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Publication Date

DOI

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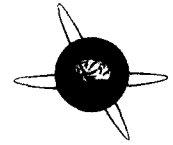
Sequential changes of auditory processing during target detection: motor responding versus mental counting

A. Starr*, T. Aguinaldo, M. Roe, H.J. Michalewski

Department of Neurology, University of California, Irvine, CA 92697-4290, USA

Abstract

Brain potentials evoked to non-targets in an auditory target detection task changed in amplitude, duration, polarity, and scalp topography as a function of position in the stimulus sequence relative to the target. (1) A negative prestimulus readiness like-potential, or RP, the poststimulus N100, and a late slow wave to non-targets immediately after the target were reduced in amplitude compared to non-targets immediately before the target. The amplitudes of these potentials after the target then increased in size as a linear function of the number of non-targets in the sequence. (2) The amplitudes of the positive components, P50 and P200, were larger to non-targets immediately after the target than to non-targets immediately before the targets. P50 amplitude then decreased to subsequent non-targets in the sequence in a linear manner; P200 amplitude was reduced equivalently to all subsequent non-targets. (3) The duration of the P200 component could extend into the time domain when the P300 to targets would occur. The P200 component to non-targets was therefore designated 'P200/300'. The duration of the P200/300 component was shorter to non-targets immediately after the target than to non-targets immediately before the targets. P200/300 duration then extended in a linear manner to subsequent non-targets in the sequence and approached the peak latency of the P300 evoked by targets. (4) The anterior/posterior scalp distribution of P50 and the polarity of the late slow wave to non-targets changed as a function of non-target position in the sequence. The subject's response to the targets (button press or mental count) influenced these sequential effects. Linear trends for sequence were present in the press but not the count conditions for the amplitude of the RP, N100, and P300; linear trends for P50, P200/300 duration, and the late slow wave were found in both the press and count conditions. Reaction time was speeded as a function of the number of preceding targets. These dynamic changes in the processing of auditory signals were attributed to an interaction of attention and the subjective expectancies for both the appearance of a target stimulus and the requirement to make a motor response. © 1997 Elsevier Science Ireland Ltd.

Keywords: Stimulus sequence; Auditory evoked potentials; Response preparation

1. Introduction

In target detection paradigms, it is typical for brain potentials to targets and to non-targets to be separately averaged (e.g. Polich and McIsaac, 1994). One assumption made in this averaging procedure is that brain activity to targets and to non-targets does not change during the stimulus sequence. Such an assumption is probably appropriate for studies of sensory processes at the level of receptors and initial portions of the sensory pathways as in the short latency auditory brainstem potentials, or in the short latency components of somatosensory evoked potentials (Starr, 1978). In contrast, the long latency cortical components to both targets and to non-targets in a target detection task can vary considerably in latency from trial to trial (Michalewski

et al., 1986) or in amplitude depending on the preceding stimulus (Squires et al., 1976). These alterations in evoked potential components to identical stimuli presumably reflect changes of neural processing initiated during the stimulus sequence.

Sorting and computing averages to subgroups of targets or non-targets based on the order of the immediately preceding stimulus sequence can reveal significant differences on measures of sensory (N100, P200) and cognitive (P300) potentials, and even for the potentials that precede the stimulus (slow negative shift) (e.g. McCarthy and Donchin, 1976; Squires et al., 1976; Hermanutz et al., 1981; Sams et al., 1984; Verleger, 1987; Hirata and Lehmann, 1989). Further study of the negative shift that precedes a stimulus may provide insight into mechanisms acting on the subsequent evoked potentials throughout the stimulus sequence. For instance, changes in the negative potential with stimulus

* Corresponding author. Tel.: +1 714 8246088; fax: +1 714 8242132.

sequence appeared to be particular for motor response expectancy since the negative potentials were evident when subjects made a button press to the target but not when they kept a mental count of the target (Starr et al., 1995). This prestimulus negativity between trials in the stimulus sequence was considered a readiness-like potential or RP in keeping with other studies of prestimulus negative shifts accompanying motor response preparation (e.g. Deecke et al., 1969; Donchin et al., 1972; Rohrbaugh et al., 1976). Moreover, a significant correlation has been found between the amplitude of the slow negative shift and the subsequent reaction times (Ortiz et al., 1993; Starr et al., 1995), whereas the relationship of reaction time speed and changes in other evoked potential components was variable (Verleger, 1987).

Brunia and colleagues (Brunia, 1993; Chwilla and Brunia, 1991) have proposed that negative shifts preceding stimuli requiring a motor response are actually comprised of several components including (1) a contingent negative variation (CNV), reflecting expectancy; (2) a premotor readiness potential (RP) accompanying motor preparation; (3) and a stimulus preceding negativity (or SPN) reflecting attention to the stimulus in preparation for a motor response. The relationships of the factors governing prestimulus negative shifts to other cognitive processes that affect the amplitude and/or latency of stimulus evoked brain potentials, including for example, attention (Hillyard et al., 1973; Picton and Hillyard, 1974), habituation (Lammers and Badia, 1989), and dishabituation (Megela and Teyler, 1979) are not known.

In this paper, we have examined the relationship between prestimulus negative potentials (i.e. a readiness-like potential), reaction time, and the subsequent stimulus evoked potentials into subgroups of non-target stimuli sorted according to position in the sequence. The hypothesis examined was that both the sensory and cognitive processes involved in detecting and responding to the infrequent and random appearance of the target stimuli become organized by subjective expectancies based on the immediately preceding stimulus sequence and the response instructions. We have, therefore, made a systematic analysis of the potentials (P50, N100, P200, P300, late slow wave) to non-targets both preceding (readiness potential) and following target stimuli as a function of the response required (a button press, mental count) to the detection of a target. The results demonstrated that all of the evoked potential components examined were affected by the position of the non-target in the stimulus sequence and that some of these changes were differentially affected by the requirement to make a motor compared to a mental response.

2. Materials and methods

2.1. Subjects

The subjects were 13 young individuals (nine women,

four men), aged 27–48 years (mean = 37.3) without a history of neurological problems or psychiatric illness. Eleven of the thirteen subjects were right-handed and two were left-handed. Individuals were recruited, signed informed consent forms and were tested following University guidelines for approved projects involving human subjects.

