Auditory event-related potentials as a function of abstract change magnitude

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INTRODUCTION

The auditory system can extract invariant relationships from the variant acoustic environment. This ability is essential for cognitive functions such as speech or music perception. In this way, the auditory system can identify a phoneme independently of the speaker, or recognize a melody independently of the musical instrument that plays it. For this purpose, it is necessary to maintain a transient storage of the sensory features of past stimuli for their integration with successive incoming stimuli, in what has been called auditory sensory memory, lasting for several seconds [1].

The internal representation of auditory stimuli kept in sensory memory can be demonstrated by presenting low-probability deviant stimuli among repetitive stimuli (the standard stimuli). When the auditory system discriminates the deviant stimuli, the mismatch negativity (MMN) component of the auditory event-related brain potentials (ERPs) is elicited [2]. MMN is generated in the auditory and prefrontal cortices approximately 150 ms after the onset of the discrepancy between the deviant and the standard stimuli [3]. The brain mechanism underlying this mismatch detection has been proposed to start a sequence of brain processes leading to an involuntary orienting of attention towards the eliciting sound, which is reflected in the subsequent P3a and reorienting negativity (RON) components of ERPs [3,4].

Studies with the MMN originally focused on the processing of simple sound features, such as frequency, intensity, duration and location [2]. Since 1992, however, a group of studies focused their interest on the processing of rules governing the relationship between different stimuli, regardless of their physical features. For instance, in the first study of this series, tone pairs of ascending frequency as standard stimuli, and descending frequency as deviant stimuli (50 ms each tone, with a silent intertone gap of 40 ms) were presented to volunteers while they were reading a book [5]. The pairs were randomized on five different frequency levels, thus forming no physically constant pair. Instead, the constant feature of the stimulation was the direction of the frequency change within the pair. Results showed an MMN elicited to the descending pairs, thus demonstrating that the brain was able to encode the frequency relationship between the tones within the pair, regardless of their individual frequencies. These results were replicated with a similar paradigm using 10 different frequency levels [6]. The amplitude of the MMN obtained with these 10 frequency levels was similar to that obtained with five levels, thus supporting the explanation in terms of extraction of an abstract relationship instead of extraction of individual information within the pair. Further studies showed similar effects with different directions of change (i.e. deviant as ascending), different magnitudes of the pitch difference (i.e. deviant pairs with two or three musical notes of difference within the pair [7]), or by varying the intensity change of the sound instead of the pitch dimension [8]. Moreover, these abstract rules can be probed in children [9] and even in the human newborn brain (Carral V, Huotilainen M, Ruusuvirta T, Fellman V, Naätänen R, Escera C, in preparation).

The aim of the present study was to determine the accuracy with which abstract rules governing the relationship between pairs of stimuli are represented in the human brain, as reflected by the MMN and P3a ERP components. For this purpose, neuroelectric responses were measured to event-related potentials were recorded in healthy volunteers to test the accuracy of the human brain to extract, preattentively, auditory abstract rules. The abstract rule was determined by the frequency relationship between two pure tones forming a pair. The standard pairs had identical tone frequency, whereas the deviant pairs had the second tone two, four, six or eight musical steps higher or lower in frequency than the first one. All abstract changes elicited mismatch negativity, which was not affected by the magnitude of change. However, the subsequent P3a increased as a function of the magnitude of the abstract change. These results suggest that mismatch negativity detects violations of abstract rules, and the amount of violation is analyzed in subsequent stages of auditory processing. NeuroReport 16:301–305 © 2005 Lippincott Williams & Wilkins.

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changes of increasing or decreasing magnitude in the frequency difference between two pairs of pure tones. We hypothesize that the larger the magnitude of the abstract change, the larger the amplitude of the MMN and, if present, of the P3a component.

MATERIALS AND METHODS

Participants: Sixteen healthy volunteers (18–28 years, mean age=23.2, five men) with normal hearing and normal or corrected-to-normal vision participated in the experiment. None of them had ever enrolled in regular musical training. According to the Declaration of Helsinki, volunteers gave informed consent after the nature of the experiment was explained to them.

Stimuli and procedure: The auditory stimuli were pure tone pairs consisting of two tones of 50 ms (including 10 ms rise and fall times) separated by a silent gap of 40 ms. The standard pairs \( p=0.8 \) were the same for all conditions and were formed by two pure tones with the same within-pair frequency. The deviant pairs \( p=0.2 \) were formed by two pure tones with an ascending or descending within-pair frequency (i.e. the second tone was higher in frequency than the first one in ascending conditions, the second tone being lower in descending conditions). Moreover, in different blocks, the second tone of the deviant pair was two, four, six or eight musical steps of the tempered scale higher or lower in frequency; therefore, there were four ascending frequency levels and four descending levels. There were thirteen different frequencies (1865, 1661, 1480, 1319, 1175, 1047, 932, 831, 740, 659, 587, 523 and 466 Hz), and five different physical pairs for each stimulus type (Table 1).

