a sensory event representation to the next level of processing; this representation not only encodes sensory features but also specifies how this sound is related to the current auditory context and current goals of the individual (Winkler and Schröger, 2015). Unitary sensory memory representations are then created and used to form predictions and create auditory objects (Winkler and Czigler, 2012; Winkler and Schröger, 2015). Sequential grouping cues may use Gestalt principles such as the old-plus-new heuristic (Bregman, 1990) whereby the auditory system removes continuations of previous sounds from incoming stimuli before proceeding to analyze novel input (Winkler et al, 2009; Bendixen, 2014). Units of regularities stored in auditory short-term memory may be a percept, such as spatial location or pitch (Mathias and von Kriegstein, 2014). Mill et al (2013) suggest that the auditory system constantly switches between various alternative chains before assigning the incoming sound to a final auditory object. As in other predictive processes, attention can have a strong modulating effect on the formation of auditory regularities (Winkler et al, 2009; Ramaswami, 2014). Novel auditory objects are flagged as salient as a result of higher levels of attention diverted toward them (Ramaswami, 2014).

Electrophysiological Evidence Related to Predictive Processing within the Cortex

Event-related potentials (ERPs) can act as indicators of predictive processes, spanning over large time frames and arising from either low-level regularity detection or by top-down feedback for anticipatory future events (for reviews, see Baldeweg, 2006; Winkler et al, 2009; Bendixen, 2014). The mismatch negativity (MMN) marker is most commonly used to detect auditory deviances (Näätänen and Picton, 1987; Paavilainen, 2013; Pieszek et al, 2013), but middle latency responses (MLRs) have also been investigated in relation to prediction. The MMN is typically elicited 100–200 msec in the frontocentral regions after onset of random deviant auditory input in an auditory oddball paradigm. Other deviance responses in literature include the N1 (or N100, often observed 75–130 msec after stimulus onset [Nielsen-Bohlman et al, 1991]) and P3 response (P3b or P300, observed between 300 and 900 msec after stimulus onset, contingent on attention and localized over frontal, parietal, and medial temporal regions [Donchin and Coles, 1988a,b]; P3a can also be elicited before 300 msec because of novel stimuli [Bendixen et al, 2012]).

Reduced MMN amplitudes have been found for patterned sequences compared with random sequences (Todd and Robinson, 2010). Todd and Mullens (2011) observed smaller MMN amplitudes for deviants preceding a previous deviant than for random deviants. Todd et al (2013) demonstrated the MMN amplitude to be proportional to the probability of a deviant occurring, and this effect was robust over multiple temporal scales. Lecaignard et al (2015) also observed a decrease in MMN response to predictable deviants within a sound sequence altering only in temporal predictability. When language-specific phonological rules were violated in speech input, Ylinen et al (2016) observed increased MMN amplitudes and the presence of P3a waveforms. Bendixen et al (2014) observed a larger MMN response for spoken sentences with omitted speech segments where the final speech segment had been predictable, compared with unpredictable. Strauss et al (2015) concluded based on the absence of P3 and incomplete structure of the MMN in sleep compared with wakefulness that both short-term and longer-term auditory predictive coding maybe disrupted during sleep. Based on findings regarding time scale, brain topographies, and modulation by attention, the MMN may reflect predictive error processing whereas the P3 might involve attention orientation toward deviant stimuli (Schwartze et al, 2012) and updating of neural memory representations for future events (Polich, 2007; King et al, 2014). Deviations to regular temporal structure resulted in enhanced N1 responses (Schwartze et al, 2013), whereas higher stimulus probability based on timing resulted in significant N1 suppression (Sherwell et al, 2016). Reduction in N1 responses was found for familiar melodies compared with unfamiliar melodies, regardless of octave transposition (Globerson et al, 2017).

