Auditory Predictive Coding: Neural Responses to Sound Repetition and Change

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Abstract

Predictive coding is considered one of the important mechanisms by which the brain interacts with complex environments. Effectively perceiving the external environment and making predictions about future events is of crucial significance for individual survival. The human brain continuously optimizes internal models representing the external environment in an iterative manner based on sensory input, and constantly predicts subsequent sensory input. Taking the auditory modality as an example, neural responses to sound repetition and auditory change in humans and animals (such as mismatch negativity and stimulus-specific adaptation) are important manifestations of predictive coding in the brain, expressed as repetition suppression and prediction error. Conducting cross-species research combining human and animal models within this theoretical framework will help deepen our understanding of auditory processing, and even the working mechanisms of the brain.

Full Text

Predictive Coding in Auditory Cortex: The Neural Responses to Sound Repetition and Auditory Change

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Abstract

Predictive coding is considered one of the crucial mechanisms for brain-environment interaction. Effectively perceiving the external environment and predicting future events is vital for survival. The human brain continuously optimizes its internal model representing the external environment in an iterative manner based on sensory input, constantly generating predictions about upcoming sensory information. Taking the auditory modality as an example, neural responses to sound repetition and auditory change in humans and animals—such as mismatch negativity (MMN) and stimulus-specific adaptation (SSA)—represent important manifestations of predictive coding in the brain, expressed as repetition suppression and prediction error. Conducting cross-species research that combines human and animal models within this theoretical framework will help deepen our understanding of auditory processing and even the fundamental working mechanisms of the brain.

Keywords: predictive coding; repetition suppression; prediction error; MMN; SSA

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1. Introduction

Rapid and efficient perception of the external environment and identification of the sources of sensory information constitute the primary functions of sensory systems. In the auditory domain, the environment typically contains numerous concurrent sound events with overlapping acoustic characteristics in both temporal and spectral domains. Yet, when faced with this seemingly chaotic acoustic information, the brain can effectively categorize and organize it (Bregman, 1994), enabling individuals to effortlessly select information, recognize sound patterns, and detect novel stimuli. Näätänen, Tervaniemi, Sussman, Paavilainen, and Winkler (2001) refer to this cognitive activity occurring in sensory cortex as "primitive sensory intelligence." Unlike traditional views that the brain passively receives bottom-up information input, this perspective emphasizes top-down modulation of sensory information by the brain. More importantly, the brain continuously optimizes its internal model representing the external environment based on sensory input in an iterative fashion, constantly predicting subsequent sensory input. This concept was first proposed by Rao and Ballard (1999) in the visual modality, conceptualizing visual processing as a form of predictive coding. Specifically, sensory systems process information at each hierarchical level through predictive coding. Each level receives bottom-up input and top-down predictions. When input information contradicts existing predictions, an error signal is generated and transmitted upward to adjust predictions at higher levels. The revised predictions are then conveyed downward as predictive signals, which generate expectations at lower levels to suppress prediction error. Later, the concept of predictive coding was widely applied to the auditory modality (Friston, 2005; Rubin, Ulanovsky, Nelken, & Tishby, 2016), largely due to extensive research on auditory mismatch negativity (MMN) and stimulus-specific adaptation (SSA).

Predictive coding is considered one of the essential mechanisms for brain interaction with complex environments. Based on this theoretical framework, numerous theoretical, empirical, and computational modeling studies have rapidly emerged. To better understand how predictive coding operates in auditory cortex, this article summarizes empirical research on neural responses to sound repetition and auditory change in humans and animals, and discusses two primary pieces of evidence for predictive coding in the auditory modality: repetition suppression and prediction error. Specifically, the article first reviews relevant research on human auditory MMN, explaining from a predictive coding perspective how top-down brain activity influences different processing stages involved in MMN. Then, using animal models and focusing on SSA, the article further discusses the neural basis of predictive coding. Finally, the article examines the current dilemmas and future development trends of predictive coding as a theoretical framework, highlighting the importance of conducting cross-species research to deepen our understanding of auditory processing mechanisms.