2.2. Target detection task

Subjects were asked to detect each occurrence of an auditory 'high' pitched target note (D, one octave above middle C) occurring infrequently ($P = 0.2$) among 'low' pitched notes (middle C) in two conditions: press and count. For the press condition, subjects were instructed to listen to the stimulus sequence and to press a reaction time button using the thumb of the dominant hand as soon as they heard the high-frequency target note. In the count condition, the subjects were told to listen to the stimuli and to 'make a mental count' of the target as soon as they heard the high-frequency note. The response button was removed in the count condition. The notes were generated by a microcomputer and consisted of the fundamental and its harmonics. The auditory signals (250 ms duration, 60 dB nHL intensity) were presented by earphones every 2.0 s. The high-pitched target notes were randomly interspersed among the low-pitched notes with the constraint that two targets could not occur in succession. Each test condition consisted of 300 stimuli comprised of 240 frequent low notes and 60 target high notes. The order of presentation of the press and count conditions was counterbalanced and the same stimulus sequence was used for all subjects. The subject sat in a comfortable chair in a sound-attenuating chamber and was instructed to look at a fixation spot straight ahead. Subjects were asked to refrain from blinking during the test period.

2.3. Brain and muscle (EMG) potential recordings

Disc electrodes were placed over Fz, Cz, Pz, C3', and C4' (C3' and C4' were located 1 cm anterior to C3 and C4, respectively) and were referenced to linked electrodes at A1 and A2. The electrode over the dominant hemisphere (the left hemisphere in 11 subjects and the right hemisphere in two subjects) was called the $C^{dominant}$ electrode; the electrode over the non-dominant hemisphere (the right hemisphere in 11 subjects and the left hemisphere in two subjects) was called the $C^{non\text{-}dominant}$ electrode. Eye blinks were monitored by electrodes situated above and at the lateral lower lid of the right eye. Muscle potentials (EMG) of the thenar muscles of the dominant hand were recorded between an electrode over the belly of the opponens muscle of the thumb and an electrode over the tendon at the metacarpophalangeal joint of the thumb. The brain potentials were amplified 200 000 times and the eye potentials were amplified 100 000 times and both were filtered (3 dB down) between 0.01 and 100 Hz (time constant = 16 s). Skin impe-

dances measured between scalp sites were below 3.0 kΩ. The muscle potentials were amplified 20 000 times and were filtered (3 dB down) between 30-10 000 Hz.

2.4. Computer interface

The microcomputer that controlled the stimulus sequence also recorded reaction times in the press condition. A second computer digitized the brain and muscle potentials. The digitized activities (256 points/channel) of the session were stored in computer memory and later saved as individual trials to disk for off-line analysis. The analysis epoch was 1.44 s (dwell = 5.625 ms) and included a prestimulus period of 0.76 s duration. This dwell time could have affected the sampling of the higher frequency components (>60 Hz) of the brain potentials. The data from the EMG potentials were used to monitor button press activity and were not used in the analysis. Reaction times were derived from the activation of a microswitch.

2.5. Averaged potentials

Averaged brain potentials were computed from the individual stored files for each condition. The type of stimulus (infrequent targets or frequent non-targets) and the reaction time for the button press were included in each file. The digitized waveforms from each trial were displayed and examined on the computer screen. Trials were sorted and averaged by stimulus type (targets or non-targets). Each channel average was baseline corrected to remove any DC offset. Accuracy in the press condition was recorded by the microcomputer; in the count condition, accuracy was based on the number of targets counted by the subject. Error rates were approximately 1–2% for press and count conditions.

Only those trials with correct responses in the press condition (button press for high notes and no button press for frequent low notes) were included in the averages. If a trial was compromised by potentials from eye blinks (up to 10% of the trials), a compensatory adjustment of the potentials was made. An algorithm, modified after Gratton et al. (1983), used the recorded eye channel as a template for subtraction of a scaled potential from each electrode site. The adjusted potentials were examined and added to the average if the blink artifact was removed. The validity of this adjustment procedure was examined in several subjects by comparing the averages which excluded trials because of eye-movement artifact to the averages with trials which compensated for the contribution of eye-movement artifact. Superimposition of the potentials averaged by the two methods did not reveal prominent differences.

Averaged potentials to non-targets were computed as a function of position in the sequence relative to the targets for each subject. Non-targets immediately preceding the target were designated as T − 1 (before) and non-targets immediately following the target as T + 1 (after). Note

that the composition of the T − 1 averages (i.e. non-targets immediately before the target) was made independent of the number of preceding non-targets in the sequence. Therefore, the non-targets were also sorted and averaged according to the relative position following the target (i.e. T + 2, T + 3... T + 7). The number of trials in each category available for analysis varied as a function of position in the stimulus sequence. The trials which comprised T + 6 and T + 7 groups were combined into a T > 5 grouping to make the number of trials comparable to the T + 4 and T + 5 groups. The trials which made up the T > +7 group were not included in the analysis. The four non-targets at the start of the stimulus sequence were not analyzed since no target had yet occurred. Trial counts for non-target position in the sequence relative to the target were: T + 1 (60 trials), T + 2 (57 trials), T + 3 (42 trials), T + 4 (29 trials), T + 5 (21 trials), T + 6 (14 trials), T + 7 (8 trials), and >T + 7 (5 trials).

Mean reaction time to targets was computed as a function of the number of preceding non-targets in the press condition. Sixty trials were available for analysis. The analysis was restricted to the T + 3, T + 4, T + 5, and T > 5 (the latter consisting of the combined T + 6 and T + 7 groups). There were too few targets in other positions in the sequence to include in the analysis. Trial counts for target position in the sequence relative to the immediately preceding target were: T + 1 (0 trials), T + 2 (2 trials), T + 3 (15 trials), T + 4 (13 trials), T + 5 (9 trials), T + 6 (7 trials), T + 7 (6 trials), T + 8 (4 trials), T + 9 (3 trials), and T + 10 (1 trial).