Detection of auditory regularity violations within oddball paradigms can also be observed at much earlier latency ranges than that corresponding to the MMN, particularly with the MLR (Slabu et al, 2010; Althen et al, 2011; Grimm et al, 2011; Recasens et al, 2014) that occur within 10-60ms after stimulus onset in the ACs (Picton et al, 1974). Bendixen et al (2009) found that ERPs generated within the first 50ms after the expected onset of a fully predictable tone are identical to those elicited on presentation of the actual tone. These may detect low-level simple irregularities (but not to more complex violations and may not generate predictions), supporting the hierarchical nature of auditory predictive processing. Early modulations may also detect the most salient source of acoustic information and aid in auditory streaming (Bregman, 1990; Winkler et al, 2009; Bendixen, 2014). Cornella et al (2012) found that changing perceived location but not stimulus repetition in a complex tone paradigm led to changes in MLR responses. Stimulus location and repetition change both resulted in MMN changes. Leung et al (2012) found that only frequency deviants led to enhanced MLR responses; frequency, duration, intensity, and interaural time difference deviants all generated significant MMNs. Cornella et al (2015) found that for chirps delivered in either a predictable or random location or omitted, an attenuation in MLR was only present for regular chirps compared with random chirps. In the late latency response range, both changes in predictability and omissions led to significant differences in cortical responses.

There has been considerable debate whether the MMN origin reflects prediction signal error or is the result of neural adaptation (Ulanovsky et al, 2003; Pérez-González et al; 2005; Näätänen et al, 2005, 2007; May and Tiitinen, 2010; Fishman, 2014) (Figure 2). Gain adaptation of neurons responding to the repeated stimuli in the oddball paradigm can cause habituation of the volume over time. The deviant stimulus induces activation of less suppressed cells; therefore, relatively greater amplitude is recorded as an ERP response. To separate out the deviant responses evoked by changing a feature of the stimulus from that evoked due to potential prediction error, Symonds et al (2017) developed a unique tone-sequence stimulus in which only temporal expectations were violated (the time duration of each sequence) without altering any stimulus parameters. The expectation violation response differed in timing, scalp distribution, (specific left-lateralized frontal MMN), and the extent of modulation from attention from the traditional MMN response. The authors suggest that the MMN response may be formed from multiple overlapping processes and is not exclusively reflective of prediction error. Therefore, there is some limitation to the extent to which findings using MMN can be applied. Another disadvantage is that the repetitive long string of tonal stimuli played is less representative of complex real-world auditory phenomenon (Winkler et al, 2009; Bendixen et al, 2012; Bendixen, 2014; Bendixen et al, 2014). Bendixen et al (2015) used noise to degrade the quality of tone sequences and measured cortical responses; the covering of a predictable tone was not significantly different to the covering of an unpredictable tone. The specific stimuli and paradigm used in testing predictive processing therefore seem to have a considerable effect on results.

Role of Attention in Prediction

Attention (broadly referring to the ability or power to concentrate mentally [Zenner et al, 2006; Fritz et al, 2007]) appears to serve the purpose of enhancing rather than generating predictive processes. Regularity formation and deviation detection can act independently of attention (Takegata et al, 2005; Winkler et al, 2005;