Pairs were binaurally delivered through headphones with a constant interstimulus interval (SOA) of 700 ms from onset to onset, at an intensity of 85 dB SPL. Volunteers were each presented with eight different blocks of 1020 pairs of tones. The deviant pairs were randomly interspersed with the standard pairs (\( A, A^+ \) or \( A, A^- \) or \( D, D^- \) or \( D, D^+ \)). To analyze statistically the MMN and P3a components, the mean amplitude of the deviant and standard ERPs in a latency window of 50 and 60 ms centered at their respective peaks was measured. ANOVAs including the factors stimulus (standard vs. deviant), direction of change (ascending vs. descending), magnitude of change (two, four, six vs. eight levels) and electrode (F3, Fz, F4, C3, Cz vs. C4) were conducted over the mean amplitude of each component. Additional linear regression analyses were computed in order to test whether the amplitude of the MMN and P3a, measured at Cz in the difference waves in the same latency windows as above, increased as a function of the magnitude of the frequency difference between the standard and deviant pairs.

RESULTS

All volunteers performed the CPT with a level similar to other studies (hit rate of 88.6%, ranging from 74.9% to 97.2%; reaction time of 477 ms, ranging from 417 to 542 ms; see Ref. [10], indicating that attention was kept away from the auditory stimulation.

Figure 1 shows the ERPs elicited to standard and deviant tone pairs for the four change levels in ascending and descending conditions. As can be seen, the deviant ERP

| Frequency values (in Hz) of the different tones used in the standard and deviant stimulus pairs (\( A, A^+ \) or \( A, A^- \) or \( D, D^- \) or \( D, D^+ \)). |
|----------------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|
| \( 1865-1865 \) | \( 1480-1865 \) | \( 1175-1865 \) | \( 932-1865 \) | \( 740-1865 \) | \( 1865-1480 \) | \( 1865-1175 \) | \( 1865-932 \) |
| \( 1319-139 \) | \( 1047-139 \) | \( 932-1480 \) | \( 740-1480 \) | \( 659-1661 \) | \( 1319-1047 \) | \( 1480-932 \) | \( 1480-740 \) |
| \( 831-932 \) | \( 831-1047 \) | \( 740-1175 \) | \( 659-139 \) | \( 587-1480 \) | \( 1047-831 \) | \( 1175-740 \) | \( 1319-659 \) |
| \( 659-659 \) | \( 659-831 \) | \( 587-932 \) | \( 587-1175 \) | \( 523-1319 \) | \( 831-659 \) | \( 932-587 \) | \( 1175-587 \) |
| \( 466-466 \) | \( 466-587 \) | \( 466-740 \) | \( 466-932 \) | \( 466-1175 \) | \( 587-466 \) | \( 740-466 \) | \( 932-466 \) |

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started to differ from the standard one circa 180 ms from pair onset, that is, 90 ms from deviance onset, and peaked at about 130 ms from deviance onset. The ANOVA revealed a significant main effect for the stimulus factor in the MMN latency window (F(1,15) = 14.854, p = 0.002), thus confirming the generation of MMN in all deviant conditions. However, the deviant–standard ERP difference in the MMN range was of similar amplitude for all change levels in the ascending and descending conditions, as indicated by the lack of significant interaction between the stimulus and the magnitude of change factors (F(3,15) = 0.827, p = 0.471). This can be better seen in the deviant minus standard difference waveforms shown in Fig. 2, where MMN appears with a similar latency and amplitude for all conditions. Hence, linear regressions of MMN amplitude were not significant for the ascending (F(1,15) = 2.061, p = 0.156) nor for the descending (F(1,15) = 0.030, p = 0.864) conditions.

Following the MMN, a clear and significant (main effect stimulus factor: F(1,15) = 7.184, p = 0.017) P3a component was elicited in all ascending and descending conditions (Figs. 1 and 2). Moreover, contrary to what happened with the MMN, the P3a amplitude increased with the magnitude of abstract change, as revealed by the significant interaction between the stimulus and the magnitude of change factors in the P3a latency range (F(3,15) = 4.743, p = 0.008). Regression analysis confirmed that the amplitude of P3a increased linearly with the magnitude of the abstract change, both for the ascending (F(1,15) = 5.232, p = 0.026) and for the descending (F(1,15) = 4.592, p = 0.036) conditions.

**DISCUSSION**

The generation of MMN in the present data corroborates that the human auditory system can extract, preattentively, abstract rules from the acoustic environment, as previously reported in the literature [5–8]. However, in contrast to our expectations, we did not observe an increment of the MMN amplitude as a function of the deviance increment. In previous studies, using changes in simple sound features as deviant stimuli, the amplitude of MMN was shown to be directly and proportionally related to the degree of difference between the standard and the deviant stimuli, for stimuli differing in frequency [11,12] and duration [13]. In the present study, however, the amplitude of MMN was
similar in all deviant conditions. At least three possible explanations can be outlined to account for this lack of modulation of MMN amplitude as a function of the magnitude of abstract change.

