



Early indices of deviance detection in humans and animal models



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ABSTRACT

Detecting unexpected stimuli in the environment is a critical function of the auditory system. Responses to unexpected “deviant” sounds are enhanced compared to responses to expected stimuli. At the human scalp, deviance detection is reflected in the mismatch negativity (MMN) and in an enhancement of the middle-latency response (MLR). Single neurons often respond more strongly to a stimulus when rare than when common, a phenomenon termed stimulus-specific adaptation (SSA). Here we compare stimulus-specific adaptation with scalp-recorded deviance-related responses. We conclude that early markers of deviance detection in the time range of the MLR could be a direct correlate of cortical SSA. Both occur at an early level of cortical activation, both are robust findings with low-probability stimuli, and both show properties of genuine deviance detection. Their causal relation with the later scalp-recorded MMN is a key question in this field.

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1. Introduction

Sensory systems of animals and humans can adjust their sensitivity depending on stimulation context. Sensory responses may depend not only on the incoming stimulus, but also on the history of past stimulation. For example, low-probability stimuli very often evoke enhanced responses (relative to the same stimuli when common). Probability-dependent modulations of auditory responses may serve the important function of deviance detection, which allows for the rapid spotting of unexpected or irregular stimuli in an otherwise predictable environment. In the laboratory, this function is quantified by contrasting the brain's response to predictable (e.g., repeated) ‘standard’ stimuli with the response to unexpected ‘deviant’ stimuli—typically yielding larger responses for deviants compared to standards.

While there are no disagreements about these findings, their interpretation has been hotly debated. Larger responses to rare stimuli may represent the detection of regularity violation, but the same findings could simply be the result of sensory adaptation, that is, an attenuation of the neural response to the repeated standard

stimulus, while activating unadapted neuronal population with the deviant stimulus. Such a process would show larger responses to rare sounds, but not because they violate regularity—rather, the larger responses to rare sounds occur simply because the rare sounds are rare. Contrary to such adaptation-driven explanations, enhanced responses to deviants have been attributed to mechanisms such as a memory comparison process (Näätänen, Paavilainen, Rinne, & Alho, 2007) or a process of prediction and sensory hypothesis testing (Winkler, Denham, & Nelken, 2009). Such models assume that representation of regularities in the stimulus history (or the predictions based on these regularities) influence the processing of newly incoming input. In consequence, to demonstrate true deviance sensitivity (rather than simple sensitivity to the rarity of the deviant), it is necessary to show not only that rare stimuli evoke larger responses, but also that these larger responses relate to the predictability of the common sounds in the sensory sequence.

Current reviews elaborate on this debate (Fishman, 2014; May & Tiitinen, 2010; Näätänen, Jacobsen, & Winkler, 2005) focusing on the mismatch negativity (MMN), a marker of deviance detection measured at the human scalp. They discuss the relation between MMN and possible intracranial correlates from animal models that can be obtained using similar paradigms, mostly under the heading of stimulus-specific adaptation (SSA, Ulanovsky, Las, & Nelken, 2003). However, given the difficulties in relating scalp-recorded

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potentials with underlying neural processes, it is unclear (and in fact unlikely, as we will argue below) that SSA is a correlate of MMN. Instead, recent studies show that indices of deviance detection can be observed in humans and animal models at different stations along the sensory processing pathway, at substantially earlier latencies than the MMN (Escera & Malmierca, 2014; Kraus et al., 1994; Nelken, 2014). In this paper, we will provide a short review of the recent literature on early deviance detection in humans and animal models. With regard to human studies, we will place a stronger focus on markers of deviance detection occurring earlier than the MMN; with regard to animal studies we mainly focus on early cortical intracranial responses in typical deviance detection paradigms. We will argue that these early indices of deviance sensitivity in human and animal findings are likely to be closely related to each other, and sketch implications on our understanding of mechanisms that allow us to detect low-probability and/or irregular sounds.

2. Deviance detection in humans: MMN, MLR

In humans, studies of deviance sensitivity of auditory event-related potentials (ERPs) have a long history. The MMN is the best-studied electrophysiological marker of deviance detection. It is elicited in oddball paradigms or variations thereof and is measured as the difference between the deviant and standard ERP peaking between 100 and 250 ms (Näätänen, Gaillard, & Mäntysalo, 1978; Näätänen et al., 2007).