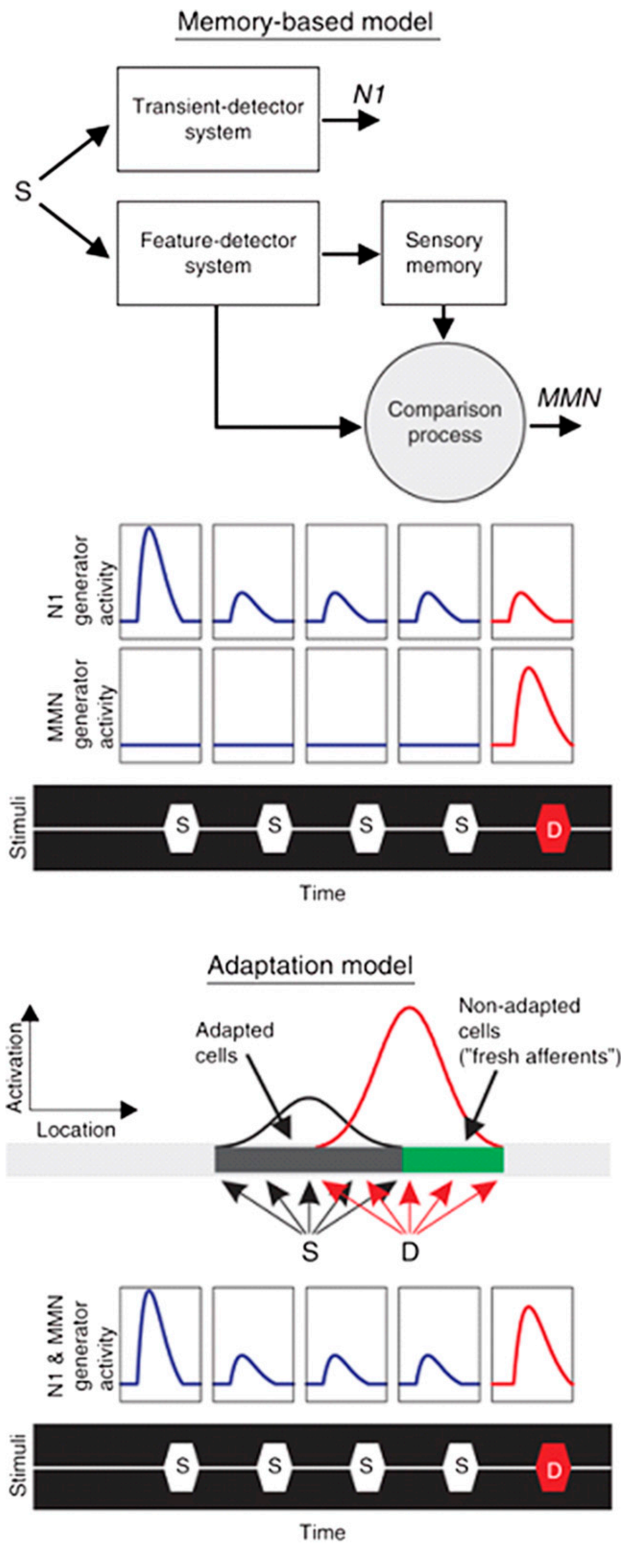

Figure 2. Schematic representations of the memory-based and adaptation model of the mismatch negativity (MMN). Top: In the memory-based model, a stimulus is analyzed by an N1-generating transient-detector system and a separate MMN-generating system that first analyses the stimulus for its features (frequency, intensity, duration, etc.). The result is deposited in sensory memory. A comparison process compares the features of incoming stimuli with representations of past stimuli in the sensory memory store, and when the two differ, an MMN response is generated. Also shown is the beginning of a stimulus sequence, four standards (S) followed by a deviant (D), and the event-related responses produced by the separate N1 and MMN generators to the stimuli. The N1 is largest for the first standard. In contrast, the MMN generator reacts only when the deviant follows an already established memory trace for the standards (red curve). Therefore, it produces no response to any of the standards, including the first stimulus in the sequence. Bottom: In the adaptation model, the standards and deviants activate overlapping neural populations. The repetitive standard leads to cells tuned to the standard to become adapted. When the deviant is presented, nonadapted cells—"fresh afferents"—contribute to an enhanced response. Being in a nonadapted state, the MMN generator responds vigorously to the first standard of the sequence. It also produces attenuated responses to the subsequent standards. In this model, the N1 and MMN are generated by the same neural populations, and the MMN is, essentially, an enhanced N1 response. Reproduced with permission from (May and Tiitinen, 2010, p. 68). (This figure appears in color in the online version of this article.)

Symonds et al, 2017). Chennu et al (2016) observed using electroencephalography (EEG) and magnetoencephalography (MEG) that attention modulates the strength and precision of prediction errors generated for omissions. Auksztulewicz and Friston (2015) used MEG to show that MMN deviance responses were enhanced by attention; this was linked to an increased gain of inhibitory interneurons. Hsu et al (2014) observed enhanced N1 waveforms for consciously attended versus unattended stimuli. The greatest N1 amplitude was observed in the attended condition for predictable stimuli, compared with random stimuli. Attention and intention of the listener may modulate signal detection and the gain of the prediction error signal sent to higher-order levels of processing (Bouwer and Honing, 2015; Schröger et al, 2015).