2.1 Auditory MMN

MMN is considered a robust neural index of deviance detection (Näätänen, Paavilainen, Rinne, & Alho, 2007; Winkler, 2007). The classic paradigm for eliciting MMN is the oddball paradigm, in which two or more sound stimuli are presented alternately at different probabilities (Näätänen, Pakarinen, Rinne, & Takegata, 2004). Different sound stimuli can vary in spatial domain (e.g., location), spectral domain (e.g., pitch, timbre), or temporal domain (e.g., stimulus duration, inter-stimulus interval) (Näätänen et al., 2007). Frequently repeated sounds and occasionally presented sounds are referred to as standard and deviant stimuli, respectively. MMN refers to the difference wave between neural responses evoked by standard and deviant stimuli, typically occurring 150–250 ms after deviant stimulus presentation. MMN is distributed primarily over fronto-central scalp regions (Näätänen, Paavilainen, & Reinikainen, 1989), with major generators localized in auditory cortex and prefrontal cortex (Näätänen et al., 2007). MMN latency and amplitude are influenced by factors such as the acoustic difference between standard and deviant stimuli (Sams, Paavilainen, Alho, & Näätänen, 1985), deviant stimulus probability (Taaseh, Yaron, & Nelken, 2011), and the complexity of temporal stimulus information (Lumaca, Trusbak Haumann, Brattico, Grube, & Vuust, 2018). Notably, as the difference between standard and deviant stimuli increases, MMN latency advances and may overlap with the auditory N1 component, making them difficult to separate. However, N1 is more related to stimulus physical properties and is less affected by differences between stimuli. Therefore, MMN latency changes with varying degrees of deviance, whereas N1 latency remains relatively stable (Näätänen & Picton, 1987).

Although MMN is thought to reflect pre-attentive processing without conscious involvement, its amplitude and latency are still influenced by top-down attention and expectation (Chennu et al., 2013; Heilbron & Chait, 2018), with these two factors operating differently (Auksztulewicz & Friston, 2015; Cacciaglia, Costa-Faidella, Zarnowiec, Grimm, & Escera, 2019). In some cases, MMN under attentional conditions may overlap with the N2b component, which reflects attentional deviance detection. Generally, N2b has a later latency than MMN, peaking approximately 200–300 ms after deviant stimulus presentation. Additionally, N2b has a different scalp distribution, concentrating over centroparietal regions with no polarity reversal at mastoid sites, suggesting its generator may lie outside auditory cortex (Näätänen, Simpson, & Loveless, 1982). In fact, MMN can be divided into two stages: standard formation and deviance detection. Standard formation is the cornerstone of MMN generation, establishing the foundation for deviance detection. When a deviant stimulus is detected, MMN is elicited (Sussman, 2007). Generally, the standard formation stage is influenced by top-down factors such as attention, expectation, and musical training, whereas the deviance detection stage is not affected by attention and reflects genuine pre-attentive sensory processing (Sussman, Winkler, & Wang, 2003). However, it should be noted that detecting deviant stimuli depends on extracting rules from the input sound sequence and their representation or memory trace formed during standard formation (Näätänen & Picton, 1987). The most direct evidence comes from Sussman, Winkler, Huotilainen, Ritter, and Näätänen (2002). In this study, researchers presented sound sequences to participants who were instructed to either ignore the sounds (ignore condition), attend to pitch changes (attend-pitch condition), or attend to pattern violations (attend-pattern condition). Results showed that deviant tones elicited MMN components in both ignore and attend-pitch conditions, but not in the attend-pattern condition. This is primarily because in the attend-pattern condition, local deviant tones were treated as global standard tones and therefore did not violate the established rule, indicating that auditory cortex maintenance of sound representations is affected by top-down attention, which in turn influences the MMN deviance detection process. Moreover, although the attend-pitch condition elicited an additional N2b component compared to the ignore condition, the MMN components were equivalent between these two conditions, suggesting that attention does not affect the MMN deviance detection process itself (Sussman et al., 2002; Sussman et al., 2003).