In the first place, the lack of MMN amplitude increase as a function of abstract changes may be due to a ceiling effect. Thus, even for the smaller deviant conditions of the present experiment, the MMN could have been elicited at its maximum possible amplitude. This would be indirectly supported by previous studies showing a ceiling effect in MMN duration on increasing the magnitude of frequency changes [11]. Indeed, in the present study, we use relatively large amounts of change in the deviant stimuli with regard to the standard ones, that is, 20.6%, 37%, 50% and 60.3%. In contrast, previous studies with simple tone features as deviant stimuli used very small amounts of change, such as 0.5%, 1%, 2%, 4%, 8%, 12.7%, 20.2% and 32% in the study of Tiitinen et al. [11] or 2.5%, 5%, 10% and 20% in the study of Novitski et al. [12].

The second explanation derives from the functional role of the neural processes underlying MMN generation. According to one widely accepted interpretation of MMN generation, the so-called trace-presence hypothesis [14], MMN reflects the outcome of a neural mismatch process between the memory trace of the repetitive standard stimuli kept in sensory memory and a neural representation of the incoming deviant stimulus. Thus, in this model, MMN generation depends on the detection of the deviant sound. However, a key study in the field challenged this view [15]. In that study, sequences beginning with six long standard tones (450 ms), followed by zero, two, four or six short standard tones (150 ms), and ending with a deviant, probe stimulus of 300 ms in duration, were presented. The amplitude of the MMN elicited to the probe stimulus was smaller on increasing the amount of short standard tones interspersed between them. Thus, it was suggested that the magnitude of the MMN was not related to the magnitude of the discrepancy between the standard and the deviant stimuli, but to the amount of reorganization necessary for reestablishing a model of the acoustic environment [15,16]. According to this view, MMN reflects an updating of information about the regularities of the auditory input, that is, a reconfiguration of the model of the acoustic environment. Our present data, showing the lack of MMN amplitude modulation as a function of abstract change, may be interpreted within this latter framework. In this way, in all deviant conditions of the present experiment, the amount of reorganization of the acoustic model generated by the different deviants would be the same. As a matter of fact, one might take into account that the standard stimuli (and, by extension, the model of the acoustic environment) were exactly the same for all conditions but still involving a parametric manipulation of abstract change, may help in resolving this issue.

A further explanation for the insensitivity of the MMN mechanism in detecting the magnitude of the abstract change may be based on the assumption that MMN would detect only the fact that the deviant pair did not follow the same rule as the standard pair. In this way, the analysis of the magnitude of change would be left for later stages of auditory processing, as suggested by the parallel increase in the abstract change magnitude of P3a following MMN. In support of this interpretation are the results obtained by Tervaniemi et al. [17]. These authors presented sequences of regularly descending tones along 12 frequency levels, with the deviant stimuli consisting of frequency increments or repetitions. They suggested that MMN elicited to the deviant stimuli reflected the discrepancy between the expectancy created for a descending frequency change in sensory memory and the actual sensory input involving an ascending frequency change. According to this, a neural representation was developed for the direction of the frequency change, as also proposed by Saarinen et al. [5]. Tervaniemi et al. therefore proposed that sensory memory might not only represent the features of past events but may also create expectancies about forthcoming stimuli [17]. This explanation fits our results well, and suggests that in the present study the preattentive auditory processes underlying MMN reflect the discrepancy between the deviant stimuli (i.e. tone pairs of ascending or descending frequency) and the expectancy created by the standard tones (pairs of equal frequency) in sensory memory.

Following MMN, a clear P3a was elicited to abstract changes in all ascending and descending conditions. Moreover, the amplitude of the P3a increased linearly as a function of abstract change magnitude. Elicitation of P3a to deviant pairs indicates an involuntary attention switching towards abstract deviance following change detection indexed by MMN [3,4], resulting in an evaluation of the novelty carried by the eliciting stimulus [18]. Thus, even though attention was strongly focused on visual performance, the attentional resources were captured involuntarily in order to evaluate the deviant stimuli. This process may have resulted in an identification of the abstract change significance, as suggested by the P3a amplitude increase as a function of the abstract change magnitude. Previous studies using simple tone features as deviant stimuli, particularly tone frequency, have also shown an increase in P3a amplitude as a function of deviance [19]. As P3a generation involves sources from the frontal cortex [20,21], the present results are in agreement with recent studies highlighting the functional role of the frontal lobe in encoding abstract rules [22,23].

CONCLUSION

The results obtained in the present experiment demonstrate that whereas the MMN generation process can detect abstract rule violations, the analysis of the magnitude of such rule violation is left to subsequent stages of auditory processing, as indexed by the linear increase in P3a amplitude as a function of the magnitude of auditory abstract change.

REFERENCES


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