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Neural representations of abstract stimulus features in the human brain as reflected by the mismatch negativity

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NEURAL sensory-memory representations that encode physical properties of incoming stimuli can be probed by recording the change-specific mismatch negativity of the event-related potential (ERP). The present study was aimed at determining whether invariant stimulus features, abstracted from the continuously changing acoustic environment, are encoded in these sensory-memory representations. Regularly descending tone sequences with an occasional ascending tone or tone repetition were presented to reading subjects. A significant MMN was elicited by the ascending tones. When instead of simple tones, Shepard tones creating an illusion of a continuous pitch decrement were used in the same paradigm, the MMN was elicited by both ascending and repeating tones. It was concluded that besides physical stimulus properties, abstract stimulus features are also encoded in the neural representations of sensory memory.

Key words: Audition; Mismatch negativity; Neural representations; Sensory memory

Introduction

The neural basis of sensory memory (the first phase in our memory system[1]) can be studied by recording the mismatch-negativity component (MMN) of the event-related potential (ERP).[2] The MMN is elicited when a rare, physically deviant, stimulus is presented among repetitive, standard, stimuli. Besides changes in simple stimulus features (e.g. frequency, intensity, and location[3]), those in spectrally[4–7] and temporally[8–10] complex stimuli also elicit the MMN. On the basis of MMN data, it has been suggested that acoustic information is represented in auditory cortex in short-duration neural memory traces,[11] the MMN being elicited when a stimulus deviates from that represented in the memory trace in some physical parameter.

The standard stimulus does not have to be constant for the MMN to be elicited, however.[12] Recently, the MMN was found also when an ascending frequency change within paired stimuli was randomly replaced by a descending change (or vice versa) or by a frequency repetition even though the tone pairs varied randomly between several frequency levels.[13] It was proposed that a neural representation was developed for the direction of the frequency change within a pair *per se*.

The present paper tested the hypothesis of information generalization in the neural memory traces by presenting a regularly descending tone sequence instead of tone pairs, occasional frequency increments or repetitions serving as deviant events. If the direction of frequency change *per se* was encoded by the memory system, then these events should elicit an MMN. In separate blocks, the tone sequences consisted of either sinusoidal or Shepard tones. By employing Shepard tones,[14] an illusion of circular pitch was created: the tone sequence could be repeated without any perception of a starting frequency, although physically every 13th tone was identical with one another. (A parallel between Shepard tones and the endless staircases in the visual modality has often been drawn.)

Materials and Methods

Tones of 200 ms duration (10 ms rise and fall times) were presented binaurally through headphones (75 dB SPL) with an (offset-to-onset) ISI of 250 ms. The frequencies of 12 sinusoidal tones were between 311 and 587 Hz, in one semitone steps, and they were presented in circularly looped sequences in descending order (... 349—330—311—587—555 ... Hz). The 12 Shepard tones were generated according to the formula presented by Shepard[14] from 10 sinusoidal components spaced one octave apart and weighted to obtain a bell-shaped spectrum. The frequencies of these components varied between 9.73 [f(min) instead of Shepard's 4.86 Hz] and 9400 Hz, in one semitone steps, and the amplitudes between 22 and 56 dB (SPL). (See Table 1 for an illustration of the frequencies and amplitudes of the fifth and sixth components that were highest in intensity among the components.) Also the Shepard tones were presented in descending order looped sequences.

The regularly descending pitch change between two successive tones of the sequence was designated as the Standard event (... 349—330—311 ... Hz). Deviant events of two kinds randomly occurred in separate blocks: *repetition* of a previous pitch (e.g. ... 349—330—*330*—311 ... Hz; 75 deviants in a block of 680 tones; $p = 0.12$), and *ascending* pitch

Table 1. Frequencies and amplitudes of the fifth and sixth components of the Shepard tones that had the highest intensity among the components of a Shepard tone

	Fifth component of the Shepard tone		Sixth component of the Shepard tone	
	Frequency (Hz)	Amplitude (dB SPL)	Frequency (Hz)	Amplitude (dB SPL)
Tone 1	**293.8**	56.0	587.5	53.3
2	**277.3**	55.9	554.6	53.7
3	**261.7**	55.8	523.4	54.1
4	**247.0**	55.6	494.0	54.5
5	**233.2**	55.4	466.3	54.9
6	**220.1**	55.2	**440.2**	55.2
7	207.7	54.9	**415.4**	55.4
8	196.1	54.5	**392.1**	55.6
9	185.1	54.1	**370.1**	55.8
10	174.7	53.7	**349.4**	55.9
11	164.9	53.3	**329.7**	56.0
12	155.6	52.8	**311.2**	56.0