2.6. Data reduction and analysis

For measuring amplitudes and latencies of the various components and slow potential shifts in the target detection tasks, the averaged potentials were filtered in two ways (Fig. 1). Firstly, to determine the peak latencies and amplitudes of sensory and cognitive components the bandpass filter was set to attenuate the slow potential shifts (1–16 Hz) using Fast Fourier Transform (FFT) and Inverse Fourier Transform (IFT) procedures. The measures made of the brain potentials included:

1. The maximum amplitude of P50, N100, P200, and P300 relative to the average amplitude in a 751.25 ms baseline period prior to the stimulus.
2. The peak latencies of P50, N100, and P200 from stimulus onset were determined for the T − 1 (before) and T + 1 (after) averages.
3. The duration of the P200/300 component was defined at the latency that the descending or negative going portion of the component reached an asymptote or levelled off.
4. The amplitude of the P300 component to non-targets was estimated at the peak latency of the P300 to targets for that subject.

Secondly, the amplitudes of the slow waves (the RP and the late slow wave) were measured in a 300 ms window

(average amplitude) after the waveforms were low-pass filtered (0.01–3.1 Hz, 12 dB down, using a zero-phase-shift digital filter) relative to the average amplitude in a 120 ms period at the beginning of the averaged epoch. The window for the RP was positioned between −300 ms and 0 ms (stimulus onset); the window for the late slow wave was positioned from +380 to +680 ms following stimulus onset.

Analyses of variance procedures for repeated measures were used to evaluate the measures of amplitude and latency from Cz. The effects of instruction (press, count) and non-target position relative to the target (before, after) were analyzed in a two-factor ANOVA (instruction × position). Separate analyses were conducted for the averaged amplitude of the slow negative prestimulus shift (or RP) and the amplitudes of the late slow wave, P50, N100, P200, and P300; separate analyses were used to evaluate P50, N100, and P200 latencies, and P200/300 termination.

Trend analysis was employed to evaluate non-target component measures as a function of stimulus sequence following the target. Tests for linear and quadratic trends were conducted separately for the press and count conditions when significant main effects for sequence (T + 1...T > 5) were found. A similar analysis of trend was performed on the reaction times to the targets as a function of the position of the target relative to the immediately preceding target (T + 3...T > 5). Regression procedures were applied to provide an index (r^2) of fit of the means from significant trends.

The analyses of the scalp distribution were performed on the combined measures for the press and count conditions, since no significant overall differences due to instruction were revealed for component measures (three-factor ANOVA, instruction [press, count] × position [before, after] × electrode [all sites]). Separate ANOVAs were performed to evaluate amplitude changes along the midline and between lateral sites. For the analysis along the midline, the factors were non-target position (T − 1, T + 1) and electrode (Fz, Cz and Pz); for the lateral sites, the factors were non-target position (T − 1, T + 1) and electrode ($C^{dominant}$, $C^{non-dominant}$). Results from ANOVAs employed the Greenhouse-Geisser adjustment when appropriate and differences at $P < 0.05$, or better, were considered significant. Post-hoc differences among the means were carried out using the Newman-Keuls' procedure.

3. Results

3.1. Non-target potentials immediately preceding versus immediately following targets (T − 1 vs. T + 1)

The grand-averaged potentials to the non-targets immediately before (T − 1) and immediately following (T + 1) the targets from the Cz electrode are superimposed in Fig. 1 for both the press and count conditions. A segment of the stimulus sequence is shown above (A). The low- and high-

pass filtered traces (B and C, respectively) are presented separately to highlight changes in the short duration components with the low frequencies removed (bandpass 1.0–16 Hz); for comparison, the slow potential shifts are shown (D) with the short duration components removed (filtered between 0.01 and 3.1 Hz). The measures of the components are shown graphically in Fig. 2. The corresponding mean values are presented in Table 1.

3.1.1. Readiness potential (RP)

An overall sequence effect ($P < 0.01$) indicated that the slow negative potential was larger to non-targets before (T − 1) than after (T + 1). Since the average amplitude of the RP in the count condition for T − 1 or T + 1 positions was not significantly different from baseline levels or zero (t-tests), the count and press conditions were analyzed separately (Fig. 2). In the press condition, the amplitude of the slow potential shift to non-targets immediately before (T − 1) the target was significantly larger than for the non-targets immediately after (T + 1) the targets ($P < 0.01$). For the count condition, no significant differences were indicated before or after the target.

3.1.2. P50

The amplitude of the P50 component was significantly smaller ($P < 0.001$) to non-targets immediately before the targets (T − 1) compared to non-targets immediately after the targets (T + 1) independent of instruction (press, count) (Fig. 2).

3.1.3. N100

The amplitude of N100 was significantly ($P < 0.003$) larger to non-targets immediately before the targets (T − 1) than to the non-targets immediately after the target (T + 1) in the press but not in the count condition (Fig. 2).

3.1.4. P200

The amplitude of P200 was significantly ($P < 0.001$) smaller to non-targets immediately before (T − 1) the targets than immediately following (T + 1) the targets in both the press and count conditions (Fig. 2).

3.1.5. P200/300 duration

The P200 component changed in duration with non-target position (Fig. 2). The measure used to quantify this change was the latency at which the descending or negative going portion of P200 reached an asymptote or levelled off. The label 'P200/300' was used for this component to denote that P200 duration could extend as far as 400 ms, a latency at which P300 appeared to targets. Overall, P200/300 duration was longer for the non-targets immediately preceding (T − 1) than immediately after the targets (T + 1) ($P < 0.001$). There was a significant position (before, after) by instruction (press, count) interaction ($P < 0.02$); in the press condition the duration of P200/300 before (T − 1)

EVOKED POTENTIALS TO NON-TARGETS IMMEDIATELY BEFORE AND IMMEDIATELY AFTER THE TARGET

BEFORE TARGET (T - 1) ————
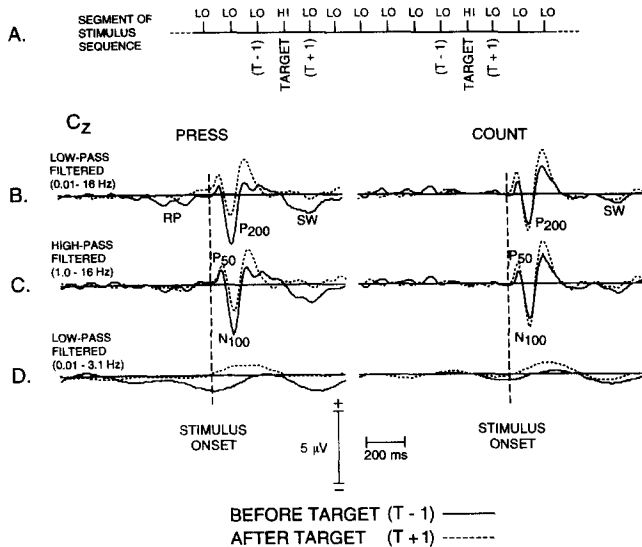AFTER TARGET   (T +1) --------