Role of Oscillatory Bands in Auditory Prediction

Oscillatory bands may serve as a neurophysiological substrate for temporal prediction. Rhythmic or repetitive neural activities are present within the cortex, termed neural oscillations (Adamchic et al, 2014). These are labeled according to bands of frequency oscillations as follows: delta (approximately 1–4 Hz), theta (approximately 4–8 Hz), alpha (approximately 8–13 Hz), and gamma (approximately 30–48 Hz) (De Ridder et al, 2006; Vanneste et al, 2010; Adamchic et al, 2014). Various brain functions are realized by simultaneous oscillations or coupling between different bands (Schutter and Knyazev, 2012). If there is a decrease in sensory input needing to be processed, oscillatory patterns may change to slower rhythms, indicating that cellular firing rates and oscillations may be coupled at the thalamocortical level (De Ridder et al, 2015b). The Thalamacortical Dysrhythmia theory (Llinás et al, 1999; Llinás et al, 2005) states that sensory deafferentation triggers a cascade of events whereby spontaneous resting state alpha rhythms subsequently move to theta-band rhythms, and persistent theta, gamma, and delta activity is established within localized brain regions (Weisz et al, 2005; De Ridder et al, 2011b; 2014a,b; 2015b). Oscillatory bands may increase neural sensitivity (increase signal-to-noise ratio) of predictable, task-relevant input (Morillon and Schroeder, 2015). Morillon and Schroeder (2015) illustrate this using the example of speech processing which involves integration of delta, theta, and low-gamma oscillations for prediction. Arnal et al (2011) propose that gamma bands transfer prediction errors to higher-order regions whereas top-down feedback information is nested on beta bands. The level of gamma activity in the cortex should therefore increase proportionally to prediction error. Fujioka et al (2012) measured an increase in beta wave amplitudes over time to always reach a maximum just before the introduction of the next sound in the sequence. Chang et al (2016) observed beta fluctuations in the AC to be modulated by frequency deviances. Dürschmid et al (2016) conducted a study using subdural electrocorticographic electrodes and demonstrated that longer-term global irregularities correlated with frontal gamma activity; short-term irregularities correlated with temporal cortex activation. Sedley et al (2016) also conducted an experiment using electrocorticography in three patients having neurosurgical treatment for epilepsy. A stream of complex tones was presented which were perceived as being random, although the pitch changes followed specific rules. Prediction errors were found to be explained partly by changes in local gamma-band oscillations; the accuracy of predictions was related to alpha-band levels; and changes to predictions were related to beta oscillations.

Tinnitus as an Auditory Object in ASA

The Adaptation Level Theory model of tinnitus views tinnitus as an auditory object which is formed and processed by ASA in the early stages (Searchfield et al, 2012; Searchfield, 2014). Tinnitus retains characteristics of various objects such as complex sound quality and typically has a defined spatial location (Griffiths and Warren, 2004; Snyder and Alain, 2007). However, as a phantom sound, tinnitus has no stored schema, meaning or explanation, and it does not interact with external sounds in typical ways, as observed in psychoacoustic masking studies (Leech et al, 2009). Generalization of the object based on other senses is difficult as there is also no concurrent information arriving from other modalities, such as vision and/or touch, which can be used to corroborate and identify a sound source (Feldmann, 1992). These discrepancies disrupt later-stage auditory object processing, driving saliency of the tinnitus signal, and making it difficult to habituate to (Grossberg et al, 2004; De Ridder et al, 2011a; Searchfield et al, 2012; Searchfield, 2014). The Adaptation Level Theory model defines aversive memory representations, reduced working memory capacity, and strength of auditory prediction errors generated (also related to attention factors) as individual residual factors which can influence final magnitude judgments of tinnitus loudness and distress.