Based on the early occurrence of deviance responses in animal research, a series of studies have hypothesized that markers of deviance detection earlier than the MMN should be observable at the human scalp. Indications, that deviance is detected before the occurrence of MMN (at around 80–100 ms) also come from microsaccadic recordings (Widmann, Engbert, & Schröger, 2014). The existence of such earlier discrimination mechanisms has been verified by showing deviance sensitivity to sounds in the time range of the middle latency response (MLR; a set of positive and negative deflections peaking between 10 and 50 ms after stimulus onset) of the auditory evoked potential. Frequency deviants in a simple oddball paradigm elicit an enhanced Nb component of the MLR peaking at about 40 ms after deviant onset (Grimm, Escera, Slabu, & Costa-Faidella, 2011; Slabu, Escera, Grimm, & Costa-Faidella, 2010), location or ITD deviants elicit a larger Na component peaking at about 20 ms (Cornella, Leung, Grimm, & Escera, 2012; Grimm, Recasens, Althen, & Escera, 2012; Sonnadara et al., 2006), intensity deviants modulate the late portion of the Pa component (Althen, Grimm, & Escera, 2011) and deviants that are rarely presented at a shorter stimulus-onset asynchrony (SOA) elicit enlarged Pa and Nb components (Leung, Recasens, Grimm, & Escera, 2013). Nb modulations to frequency deviants are robust enough to tolerate the variations of other features within the auditory sequence as shown in the so-called optimal paradigm (Leung, Cornella, Grimm, & Escera, 2012), they persist with higher stimulus complexity, e.g., in response to pitch changes in a sequence of missing fundamental sounds (Alho, Grimm, Mateo-Leon, Costa-Faidella, & Escera, 2012), and also occur when a pitch change is embedded in a complex auditory scene consisting of several parallel streams (Puschmann et al., 2013). The sources of the modulatory effect on the magnetic counterpart Nbm in response to frequency deviants have been localized in regions anterior and medial in comparison to the sources of the MMN likely covering primary auditory cortex (Recasens, Grimm, Capilla, Nowak, & Escera, 2014a). Whereas MMN can be elicited to violations of complex and abstract type of regularities (e.g., Bendixen & Schröger, 2008; Paavilainen, 2013; Paavilainen, Arajärvi, & Takegata, 2007), such complex regularities are not signaled by deviance-related modulations in the MLR

time range. That is, in sequences containing tones of alternating frequency (ABAB; see Cornella et al., 2012) or tones that follow a specific frequency pattern (e.g., AAABAAAB; see Recasens, Grimm, Wollbrink, Pantev, & Escera, 2014b), regularity-violating repetitions of a frequency elicited MMN that was not preceded by earlier modulations of the ERPs. A similar pattern of results was found for deviants that were defined by an irregular combination of different features (Althen, Grimm, & Escera, 2013). That is, to date deviance-related modulations in the MLR time range have only been reported to physical feature changes occurring with low probability—which could lead to the conclusion that at this level of processing deviance-related modulations of the MLR reflect mainly the rarity of the deviant (rather than the regularity of the standard).

Nevertheless, findings under a respective control condition indicate that it is (at least partly) genuine deviance detection that is contributing to the MLR enhancement for frequency deviants (e.g., Grimm et al., 2011; Recasens et al., 2014a; Slabu et al., 2010), whereas results were inconclusive for intensity deviants (Althen et al., 2011). In this so called control or many-standards condition, stimuli that vary along a feature dimension are presented randomly and with equal probability each (Jacobsen & Schröger, 2001; Jacobsen, Horenkamp, & Schröger, 2003; Schröger & Wolff, 1996). In that way, deviant and standard ERPs can be compared to ERPs of physically identical stimuli when they occur with low probability in a non-regular context, with differences ideally reflecting either adaptation to high-probability input (standard vs. control) or a genuine deviance response (deviant vs. control) or both.

Yet in practice, due to cross-frequency adaptation, a true equivalence in the state of adaptation for the deviant tone in the oddball and many-standards conditions is difficult to reach. For example, for testing deviance sensitivity for frequency, the control sequence is constructed so that the frequency separation between standard and deviant in the oddball paradigm corresponds to the frequency separation between deviant and the closest standard in the many standard condition. In consequence, the adaptation level of the deviant tone in the many-standard condition is certainly not larger, but may in fact be smaller, than that of the deviant in an oddball condition, where a high percentage of context tones occur at the minimal frequency separation (Taaseh, Yaron, & Nelken, 2011). Thus, while a deviant response that is larger than the control response is a *prima facie* evidence for deviance detection, the reverse implication is not correct—inconclusive results as in the case of the two being equal to each other, for example, are no proof for the absence of true deviance sensitivity.

Taken together, it seems that deviance detection develops along the processing hierarchy, with deviance from simple feature repetitions being detected earlier (in the MLR time range) while deviance from complex and abstract regularities are signaled only later (in the MMN time range). Nevertheless, like for the MMN, deviance-related effects in MLR can at least partly be attributed to true deviance sensitivity.

3. Stimulus-specific adaptation in animal models

Stimulus-specific adaptation is a reduction in the neural response to a stimulus with high probability of occurrence, which is not generalized, or only partially generalized, to other stimuli. SSA is usually measured with sequences of common and rare sounds. Since neurons in the auditory system have feature selectivity, the response of a neuron to e.g., a rare sound in a sequence may be larger not because the sound was rare but rather because that sound is preferred by the neuron. In consequence, SSA is quantified by comparing the responses to the same physical sound tested once in a sequence in which it was common and then again in a sequence in which it was rare.

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