Fig. 1. A segment of the stimulus sequence represented at the top (A) shows how non-target evoked potentials were sorted as a function of position relative to the target, before (designated as T − 1) and after (T + 1). Below are the superimposed grand-averages recorded from Cz before, T − 1, (solid line) and after, T + 1, (interrupted line) the target for the press and count conditions. The averages are shown for different filter settings: (B) relatively wide-band low-pass filtered (0.01–16 Hz), (C) high-pass filtered (1.0–16 Hz), and (D) low-pass filtered (0.01–3.1 Hz). The short duration components are labelled by polarity (P or N) and approximate latency in ms, the slow negative shift before stimulus onset is labelled by readiness potential (RP), and the late slow wave peaking at approximately 550 ms is labelled by SW. Note the presence of an RP to T − 1 (before) in the press but not in the count condition, while an RP is absent to T + 1 (after) in both the press and count conditions. N100 amplitude is smaller to T + 1 than T − 1 in the press but not in the count condition. P200 amplitude is larger to the T + 1 than T − 1 in both the press and count conditions. P200/P300 duration is prolonged to T − 1 in the press but not in the count condition. A late slow (SW), particularly evident in the press condition, then follows to the T − 1 (before) but not the T + 1 (after) averages.

the target was later than after the target (T + 1); in the count condition, duration no significant P200/300 duration differences were indicated.

3.1.6. P300

No significant effects for non-target position (T − 1, T + 1), instruction (press, count) or interactions of these factors were found for the amplitudes of P300 (the amplitude of the P200/300 component at the peak latency of the target P300 for each subject).

3.1.7. Late slow wave

The negative late slow wave at Cz following the P200/300 component complex was significantly larger to non-targets immediately preceding the targets (T − 1) compared to non-targets immediately after the targets (T + 1) (P <

0.03; see Figs. 1, 2 and 3). Differences due to the effects of instruction (press, count) did not reach significant levels.

3.1.8. P50, N100, and P200 latencies

No significant effects for instruction (press, count), for sequence (before, after) or for the interaction of instruction and sequence were found for the latencies of P50, N100, or P200.

3.2. Trends of sequential changes of non-target potentials following the target (T + 1... T > 5)

In Fig. 3, the stimulus sequence relative to the target (i.e. T + 1...T > 6) (A), target potentials (B), and the potentials to non-targets sorted according to position in the stimulus sequence are shown (C and D) and the means of the component measures are graphed in Fig. 4. The low-pass filtered (0.01–16 Hz) traces (Fig. 3C) are compared to the high-pass filtered (bandpass 1.0–16 Hz) traces (Fig. 3D) to highlight the changes in the short duration components with the low
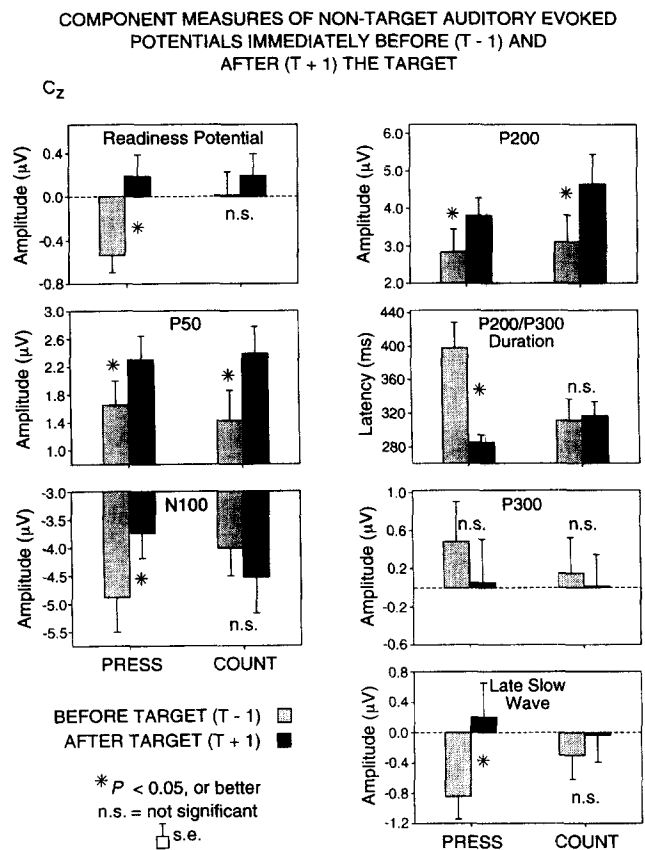
COMPONENT MEASURES OF NON-TARGET AUDITORY EVOKED POTENTIALS IMMEDIATELY BEFORE (T - 1) AND AFTER (T + 1) THE TARGET

BEFORE TARGET (T - 1) ▣
AFTER TARGET (T + 1) ■

$*P < 0.05$, or better
n.s. = not significant
⊡ s.e.

Fig. 2. Means and standard errors of component measures from Cz to non-targets immediately before (T − 1, light bars) and immediately after (T + 1, dark bars) the targets are illustrated for the press and count conditions. Amplitudes are shown relative to baseline levels. Significant differences (P < 0.05, or better) are indicated (*) for sequence (before, after) for the press and the count conditions; non-significant differences are indicated by n.s.