Note the gradually shifting amplitude weights of the components, especially in Tones 5 to 7 (the frequency of the loudest component is marked with bold). Together with the broad spectrum distributed in 10 octaves, this cyclic change of the amplitude maximum causes the perception of pitch level (height) to disappear. The pair-wise comparisons of successive tones create an illusion of an ever descending tone sequence.

change (e.g. ... 349—330—*349*—330—311 ... Hz; 75 deviants in a block of 820 tones; $p = 0.10$). Each block was presented three times with sinusoidal and three times with Shepard tones. The experiment was conducted in an acoustically and electrically shielded room in two sessions: the Shepard-tone blocks in the first day and the sinusoidal-tone blocks in the second day, the presentation order of the blocks within a session being counterbalanced. During the experiment, subjects ($n = 8$, 21–31 years, five males) were reading.

The EEG was recorded (continuous sampling; 250 Hz; bandpass 0.1–100 Hz; −3 dB points) with Ag–AgCl electrodes at six scalp locations: Fpz, Fz, Cz, Pz, and both mastoids, with the nose as a reference. The EOG was monitored at the outer canthus of the right eye. The amplified and digitized EEG was stored on a computer disc for averaging. Epochs with EEG change exceeding 150 μV at any EEG or EOG electrode were omitted from averaging. The analysis period was 690 ms including a 100 ms prestimulus baseline. Frequencies higher than 30 Hz were filtered from ERPs with FFT-filter.