Prediction Error and Tinnitus

There is a recent theoretical proposition that constant auditory prediction errors may contribute toward tinnitus perception and distress (De Ridder et al, 2014b, 2015b). According to the article by De Ridder et al (2014b), deafferentation at the peripheral auditory level results in missing input reaching the cortex for certain frequencies. If this deafferentation is sufficiently large, prediction errors occur and tinnitus becomes salient (flagged as novel). Subsequent central plasticity processes occur, including neuronal hyperactivity, synchronized neural activity, cortical map changes, and memory retrieval, ultimately giving rise to the sensation of tinnitus. Reduced sensory input and incomplete memory updating can correspond with decreased alpha-band activity, increased beta activity for prediction error propagation, and increased gamma activity within functional tinnitus regions in the cortex (De Ridder et al, 2015b). With limited deafferentation, missing information can be retrieved from neighboring auditory cortical regions (De Ridder et al, 2015b). However, if the deafferentation spans across many frequencies, missing information may be retrieved from parahippocampal auditory memory using theta carrier waves; persistent theta–gamma coupling may form the neural basis for conscious perception of tinnitus (Lisman and Jensen, 2013; De Ridder et al, 2015a,b).

The role of prediction error in tinnitus generation and maintenance has only just begun to be empirically studied. Roberts et al (2013) reviewed how auditory attention focused on this prediction error due to missing auditory input may result in the neuroplastic changes of tinnitus. Two studies examined MMN responses between tinnitus and matched normal-hearing controls and reported significant MMN amplitude reductions for pitch, duration, and silent gap deviants among the tinnitus group (Mahmoudian et al, 2013) and for frequency deviants located at the audiometric normal lesion edge (Weisz et al, 2004). De Ridder et al (2014a) reported 97% of tinnitus patients who remembered their dreams after rapid eye movement sleep did not perceive tinnitus while dreaming. Factors such as the absence of P3 and incomplete structure of the MMN in sleep compared with wakefulness (Strauss et al, 2015) suggest that predictive processing maybe disrupted during sleep; therefore, prediction errors may not be elicited in this state. However, this remains as indirect, speculative evidence. It would be beneficial to measure behavioral responses or design objective methods of measuring neural prediction processes in the tinnitus population and compare this with control groups to detect differences.

Studies examining oscillatory activity in tinnitus have been conducted and, to date, show contradictory findings. Weisz et al (2005) found reduced resting state alpha-band and increased delta-band activity among participants with tinnitus, especially in the right temporal and left frontal areas, when contrasted with normal-hearing controls. These activity levels significantly correlated with the extent of tinnitus distress. Adamchic et al (2014) found higher delta-, theta-, beta-, and gamma-band activity and lower alpha-band activity among the group of patients with tinnitus compared with healthy controls. Mohan et al (2016) examined 311 patients with tinnitus and 256 healthy controls and found distinct brain networks to be active and different network connectivity for all frequency bands (except gamma) between the two groups; the neural networks considerably overlapped in the gamma-band frequencies. Increased levels of theta–gamma coupling among patients with tinnitus have been observed using EEG (van der Loo et al, 2009; De Ridder et al, 2015a) and MEG (Llinás et al, 1999; Llinás et al, 2005; Weisz et al, 2007) as well as intracranial recordings (De Ridder et al, 2011b). Some studies report oscillatory activity differences as follows: in the beta-band range (Moazami-Goudarzi et al, 2010; Pawlak-Osińska et al, 2013), the gamma band (Ashton et al, 2007; Weisz et al, 2007; Ortmann et al, 2011) or alpha band (Weisz et al, 2007; Schlee et al, 2014). Other studies did not find any changes in beta or gamma-band activity (Weisz et al, 2005; Lorenz et al, 2009; Hébert et al, 2011; Adjamian, 2014; Meyer et al, 2014; Schlee et al, 2014; Zobay et al, 2015) or any changes in alpha-band activity (Ashton et al, 2007; Lorenz et al, 2009; Moazami-Goudarzi et al, 2010; Vanneste et al, 2010; Hébert et al, 2011; Ortmann et al, 2011; Vanneste et al, 2011; Tass et al, 2012; Adjamian, 2014; Meyer et al, 2014; Zobay et al, 2015) among individuals with tinnitus.