Table 1

Mean values of component measures for target and non-target potentials at Cz

Component/measure	Position in sequence							
	T − 1	Target	T + 1	T + 2	T + 3	T + 4	T + 5	>T + 5
RP (amplitude)								
Press	−0.66	−1.17	0.36	−0.17	−0.49	−0.85	−0.96	−1.47
Count	0.09	−0.33	0.21	0.20	−0.49	−0.52	−0.66	−0.04
P50 (amplitude)								
Press	1.66	2.00	2.31	1.94	1.66	1.35	0.88	1.19
Count	1.44	1.92	2.39	2.19	1.90	1.32	0.99	1.47
N100 (amplitude)								
Press	−4.88	−5.09	−3.72	−4.57	−5.13	−4.96	−5.65	−5.25
Count	−4.01	−4.40	−4.52	−4.17	−4.60	−4.76	−5.04	−5.15
P200 (amplitude)								
Press	2.84	3.26	3.68	2.87	2.62	3.28	2.89	3.08
Count	3.12	3.92	4.65	3.84	3.90	3.36	3.28	4.35
P300 (amplitude)								
Press	0.48	6.07	0.05	−0.25	−0.76	0.10	1.25	0.99
Count	0.14	6.86	0.00	0.29	−0.13	−0.55	−0.07	0.49
P200/300 termination (latency)								
Press	397	n/a	284	318	369	402	408	417
Count	331	n/a	318	331	363	380	366	387
Late slow wave (amplitude)								
Press	−0.86	0.75	0.20	−0.82	−1.30	−1.18	−0.82	−1.16
Count	−0.29	0.92	−0.03	−0.10	−0.82	−0.99	−1.12	−0.81
Reaction time								
Press	n/a	370	n/a	n/a	408	363	355	348

Component peak latency (ms) and peak or average amplitude (μV) are arranged as a function of instruction (button press or mental count of targets) and the position of non-targets in stimulus sequence relative to the target, e.g. first stimulus after target (T + 1), second (T + 2), etc.
n/a, not applicable.

frequencies attenuated. The corresponding mean values are given in Table 1 and the results for the analysis of trends for the press and count conditions (ANOVA) are provided in Table 2.

3.2.1. Readiness potential (RP)

The negative potential preceding stimulus onset increased in amplitude with the number of non-targets appearing in sequence. The change in amplitude of this negative shift showed a significant linear trend for the press ($r^2 = 0.87$, $P < 0.001$; see Fig. 4) but not for the count condition. A significant quadratic trend ($r^2 = 0.37$; $P < 0.025$) was indicated for the count condition.

3.2.2. P50

The P50 component decreased in amplitude as the sequence progressed in both the press and count conditions. The decrease followed a significant linear trend in both press ($r^2 = 0.87$, $P < 0.01$) and count ($r^2 = 0.75$, $P < 0.01$) conditions (Fig. 4).

3.2.3. N100

The amplitude of the N100 increased with a significant linear trend as the stimulus sequence progressed (T + 1...T > 5) in the press ($r^2 = 0.73$, $P < 0.01$) but not the count condition.

3.2.4. P200

No significant linear trends were indicated for the amplitudes of P200 in either the press or count conditions (Fig. 4). However, a significant quadratic trend was present in the count condition ($r^2 = 0.78$; $P < 0.01$).

3.2.5. P200/300 duration

The duration of the P200/300 was prolonged with stimulus sequence in a linear manner for both the press ($r^2 = 0.92$, $P < 0.001$) and count ($r^2 = 0.83$, $P < 0.01$) conditions.

3.2.6. P300

A significant linear trend was found for the amplitude of P300 for the press ($r^2 = 0.50$, $P = 0.02$) but not for the count condition.

3.2.7. Late slow wave

The amplitude of the late slow wave increased with the number of non-targets that appeared in the sequence. The change in amplitude of the late slow wave showed a significant linear trend for both the press ($r^2 = 0.43$, $P < 0.01$) and count ($r^2 = 0.67$, $P < 0.001$) conditions (Fig. 4).

3.2.8. Reaction time, T + 3... > T + 5

Reaction times to targets shortened as a function of the number of immediately preceding non-targets in the se-

quence (Fig. 5). Significant linear ($r^2 = 0.80$, $P < 0.01$) and quadratic ($r^2 = 0.98$, $P < 0.025$) trends were indicated for RT as a function of target position in the stimulus sequence.

3.3. Scalp distribution of components and stimulus position

The distribution of the evoked potential components over the scalp for Fz, Cz Pz $C^{dominant}$ and $C^{non-dominant}$ sites for targets and for non-targets before (T − 1) and after (T + 1) are shown in Fig. 6 for the press condition. A summary of the results along the midline and the lateral sites for non-targets is shown in Table 3.

Components with a frontal prominence included P50 and

the late slow wave. A marginal ($P < 0.08$) sequence by electrode interaction for P50 and a significant ($P < 0.001$) sequence by electrode interaction for the late slow wave were indicated. The P50 to non-targets had a frontal prominence in the T + 1 position whereas P50 did not differ in amplitude along the midline electrodes for the T − 1 position. The late slow wave in the T − 1 position was negative at the three midline sites with a Fz prominence; in contrast, for the T + 1 position the late slow wave distribution was slightly positive at Fz, isoelectric at Cz, and slightly negative at Pz. Components with a significant overall central-parietal prominence included P200 ($P < 0.001$) and the readiness potential ($P < 0.001$). A significant overall cen-
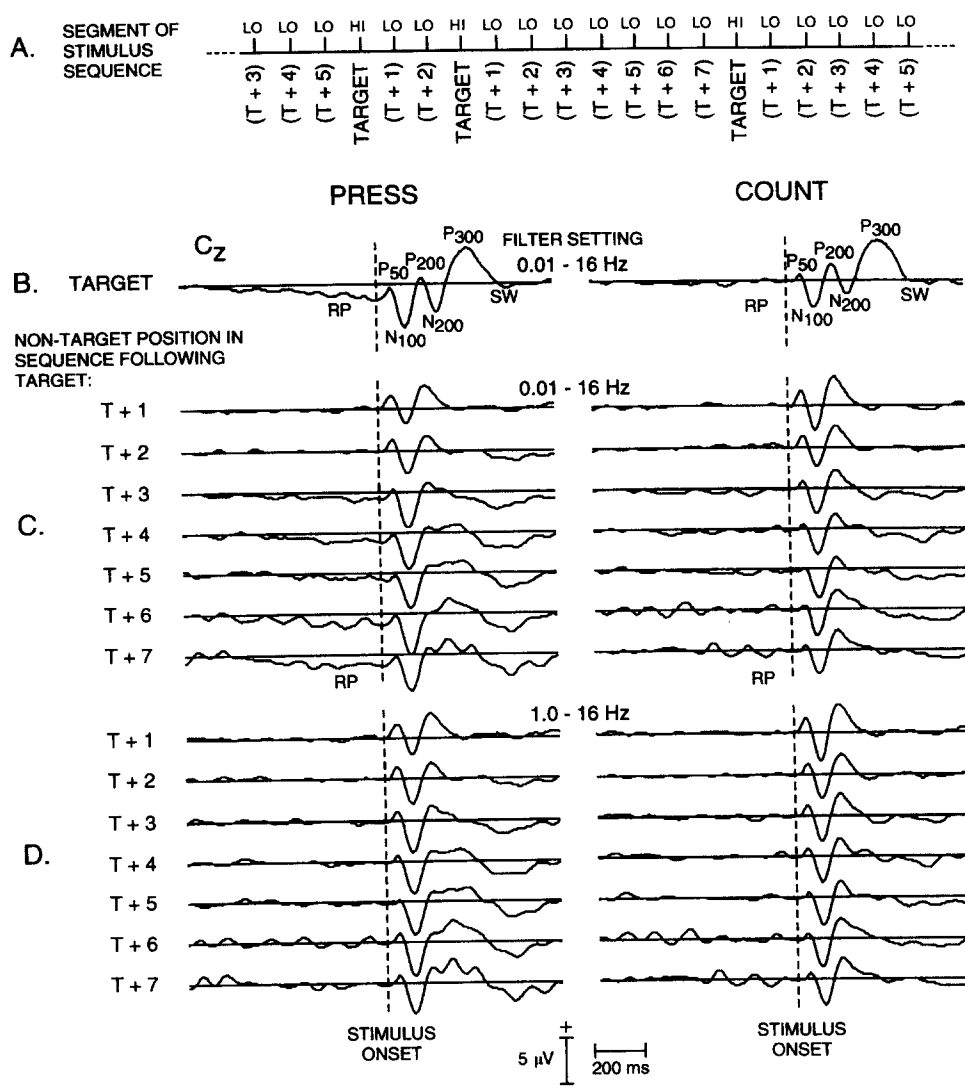