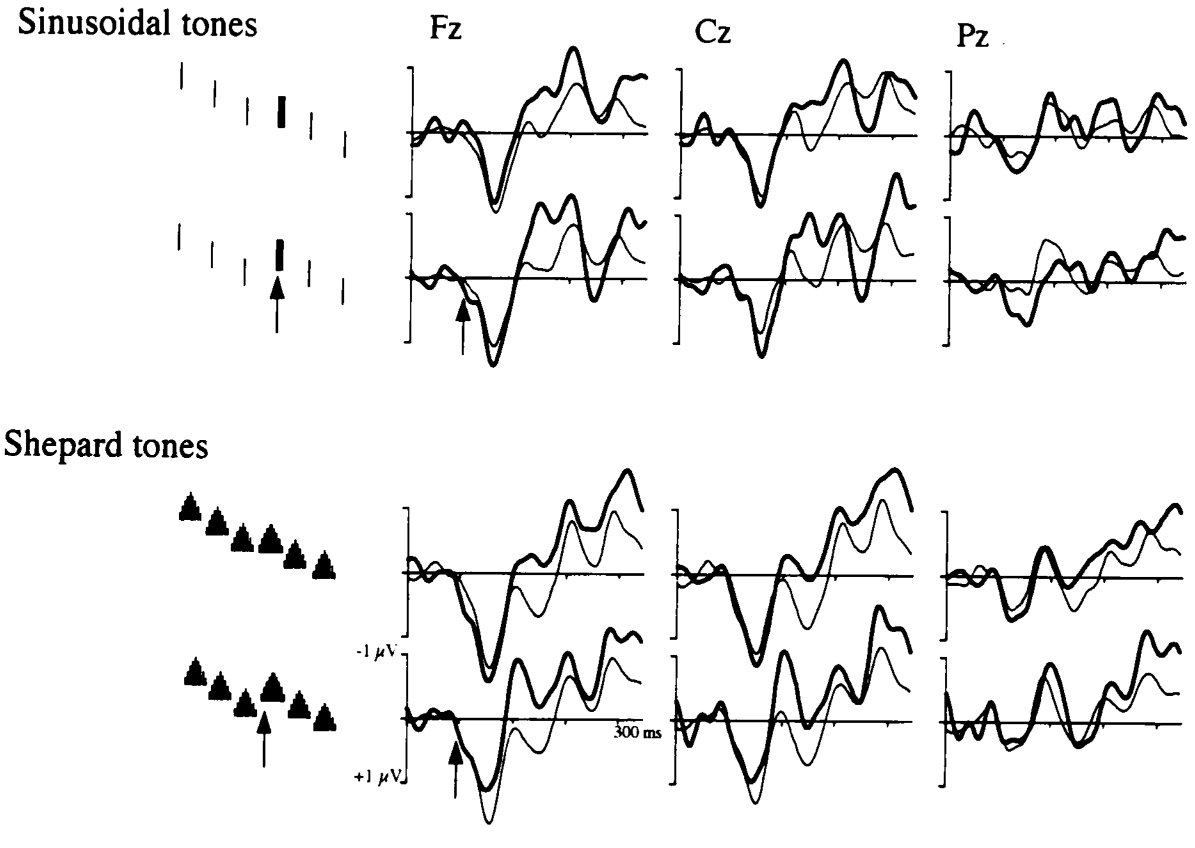

FIG. 1. ERPs to *repetition* and *ascending* deviant tones (thick line) randomly presented in a continuously descending tone sequence (standard; thin line) recorded at Fz, Cz, and Pz electrodes. Tone sequences consisted of either sinusoidal or spectrally complex Shepard tones. The P1–N1 wave was elicited equally by standards and deviants, the MMN being elicited by deviants only.

Table 2. The peak latency at Fz and mean amplitude (30 ms around the peak latency) of the MMN at Fz and Cz electrodes, measured from the deviant–standard difference waves

	Peak latency (ms)	Amplitude at Fz (μV)	Amplitude at Cz (μV)
Sinusoidal tones			
Repetition	148	−0.67 ns	−0.67 ns
Ascending	144	−0.96**	−0.95*
Shepard tones			
Repetition	140	−0.85**	−0.77*
Ascending	116	−1.07***	−0.97**

$t(7)$: $p < 0.1$*; $p < 0.05$**, $p < 0.01$***; one-tailed t-test.

Grand-average ERPs and difference wave forms (the ERP to the descending frequency change subtracted from that to the ascending frequency change or repetition) were calculated. The MMN peak latency in the grand-average difference waves at Fz was measured as the largest negative peak between 0–300 ms after stimulus onset. MMN amplitudes were measured at Fz from the difference waves as the mean amplitude during the 30 ms time window centred around this peak latency. One-tailed t-tests were used to determine whether these MMN amplitudes differed statistically significantly from zero.

Results and Discussion

The *repetition* and *ascending* deviants elicited the MMN (see Fig. 1). At the Fz electrode, this negativity was statistically significant with the Shepard tones for both deviants, and with the sinusoidal tones for *ascending* deviants (see Table 2). The negativity peaked at 116–148 ms from stimulus onset. The MMN amplitudes were larger for *ascending* than *repetition* deviants, and for Shepard tones than for sinusoidal tones. These tendencies, although insignificant ($F(3,24) = 0.22$; one-way ANOVA with repeated measures), can be explained by differences in stimuli used. With an *ascending* deviant, the discrepancy between the sensory input and the neural representation of descending standard event was larger than when a repetition deviant was delivered. The larger MMN with Shepard tones than with simple sinusoidal tones might be accounted for by the fact that several harmonics of these complex tones are, presumably, coded by a larger neuronal population.[7]

The present data give rise to several conclusions concerning neural traces underlying the MMN generation. First, these traces seem to be able to encode also abstract frequency information.The present stimulus sequences consisted of tones of 12 different frequencies, the only invariant feature being the descending frequency change between each two consecutive tones. The MMN was elicited by a violation against this abstract feature, by deviation in the direction of the frequency change. Thus it appears that even at the level of preattentive sensory processing such invariances (concepts) are derived and encoded into memory trace.

Second, the trace system involved seems to be able to integrate auditory information at least over several hundreds of milliseconds. In order to represent descending standard frequency change between two tones, the memory trace must integrate the frequency information of at least two successive tones, i.e. over a period 450 ms (the regular onset-to-onset ISI of the present study), that is, the relationship between these tones is encoded in sensory memory over time.

Third, the present data might also provide preliminary evidence for the possible extrapolatory nature of sensory memory.[3] In addition to merely representing information about past events, this memory system might also anticipate, that is, create expectancies for incoming stimuli in immediate future. The MMN recorded here might rather reflect the discrepancy between expectancy for a descending frequency change created in sensory memory and the sensory input from an ascending frequency change than just the present sensory input violating the sensory representation of preceding stimuli.

Conclusion

Besides physical stimulus properties, information about invariant stimulus features from physically changing acoustical environment is also generalized and integrated over time to the neural representations of sensory memory as reflected by the MMN.

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