Current academic explanations for MMN primarily rely on two hypotheses: the adaptation hypothesis and the memory-trace hypothesis. The adaptation hypothesis explains MMN primarily at the neuronal level, proposing that neurons are highly selective for features distinguishing standard and deviant stimuli—that is, the populations of neurons responding to standard and deviant stimuli are not identical. Frequently repeated standard stimuli cause adaptation in neurons responsible for N1 responses to standards, whereas neurons responding to deviants remain unadapted, resulting in enhanced N1 responses when deviants occur. This hypothesis suggests this neural response is a form of stimulus-specific adaptation, with no distinct brain region responsible for generating MMN. Therefore, MMN is not an independent component but rather a delayed and attenuated N1 component (Jääskeläinen et al., 2004; May & Tiitinen, 2010). However, existing experimental data cannot fully support this hypothesis (Näätänen, Jacobsen, & Winkler, 2005). For example, deviant tones can elicit MMN without evoking N1 (Yabe, Tervaniemi, & Reinikainen, 1997; Yabe et al., 1998). In contrast, the traditional memory-trace theory posits that MMN is an independent signal reflecting a mismatch component. When the brain receives auditory input, it compares this input with a memory template formed based on previous sound sequences. When the brain detects inconsistency between new input and the memory template, MMN is generated. Therefore, this hypothesis suggests MMN reflects a higher-level comparison system: when the brain detects a discrepancy, the system generates an error signal and adjusts the memory template (Näätänen et al., 1989). Similar to traditional memory-trace theory, predictive coding theory also emphasizes that MMN reflects not simple adaptation but rather a mismatch signal. However, unlike traditional memory-trace theory, predictive coding theory proposes that the error signal generated by the system results from mismatch between sensory input and predictive models. In other words, MMN reflects the process of brain representation updating when input does not match predicted stimuli, representing an active prediction process about future events (Friston, 2005, 2010; Winkler, 2007). Currently, increasing evidence suggests the brain interacts with complex environments through active prediction rather than passively receiving external information via sensory systems (Friston, 2018).

MMN refers to the difference between neural responses evoked by deviant and standard stimuli. Therefore, increased MMN amplitude may result from either enhanced brain responses to deviant stimuli during deviance detection or reduced brain responses to standard stimuli during standard formation. For example, research has found that as the number of standard stimuli increases, the main reason for MMN amplitude enhancement is not that reduced deviant probability elicits larger negative waves, but rather that standard stimuli evoke a positive slow wave (including P50, N1, and P2 components) between 50–250 ms after presentation. This slow wave is also called repetition positivity (Haenschel, Vernon, Dwivedi, Gruzelier, & Baldeweg, 2005). In other words, the two distinct neural response stages contained within MMN (standard formation and deviance detection) manifest as repetition suppression and prediction error, respectively. The following sections discuss how auditory cortex processes sound repetition and auditory change through predictive coding from these two perspectives.

2.2 Repetition Suppression

As standard stimuli repeat, the brain gradually forms representations of sound regularities, which neurophysiologically manifests as repetition suppression (Baldeweg, 2006) with neural generators involving both auditory and non-auditory regions (Recasens, Leung, Grimm, Nowak, & Escera, 2015). In fact, researchers from different fields frequently use habituation, refractoriness, and adaptation to explain repetition suppression phenomena (Budd, Barry, Gordon, Rennie, & Michie, 1998). These different terminological perspectives have somewhat hindered understanding of repetition suppression and created confusion. Specifically, habituation is primarily a psychological concept referring to response attenuation due to loss of novelty after repeated stimulus presentation. The habituation hypothesis makes three predictions: (1) following habituation, dishabituation must occur regardless of how the stimulus changes (increase or decrease); (2) habituation gradually forms with stimulus repetition, so responses to repeated stimuli should gradually weaken; and (3) habituation is not affected by inter-stimulus interval (ISI) in the short term. However, the prediction regarding dishabituation has not received experimental support (Barry, Cocker, Anderson, Gordon, & Rennie, 1992; Muenssinger et al., 2013; Rosburg et al., 2006). Additionally, Ritter, Vaughan, and Costa (1968) found that electrophysiological measures rapidly decreased after just a few stimulus repetitions rather than gradually, and this phenomenon only occurred with an ISI of 2 s, not with an ISI of 10 s, suggesting that neural response attenuation caused by stimulus repetition is not a simple habituation phenomenon. Refractoriness and adaptation describe neurophysiological phenomena where neural response attenuation results from post-action potential refractoriness in auditory neurons or neuronal adaptation (May & Tiitinen, 2010). However, neuronal refractory periods are on the millisecond scale, making refractoriness inappropriate for explaining MMN. For this reason, O’ Shea (2015) suggested replacing refractoriness with adaptation, though this approach requires cautious treatment (Stefanics, Kremlacek, & Czigler, 2016).