Fig. 3. A portion of the stimulus sequence at the top (A) shows how non-targets were sorted according to position after the targets (T + 1, T + 2... T + 7). The grand averaged potentials below are derived from Cz. In (B), averages to targets (0.01– 16 Hz) are shown with the components identified as in Fig. 1. In (C) and (D), the grand-averages of non-targets were sorted according to position following targets. The relatively wide-band low-pass filtered (0.01–16 Hz) averages (C) and the high-pass filtered (1.0–16 Hz) averages (D) are shown in the figure. The potentials for the press condition are on the left and for the count condition on the right.

Table 2

Summary of the analysis of trends for non-target position following targets, T + 1... T>5, for linear and quadratic functions for the press and count conditions at Cz

Component/measure	Linear		Quadratic	
	Press	Count	Press	Count
RP	*	n.s.	n.s.	*
P60	*	*	n.s.	n.s.
N100	*	n.s.	n.s.	n.s.
P200	n.s.	n.s.	n.s.	*
P200/P300 duration	*	*	n.s.	n.s.
P300	*	n.s.	n.s.	n.s.
Late slow wave	*	*	n. s.	n.s.
Reaction Time (RT)	*	n/a	*	n/a

Trend results are shown for reaction time (RT) in the press condition.
*, Significant ($P < 0.05$, or better) linear and/or quadratic trends; n.s., not significant; n/a, not applicable.

tral distribution was found for N100 amplitudes ($P < 0.005$).

Components that lateralized to the dominant hemisphere ($C^{dominant} > C^{non-dominant}$) included P50 ($P < 0.03$) and P200 ($P < 0.01$). The late slow wave lateralized ($P < 0.05$) to the non-dominant hemisphere ($C^{non-dominant} > C^{dominant}$). No significant amplitude differences between lateral sites were indicated for N100 or RP.

4. Discussion

The results of this study demonstrated that component measures of evoked potentials to non-targets in a target detection task vary as a function of both the position of the non-target in the stimulus sequence and the type of response the subject made to targets. The amplitude of the stimulus preceding slow negative shift (readiness potential) and N100 increased and the duration of the P200/300 component lengthened with non-target position following the target when subjects pressed a response button to targets. These sequential changes were either absent (RP, N100) or reduced in extent (P200/300 duration) when subjects kept a mental count of the targets. In contrast, the amplitudes of P50, P200, and the late slow wave with non-target position did not differ between the press and count conditions. For some components the site of scalp maximum (P50) or polarity (late slow wave) also varied with stimulus sequence independent of response instruction (press, count) compatible with a change in generator sources. While there was an equivalent number of non-targets in the sequence analysis before (T − 1) and after (T + 1) the target, the non-target potentials averaged after the target (i.e. T + 2, T + 3...T + 7) were based on an unequal number of trials. These averages were subject to differences in the signal-to-noise ratio which may have contributed to increased component variability and affected the analyses of component measures.

The results from prior studies of stimulus sequence and component amplitudes in target detection during mental counting of the targets have been inconsistent. Both N100 (Hermanutz et al., 1981) and P300 (Squires et al., 1976) to non-targets have been described as increasing in amplitude as a function of the number of immediately preceding non-targets in the sequence. Verleger (1987), however, found that changes in P300 amplitude with stimulus sequence differed for targets and non-targets whereas N100 changes were similar for the two stimulus types. Hirata and Lehmann (1989) showed that both the amplitude and scalp distribution of N100 and P200 differed to non-targets immediately preceding versus immediately following the target. Sams and colleagues (1984) found that the amplitude of the mismatch negativity but not the amplitude of the N100 evoked by non-targets changed as a function of the position of the non-target relative to the target. It is apparent from these papers that evoked potential components can change as a function of stimulus sequence during mental counting of targets but that the direction of the change is not consistent among laboratories. The results in the present paper and in Starr et al. (1995) indicate that changes of auditory signal processing reflected by measures of the