Correlation analysis between oscillatory band activity and tinnitus characteristics has also been conducted. Strong positive correlations between subjective tinnitus loudness and resting-state contralateral AC gamma-band activity (van der Loo et al, 2009), temporal region delta-band activity (Dohrmann et al, 2007), theta-band activity in secondary auditory regions (De Ridder et al, 2011b; Vanneste et al, 2011), anterior insula alpha-band activity, anterior cingulate cortex beta-band activity, and parahippocampal gamma-band activity (De Ridder et al, 2015a) have been demonstrated. For narrow-band noise tinnitus, tinnitus laterality corresponded with gamma-band levels in the contralateral parahippocampal region. Narrow-band noise tinnitus also resulted in lower delta-band activity and increased beta- and gamma-band activity within the lateral frontopolar cortex, the posterior cingulate cortex, and parahippocampal areas when compared with pure-tone tinnitus (Vanneste et al, 2010). Vanneste et al (2011) observed increased bilateral gamma-band activity in the ACs irrespective of tinnitus laterality (right, left, and both ears). Parahippocampal gamma activity and AC activity was linked by theta–gamma cross-frequency coupling (De Ridder et al, 2015a). Pierzycki et al (2016) however found whole scalp resting state EEG oscillatory activity did not correlate with behavioral (either psychoacoustic or psychosocial) measures of tinnitus.

Working Memory and Tinnitus

Working memory space that may be compromised by the presence of tinnitus can hypothetically affect the accuracy of predictive processing. Andersson and McKenna (2006) systematically reviewed the relationship between tinnitus and cognitive functioning and concluded that the presence of tinnitus had most impact on cognitive task performance with low or high demand; medium-demand tasks were not affected to the same extent. The authors suggest that tinnitus distress arises because of cognitive deficits (working memory and attention limitations), emotional processing bias, and negative appraisal.

Persons with tinnitus have displayed impaired performance compared with nontinnitus persons on various formal working memory and/or attention tasks including reduced auditory verbal working memory, reduced divided attention performance (Rossiter et al, 2006), deficits in learning, rates of learning, immediate recall of words, serial encoding (Pierce et al, 2012), dual tasks of attention, verbal fluency, short-term and long-term memory, reaction time (Hallam et al, 2004), decreased autobiographical memory (related to self and self-understanding) (Andersson, 2003; Andersson et al, 2013), and diminished performance on Stroop tasks measuring selective attention (Andersson et al, 2000). In a study examining memory performance under the presence of external noise, Andersson et al (2002) observed the tinnitus group scored significantly lower on a digit-symbol test with intermittent masking playing in comparison with continuous masking, whereas controls scored significantly lower with intermittent masking compared with both silence and continuous masking. However, another study testing serial recall observed no differences between tinnitus and matched control groups under identical background noise conditions, indicating potential task-specific effects (Andersson et al, 2009). Individuals with tinnitus might use different compensatory memory strategies compared with controls (Hallam et al, 2004). The nature of the cognitive task itself also plays a part in the level of difficulty experienced (Andersson and McKenna, 2006). More well-designed studies may enable identification of the precise processes which show interference because of tinnitus. Even in instances where there was no immediate decline in performance, possibilities exist for tinnitus to influence long-term performance if the task was more persistent (e.g., at work for a whole day). A discussion into the neural network changes which may occur with tinnitus and which may have involvement of memory networks (e.g., De Ridder et al, 2006; 2011a) is beyond the scope of this review.

CONCLUSIONS

Chronic tinnitus is a complex phenomenon which reduces quality of life in 15–20% of those who experience it. Certain aspects of tinnitus and external sound neural processing are analogous, and external sound processing relies significantly on regularity detection and anticipation for economical functioning. This narrative account of literature was conducted to review literature on auditory prediction and examine the feasibility of a relationship between auditory memory, predictive coding, and tinnitus generation and distress.