From a predictive coding perspective, repetition suppression is related not only to the probability of previous stimuli but also to the predictability of future stimuli. That is, repetition suppression includes both neural response suppression caused by stimulus repetition itself and suppression caused by expectations generated through stimulus repetition (Grotheer & Kovacs, 2016; Winkler, Denham, & Nelken, 2009). The earliest experimental evidence comes from Summerfield, Trittschuh, Monti, Mesulam, and Egner (2008), who manipulated stimulus repetition probability in face processing research and found reduced repetition suppression when stimulus repetition was unpredictable, indicating that repetition suppression reflects top-down perceptual prediction error when processing unexpected stimuli. In auditory modality research, early evidence comes from Costa-Faidella, Baldeweg, Grimm, and Escera (2011), who investigated how temporal predictability of stimulus presentation affects repetition suppression. Using a roving standard frequency paradigm—a variation of the oddball paradigm—sequences of three, six, or twelve tones with identical pitch were randomly presented, ensuring that the first tone in each sequence was a low-probability deviant relative to the previous sequence, while the last tone was a high-probability standard within that sequence. Experimental trials were divided into two types based on whether inter-stimulus intervals within sequences were fixed: predictable and unpredictable trials. Results showed that when participants passively listened to sound sequences, unpredictable trials exhibited weakened repetition suppression effects compared to predictable trials, manifested by the disappearance of early components of repetition positivity (such as N1) and intact later components (~>200 ms, such as P2). These results also suggest that temporal predictability (“when”) influences the formation of stimulus-specific memory traces at the auditory cortical level, an effect that may already exist at subcortical stages of auditory processing (Gorina-Careta, Zarnowiec, Costa-Faidella, & Escera, 2016).

Similarly, Wacongne, Changeux, and Dehaene (2012) frequently alternated presentation of tone pairs AB and occasionally repeated presentation of tone pairs AA, creating additional expectation for B following A. According to predictive coding hypotheses, since AA occurs with low probability and is unpredictable, no expectation suppression exists due to stimulus repetition, meaning AA should evoke larger neural responses than AB. Experimental results supported this hypothesis, and this finding cannot be simply attributed to the possible existence of higher-level neurons specifically responding to the AB pattern (i.e., the adaptation view), because when the inter-stimulus interval between AA and AB was much longer than synaptic inhibition recovery time, AA still elicited MMN. Todorovic, van Ede, Maris, and de Lange (2011) obtained similar results, finding repetition suppression for AA in auditory cortex that decreased when AA was unpredictable, demonstrating that expectation suppression exists within repetition suppression. These results all indicate that expectation of future event content (“what”) also influences repetition suppression. In subsequent research, Todorovic and de Lange (2012) orthogonally manipulated repetition and expectation, attempting to separate expectation suppression from repetition suppression for the first time. Results revealed that repetition and expectation affected auditory responses at different time points without interaction. Specifically, repetition effects occurred earlier (approximately 40–60 ms after stimulus presentation), while expectation effects occurred relatively later (approximately 100–200 ms). In contrast, both repetition and expectation influenced late responses (200–500 ms). This also suggests that sensory responses are affected by different modulatory influences throughout the time course of neural processing.

As described above, substantial experimental evidence demonstrates that during standard stimulus presentation (i.e., standard formation), the brain not only attenuates neural responses evoked by standard stimuli due to stimulus repetition itself (i.e., repetition suppression) but also extracts relationships between stimuli and establishes expectations for the next stimulus at different processing levels (i.e., expectation suppression). The former can be considered a low-level expectation based on stimulus occurrence probability itself, while the latter can be regarded as a high-level expectation based on more complex statistical regularities between stimuli. Both reflect predictive coding of repeated sounds.