COMPONENT MEASURES OF NON-TARGET AUDITORY EVOKED POTENTIALS AS A FUNCTION OF STIMULUS SEQUENCE
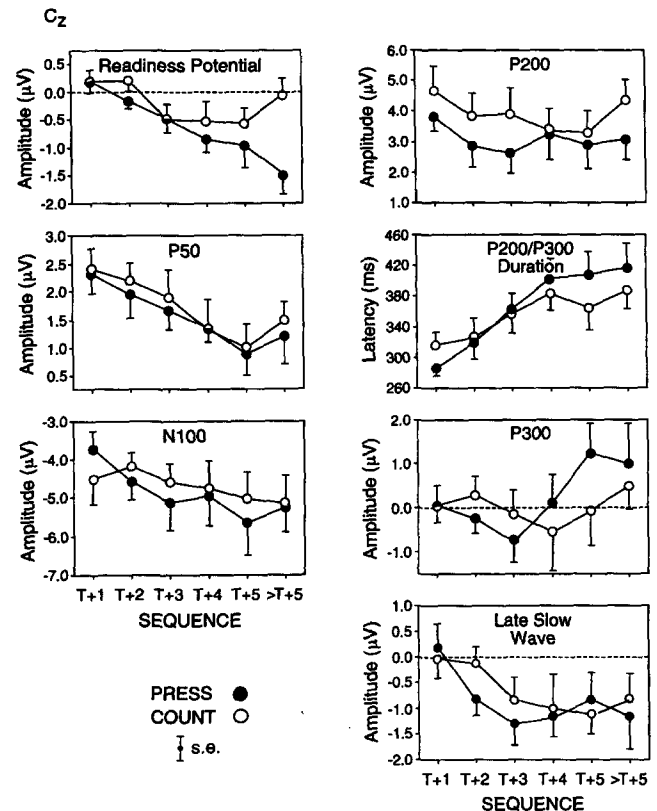

Fig. 4. Means and corresponding standard errors of component measures from Cz to non-targets plotted as a function of position in the stimulus sequence following the target (T + 1... T > 5). The presence of significant linear and quadratic trends are summarized in Table 2.

Table 3

Scalp distribution of auditory evoked potential components to non-targets for sequence (before, after) along midline (Fz, Cz, and Pz) and lateral sites[a] (C3', C4')

Component/ measure	Electrode sites			
	Midline		Lateral	
	Before	After	Before	After
RP	−Pz>Fz	−Pz>Fz	n.s.	n. s.
P50[b]	n. s.	Fz, Cz>Pz	C3' = C4'	C3'>C4'
N100	Cz>Pz	Cz>Pz	n.s.	n.s.
P200[c]	Cz>Fz; Pz>Fz, Cz>Pz	Cz, Pz>Fz	C3'>C4'	C3'>C4'
Late slow wave[d]	−Fz>−Pz	Fz> − Pz	C4'>C3'	C4'>C3'

Significant (P < 0.05, or better) midline and lateral asymmetries are noted (>).
n.s., not significant.
[a]The electrode over the dominant hemisphere (the left hemisphere in 11 subjects and the right hemisphere in two subjects) was called the C[dominant] electrode (C3'); the electrode over the non-dominant hemisphere (the right hemisphere in 11 subjects and the left hemisphere in two subjects) was called the C[non-dominant] electrode (C4').
[b]Marginal sequence by electrode interaction (midline), P < 0.08.
[c]Sequence by electrode interaction (midline), P < 0.004.
[d]Sequence by electrode interaction (midline). P < 0.001.

amplitude or latency can also be influenced by type of response required to the target (press a button, make a mental count).

4.1. Processes acting to modulate evoked potentials

1. Expectancy for a stimulus has been shown to affect both evoked potentials and RT. Matt et al. (1992) demonstrated that P300 amplitudes to targets increased and RTs shortened as expectancy increased. In the present study, the gradual broadening of the P200/300 component to non-targets with stimulus sequence into the latency period when P300 usually occurs is compatible with the premature classification of the non-target as a target based on a subjective ex-pectancy for the impending occurrence of the target. Garcia-Larrea et al. (1992) noted this component (called P250) was not present when subjects were not engaged in the task. The incremental changes of P200/300 duration are reminiscent of the gradual shortening of RT that occurred with stimulus sequence (Remington, 1969), compatible with changes in the subjective expectancy for the appearance of the target. The P200/300 to non-targets in the present study appears to be different than the P300 evoked by 'no-go' stimuli des-cribed by Hillyard et al. (1973) in a detection task both by latency and scalp distribution differences.

Expectancy has been experimentally modelled in forewarned RT experiments in which a slow negative potential shift, the contingent negative variation or CNV (McCallum, 1988), begins at the time of a warning signal (S1) and returns to prestimulus baseline levels when the imperative

stimulus (S2) appears. The CNV is observed regardless of whether the subject makes a mental or motor response to the S2 stimulus (Donchin et al., 1972; Ruchkin et al., 1986; Frost et al., 1988). Ruchkin has argued that the presence of this negative potential preceding the S2 during mental responding to S2 is an indicator of readiness to respond, albeit mentally. In contrast, Gaillard (1977, 1986) has argued that the negative potential immediately preceding S2 in the CNV reflects a motor response expectancy since CNVs are smaller with mental versus motor response preparations and are also smaller with slow compared to fast responses.

The negative shift preceding both target and non-target stimuli in the present experiments is present when a button press to the targets is required but is absent during a mental count of the same targets. We have labelled this negative shift a readiness-like potential (RP) to emphasize its origin in premotor processes. This RP-like potential may be considered as part of a CNV that develops between adjacent stimuli in the sequence. Thus, the late slow wave that follows each non-target stimulus may be the initial 'O' or orienting wave of the CNV, and the RP may represent the late 'E' or expectancy wave preceding the subsequent stimulus in the sequence (McCallum, 1988).

A systematic pattern of slow potential shifts intervening between adjacent stimuli could be identified in the present experiments (see Figs. 3 and 4). A late slow wave becomes evident beginning with the third non-target in sequence following the target (T + 3). The slow wave is of negative polarity and prominent frontally. It is followed by a RP before the next stimulus in sequence (T + 4) which is negative and prominent parietally. Both of these slow potential shifts then increase in amplitude with successive non-targets in the sequence. This pattern of slow potential shifts is altered with the appearance of the target (see Fig. 5). The late slow wave following the target becomes of positive polarity in the parietal region and is not succeeded by an RP before the next non-target (T + 1) in the sequence.

We suggest that expectancy for motor response is a major

REACTION TIME (RT) TO TARGETS SORTED
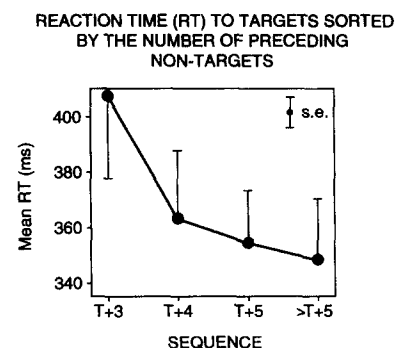BY THE NUMBER OF PRECEDING
NON-TARGETS

Fig. 5. Mean reaction time (RT) in the press condition to targets as a function of target position in the stimulus sequence relative to the immediately preceding target (T + 3... T > 5). There were no trials with a T + 1 position and only two trials with a T + 2 position.