The predictive coding model based on the Bayesian brain hypothesis and top-down feedback serves as the fundamental framework in current literature for how auditory prediction may occur. This may rely on the presence of inhibitory neural templates within the auditory system. Redundant acoustic signals are cancelled whereas novel signals are enhanced and encoded further. A hierarchical nature of regularity detection and prediction is present, with earlier processing involving low-level regularity detection and streaming, whereas later cortical processes generate predictions (corresponding with MLR and late responses [e.g., MMN] respectively). Evidence for auditory predictive processing exists in the domains of speech (especially in instances of degraded speech quality or missing speech segments), music perception, and in the identification of sound identification patterns in auditory object analysis. Attention appears to modulate the strength of predictions; however, it is not a necessary component of predictive processing itself. Much of what is understood about deviance detection comes from electrophysiological studies using the MMN waveform under the oddball paradigm. However, limitations may apply when extrapolating findings from MMN studies as it does not appear to reflect prediction error exclusively; also, the paradigm is inappropriate for modeling more complex real-life auditory phenomenon. There is empirical support for various cortical oscillatory bands to be involved in the transfer of prediction errors to higher-order regions as well as in top-down feedback of generated predictions.

Tinnitus may also be an auditory object which is formed and processed by ASA in the early stages. Certain discrepant characteristics between tinnitus and external sound potentially disrupt later stage auditory object processing, driving saliency of the tinnitus signal, and making it difficult to habituate to. De Ridder et al (2014b) suggest that constant prediction error and attentional focus can arise from missing auditory input, subsequently triggering the central compensatory processes thought to generate tinnitus. Few studies have directly examined the role of prediction error in tinnitus; most studies have examined oscillatory band activity changes with tinnitus, and this has shown largely contradictory findings. Behavioral differences and objective methods in detecting deviances for sounds corresponding to sensory deafferentation should also be investigated between tinnitus and nontinnitus individuals. Further research based on compiling EEG data from various studies (i.e., compiling large-scale databases) and applying standard protocols may enable for a clearer understanding of neural oscillatory changes in tinnitus. If differences between sound deviance detection in tinnitus sufferers compared with nontinnitus individuals exist, this can also result in auditory streaming difficulties. Durai et al (unpublished data) observed a larger N1c waveform in the absence of deviant stimuli and abnormal growth in N1c waveforms with increasing frequency deviants among individuals with tinnitus under an auditory streaming paradigm, when compared with individuals without tinnitus but matched for hearing loss. Within the context of everyday life, streaming difficulties among tinnitus sufferers can translate into difficulties in separating out different sound sources in noisy situations (e.g., following a stream of conversation in noisy environments). Errors in simultaneous grouping result in blending of sounds that should be heard as separate, and this blending can distort characteristics (e.g., frequency, quality, or timbre) of incoming sounds. It would therefore be useful clinically to provide additional counseling and/or teach individuals with tinnitus strategies for coping with hearing in complex environments, similar to techniques taught for hearing loss, such as facing the person, reducing distance between speaker and themselves, etc. This may be the basis of benefits obtained in reducing tinnitus using auditory training (Searchfield et al, 2007). Cognitive deficits (working memory and attention related) have been consistently observed among tinnitus sufferers, which can hypothetically be detrimental to optimal predictive processing and also reduce quality of life. However, working memory and attention levels are not currently assessed in standard tinnitus protocols. If it is possible to identify individuals who have such deficits, targeted therapies such as attention training or cognitive-based psychological therapy may be applied. It is possible that various factors—aversive memory representations, reduced working memory capacity, and strength of auditory prediction errors—may be residuals (Searchfield et al, 2012; Searchfield, 2014) which can vary in levels between individuals and therefore determine the final tinnitus magnitude judgement and contribute toward the heterogenous presentation of tinnitus seen clinically.

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