2.3 Prediction Error

After deviant stimulus presentation, rules established through standard stimulus repetition are violated, generating prediction error signals (Winkler & Schroger, 2015). To examine how different levels of rule violation (i.e., local and global) affect MMN, Wacongne et al. (2011) presented participants with sound sequences composed of multiple identical tones (e.g., XXXXX) and created local deviants by changing the last tone (e.g., XXXXY) and global deviants by manipulating the probability of different sequence types (e.g., 75% XXXXX, 15% XXXXY, 10% XXXX_). Results showed that when local deviants were unpredictable due to low occurrence probability (i.e., XXXXY trials within XXXXX blocks), they elicited larger MMN than when they were predictable due to high occurrence probability (i.e., XXXXY trials within XXXXY blocks). This finding aligns with predictive coding theory, indicating that higher-level predictions can counteract mismatch signals elicited by local deviants. Additionally, within XXXXY blocks, XXXXX trials without local deviants also elicited novelty responses, providing evidence for higher-level predictions in auditory cortex. However, this forward-looking hierarchical prediction is disrupted by sleep, while early processing components reflecting information mismatch such as N1 and N2 remain unaffected (Strauss et al., 2015), suggesting that independent processing stages likely exist for mismatch information: a passive adaptation stage unaffected by sleep and an active prediction stage affected by sleep.

Sensory systems are hierarchically organized with similar neuronal structures across layers, meaning similar predictive coding computational principles can apply at multiple hierarchical levels of cerebral cortex (Friston, 2005). This implies that within predictive coding theory, each level contains both prediction error generated by prediction violation and predictions transmitted top-down. However, separating prediction signals from prediction error signals has been a major challenge in predictive coding research (Heilbron & Chait, 2018). To address this issue, many studies have investigated neural responses to omitted stimuli (omission, i.e., no stimulus input) in sound sequences to indirectly demonstrate active prediction of sensory input in auditory cortex.

Specifically, stimulus omission represents an extreme case of duration change that elicits MMN, where stimulus duration equals zero (Yabe et al., 1997). Since omitted stimuli exclude interference from physical stimuli, the MMN they elicit is thought to reflect mismatch between active prediction and absence of sensory input in auditory processing. SanMiguel, Widmann, Bendixen, Trujillo-Barreto, and Schroger (2013) had participants self-generate sounds by button press and manipulated the probability of sound occurrence after button presses (88%, 50%, or 0%). Results showed that only sound omissions following button presses with high probability of sound feedback elicited MMN, demonstrating that neural responses to omitted stimuli also require predictability based on button press-generated sounds. Moreover, this predictability must be based on both stimulus timing and content; otherwise, individuals cannot form accurate predictions (SanMiguel, Saupe, & Schroger, 2013).

Chennu et al. (2016) employed a paradigm similar to Wacongne et al. (2011), presenting continuous five-tone sequences where the fifth tone could be a high-probability (74%) global standard (AAAAA or BBBBB), a low-probability (13%) global deviant (AAAAB or BBBBA), or a low-probability (13%) omitted stimulus (AAAA_ or BBBB_). By comparing these conditions with two additional control conditions where omissions were predictable, results showed that MMN was only elicited when omissions were unpredictable. This finding also indicates that neural responses to sound omissions are predictive rather than passive carry-over effects of neural oscillations, highlighting the predictive nature of omission MMN. Wacongne et al. (2011) proposed that when individuals expect a deviant stimulus to occur, its omission actually violates two expectations: a local expectation that the final stimulus in the sequence will appear (i.e., expectation that "there will be a sound") and a higher-level expectation based on probability regarding what the final stimulus in the sequence will be (i.e., expectation of "specific sound content"). It should be emphasized that omission MMN amplitude is larger under attentional than non-attentional conditions (Chennu et al., 2016; Chouiter et al., 2015), suggesting that omission MMN is modulated by attention, consistent with predictive coding models emphasizing that attention can modulate prediction strength and precision (Auksztulewicz & Friston, 2015).

More direct evidence for separating prediction and prediction error comes from Dürschmid et al. (2018), who hypothesized that prediction signals occurring before the next stimulus presentation best reflect proactive predictive processes. By reanalyzing intracranial cortical recordings from surgical patients who passively received sound sequences (Dürschmid et al., 2016), they found that compared to unpredictable deviants, high-frequency amplitude (HFA) in patients' prefrontal cortex decreased before predictable deviant presentation, which significantly correlated with reduced error signals after stimulus presentation. This suggests an intrinsic link between pre-stimulus HFA reduction and reduced neural responses to predictable deviants. Additionally, they observed that pre-stimulus HFA decreased with repeated standard presentations in unpredictable conditions. Since continuous repetition in unpredictable conditions meant increasing probability of the next stimulus being a deviant, this also demonstrates the relationship between HFA magnitude and deviant occurrence probability from another perspective, providing evidence for prediction signals independent of prediction error.

In summary, when deviant stimuli do not match predictions, the brain generates prediction error signals that are transmitted bottom-up to higher processing levels while simultaneously adjusting internal models to generate new top-down predictions that are transmitted downward to explain and eliminate prediction error, thereby reducing computational load and perceptual uncertainty, and improving processing efficiency.

3. Auditory Predictive Coding Research Based on Animal Models

Humans and animals share substantial similarities in certain neural processing mechanisms, making animal model research potentially generalizable to humans. Techniques such as local field potentials (LFPs), epidural ERPs, and multiunit recordings help reveal the neural basis of predictive coding in auditory cortex. Although most early animal studies related to auditory prediction focused primarily on stimulus-specific adaptation (SSA) in primary auditory cortex (A1) neurons, with only a small portion of animal experiments truly targeting predictive coding in auditory cortex, an increasing number of animal-based predictive coding studies suggest that cortical SSA is not simply neuronal adaptation to specific stimuli but is also influenced by top-down factors. This indicates that A1 neurons may constitute the neural basis of predictive coding. Therefore, integrating human and animal research facilitates deeper understanding and validation of predictive coding theory (Heilbron & Chait, 2018).

3.1 SSA

Similar to human MMN, SSA refers to the selective response attenuation to repeated stimuli observed in A1 neurons (Fishman & Steinschneider, 2012; von der Behrens, Bauerle, Kossl, & Gaese, 2009). Consequently, SSA is often considered single-cell-level MMN (Nelken, 2014; Ulanovsky, Las, & Nelken, 2003). Szymanski, Garcia-Lazaro, and Schnupp (2009) used an oddball paradigm to record LFPs from A1 neurons in ketamine-anesthetized rats and conducted current source density analysis. They found that the same frequency tone elicited larger neural responses when presented as a deviant than as a standard, with no significant differences in response magnitude across A1 layers. Similarly, using vowels from speech as stimulus materials, research found that neurons in deep layers (IV-VI) of auditory cortex in awake rats responded to unexpected sound stimuli (Eriksson & Villa, 2005). However, some studies indicate that deviant detection and standard adaptation in rats can already be manifested in the inferior colliculus (Malmierca, Cristaudo, Perez-Gonzalez, & Covey, 2009). Recent evidence also shows SSA exists as early as the cochlear nucleus in mice, suggesting that non-specific short-term adaptation may begin at auditory nerve fibers (Duque, Pais, & Malmierca, 2018). Notably, auditory information transmission occurs primarily through two pathways: lemniscal and non-lemniscal. For the lemniscal pathway, its neurons respond more to physical features of sound stimuli than to relationships between stimuli, so subcortical lemniscal neurons do not generate prediction error. In contrast, neurons in the non-lemniscal pathway are more modulated by cortex, can receive top-down predictions, and transmit bottom-up prediction error, providing possibilities for processing complex auditory information (Parras et al., 2017). Studies have demonstrated that complete or stronger SSA can be recorded in non-lemniscal subcortical nuclei, whereas only partial SSA can be recorded in lemniscal neurons (Malmierca et al., 2009; Polterovich, Jankowski, & Nelken, 2018). Therefore, although early subcortical SSA (< 100 ms) does not contain psychological expectation components, it may to some extent reflect early deviance detection.

Nevertheless, the exact relationship between cortical SSA and MMN remains controversial. On one hand, cortical SSA and MMN share similar characteristics (Grimm, Escera, & Nelken, 2016; Ulanovsky et al., 2003), mainly manifested in that both result from differences between stimuli. The magnitudes of both cortical SSA and MMN are negatively correlated with deviant probability and positively correlated with the difference between standard and deviant stimuli. On the other hand, substantial evidence indicates that cortical SSA is not the direct basis of MMN and that fundamental differences exist between them (Carbajal & Malmierca, 2018). For example, cortical SSA occurs earlier than MMN, observable within approximately 100 ms after deviant presentation, suggesting SSA may be a precursor to MMN recorded in A1, while MMN itself may be a combination of primary and higher-order cortical responses. Furthermore, NMDA antagonists can disrupt MMN but have no effect on cortical SSA (Khouri & Nelken, 2015).

3.2 Prediction in Auditory Cortical Neurons

Although the term SSA itself emphasizes stimulus specificity and adaptation, whether it truly represents simple neuronal adaptation to specific stimuli remains uncertain. Ulanovsky et al. (2003) found that cat A1 neurons showed larger responses to low-probability pitch and intensity, similar to MMN at the cortical level, suggesting that A1 neurons process not only sound features but also sensory memory and deviance detection. That is, the generator of MMN in A1 can be explained by SSA at the cortical level. In subsequent research, Ulanovsky, Las, Farkas, and Nelken (2004) exposed anesthetized cats to sequences of tone pairs presented independently at fixed probabilities and found that SSA elicitation depended not only on the current stimulus itself but also on stimulus sequences over extended periods (exceeding seconds). Since maintaining or processing stimulus sequences far exceeds the duration of synaptic inhibition, SSA cannot be simply considered as determined solely by synaptic plasticity (Taaseh et al., 2011; Yaron, Hershenhoren, & Nelken, 2012).

Rubin et al. (2016) reanalyzed data from Ulanovsky et al. (2004), attempting to quantify the extent to which SSA generation depends on the amount and detail of previous information. They hypothesized that the brain’ s representation of past information is a simplified representation used for predicting future events. By using information theory to quantify the complexity of these simplified representations and the predictive information they carry about future events, researchers found that neural responses in A1 neurons correlated with theoretical prediction error calculated from stimulus sequences. For some neurons, prediction error could explain over 50% of observed variance. Therefore, they inferred that A1 neurons can make predictions about the future. Additional evidence comes from Yaron et al. (2012), who conducted intracellular and extracellular recordings in auditory cortex of anesthetized and awake rats, finding that rats were sensitive to sound sequence structure, showing larger responses to random sequences than to periodic sequences, providing strong evidence for prediction in SSA. Furthermore, Rummell, Klee, and Sigurdsson (2016) recorded and compared neuronal activity in mouse auditory cortex in response to self-generated and non-self-generated sounds, finding that auditory neurons showed attenuated responses to self-generated sounds, suggesting that predictive processing may be fundamental to sound information processing at the neuronal level.

Similar to human MMN research, neuronal responses to deviant stimuli—that is, observed cortical SSA (neural response to deviants minus response to standards)—contain two components difficult to separate in classically evoked SSA: suppression of repeated stimuli and response to novel stimuli violating expectations, i.e., true deviance detection or prediction error. Taaseh et al. (2011) used a many-standard control condition that eliminated expectations evoked by repetition of a single standard stimulus, suggesting that SSA recorded under this paradigm reflects true deviance sensitivity. They found in halothane-anesthetized rat models that deviant stimuli under single-standard and many-standard control conditions elicited equivalent SSA in auditory cortex. Since fatigue effects are greater under single-standard than many-standard control conditions, researchers reasoned that when SSA is equivalent across conditions, there must be an additional component under many-standard control conditions —namely, sensitivity to deviance. This result was further confirmed in freely moving rat models (Polterovich et al., 2018), demonstrating true deviance detection in A1.

In summary, cortical SSA shares substantial similarities with human MMN and can serve as an index of deviance detection at the neuronal level. Current results from animal models including cats, rats, and mice all indicate that cortical SSA is not simply neuronal adaptation to specific stimuli but is also influenced by top-down factors, suggesting that A1 neurons may constitute the neural basis of predictive coding. However, since direct evidence for independent neurons in auditory cortex responsible for generating predictions and prediction error remains lacking, future animal research specifically targeting auditory predictive coding is needed. Additionally, animal model research on SSA can help reveal how predictive coding unfolds over time, such as the earliest stages at which predictive coding occurs in auditory processing like semantic content priming and whether this process involves subcortical neurons.

4. Summary and Outlook

Predictive coding theory conceptualizes the brain as a hierarchically organized and highly active processing system that depends on continuous prediction of sensory input and iterative adjustment of internal representations based on new input. The ultimate goal of this dynamic neural activity is to reduce prediction error. As a mechanistic theoretical model, predictive coding theory has gained tremendous popularity and been used to explain various empirical data (Clark, 2013; Friston, 2010). However, this theory currently faces significant challenges (Friston, 2018). First, its core concepts lack clear definition. For example, no consensus has been reached on the precise definition of "prediction." Theoretically, "prediction"can refer to either correlational or causal relationships between events (Denham & Winkler, 2018). Therefore, researchers' different understandings of "prediction" itself can bias their focus in predictive coding research. Second, researchers from different fields—empirical, theoretical, and computational modeling—often describe concepts from different perspectives. For example, psychology uses "habituation" while neurophysiology uses "refractoriness" to explain repetition suppression. This also creates differences in understanding predictive coding theory across disciplines. Finally, some core assumptions are not falsifiable (Kogo & Trengove, 2015). For instance, predictive coding theory posits that independent neurons in sensory cortex are responsible for predictions and prediction error, yet this assumption is difficult to verify with current technology. This also leads to a lack of direct evidence for the material basis of predictive coding (Heilbron & Chait, 2018). Therefore, some researchers suggest that predictive coding may be more of a computational mechanism (related to decision-making) than a phenomenological explanation of neural responses (Denham & Winkler, 2018; Stefanics et al., 2016).

Nevertheless, predictive coding remains the dominant theoretical framework in current sensory research and can explain many important auditory perceptual phenomena. Facing existing challenges, future research on auditory predictive coding can focus on several directions: (1) Conduct cross-species research. Based on similarities between cortical SSA and human MMN, increasing research suggests that cortical SSA may be related to the deviance sensitivity component in MMN. Moreover, current research on SSA in the auditory system has been relatively comprehensive, particularly regarding its molecular and network mechanisms and computational principles of short-term plasticity, providing an excellent model for further understanding the neural circuits of predictive coding. Therefore, future research can use identical paradigms to record human MMN and animal cortical SSA to better understand predictive coding in auditory processing and attempt to identify its material basis. (2) Utilize variations of the classic oddball paradigm or add experimental control groups to separate different components that may be contained within MMN (Harms et al., 2014; Symonds et al., 2017). For example, separating repetition suppression from expectation suppression and separating predictions from prediction error in both human and animal research can provide more reliable evidence for predictive coding in auditory processing. The use of these variations and control conditions is important for deepening understanding of predictive coding models and auditory processing mechanisms. (3) Investigate the possible material basis of predictive coding from the perspective of neural oscillations (Morillon & Schroeder, 2015). Studies have shown that neural rhythms including gamma and beta oscillations may constitute the neural basis for brain predictions of stimulus content and timing (Arnal & Giraud, 2012). Therefore, future research can examine how sound repetition and auditory change affect frequency-domain characteristics of EEG signals, understanding predictive coding mechanisms in auditory processing from different perspectives. (4) Understand more advanced auditory phenomena from a predictive coding perspective and integrate different sensory modalities to deepen our understanding of sensory processing mechanisms. Predictive coding models have already been used to explain various phenomena in advanced auditory processing, such as phonological rules (Ylinen et al., 2016), speech perception (Sohoglu, Peelle, Carlyon, & Davis, 2012), speech production (Okada, Matchin, & Hickok, 2018), speech comprehension (Bendixen, Scharinger, Strauss, & Obleser, 2014), and music perception (Koelsch, Vuust, & Friston, 2019; Salimpoor, Zald, Zatorre, Dagher, & McIntosh, 2015).

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Note: Figure translations are in progress. See original paper for figures.