SCALP DISTRIBUTION OF THE EVOKED POTENTIALS TO TARGETS AND NON-TARGETS (BEFORE, AFTER) IN THE PRESS CONDITION

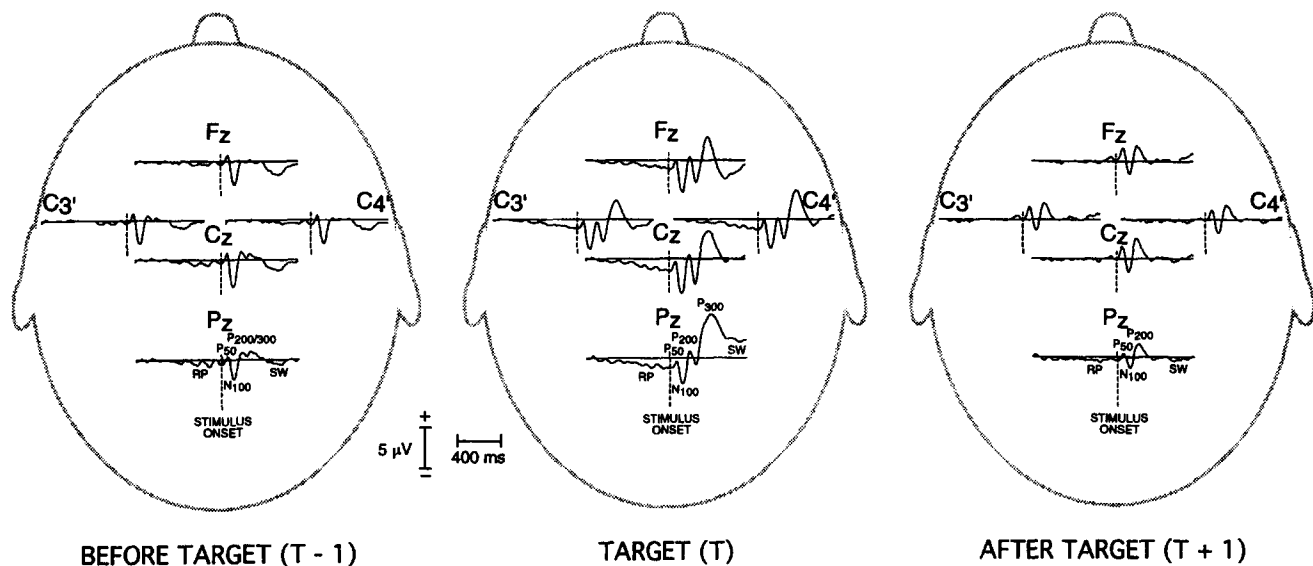BEFORE TARGET (T - 1)   TARGET (T)   AFTER TARGET (T + 1)

Fig. 6. Grand averages of the relatively wide-band low-pass filtered (0.01–16 Hz) auditory evoked potentials to the non-targets before (T − 1) the target, to the targets (T), and to the non-targets after (T + 1) the target arranged by scalp recording site for the press condition. Table 3 contains a summary of the significant amplitude differences along the anterior/posterior and lateral scalp dimensions for the various components.

factor modulating many of the evoked potential components including the RP, the N100, and the amplitude of the P300. The slopes of the functions relating the amplitudes of these components to stimulus sequence are characterized by significant linear trends only when a motor response to the targets is required. RTs to targets preceded by varying numbers of non-targets in sequence are also characterized by incremental changes but the function has a better quadratic than linear solution. The definition of these sequential trends (linear and quadratic) for evoked potential components and RTs reveals the presence of graded mechanisms modulating auditory signal processing during motor response preparation. These processes appear to be initiated after a target stimulus and have increasing influence upon each succeeding stimulus in the sequence before terminating when the next target appears and a motor response is made.

2. Attention is a mechanism that could contribute to changes of auditory processing of non-targets as a function of position in the stimulus sequence. The N100 component of auditory evoked potentials has been shown to increase in amplitude when attention is directed to the appropriate stimulus (Hillyard et al., 1973). This N100 effect is present when the task is difficult requiring considerable attention for its solution (Hillyard et al., 1973) and is absent when the task is relatively easy (Smith et al., 1970). The overall levels of attention required for the press and count conditions in the relatively easy target detection tasks are probably quite similar since the N100 in grand-averages to targets or non-targets do not differ in amplitude as a function of response requirement (Starr et al., 1995; Picton and Hillyard, 1974)

and show only slight differences in scalp distribution (Barrett et al., 1987) or change in amplitude only after repeated testing (Lew and Polich, 1993). The modulation of attention in the period between targets in the press but not the count condition could account for the gradual increase of N100 to non-targets found in the press condition in this study. This possibility could also account for the prolongation of P200/300 which was significantly longer during the press than the count condition. If the modulation of attention were to be a mechanism accounting for the observed changes of N100 and P200/300 components, it would be a specific for these components, since other components (e.g. P50 and the late slow wave) changed equivalently for both press and count conditions.

3. Gating accompanying both the preparation and the act of movement can be accompanied by an attenuation of sensory processes occurring both before and during the motor activity (Starr et al., 1969; Starr and Cohen, 1985). Gating in the auditory system has been shown to be due to both an attenuation of acoustic input accompanying movement-related contractions of middle ear muscles (Carmel and Starr, 1963) and to changes in central auditory pathway processing (Starr, 1964; Tapia et al., 1987). We do not consider gating to be a mechanism accounting for the attenuation of any of the components defined in this study. For instance, an attenuation of N100 follows the motor response to targets and requires 5–10 s before amplitudes are restored, a time period beyond the ms range usually attributed to gating (Starr and Cohen, 1985).

4. Finally, habituation/dishabituation processes have

been implicated in the changes of brain potentials to repetitive sensory stimulation that occur in the absence of any instruction to the subject to listen to or to respond to the stimuli (Megela and Teyler, 1979). Habituation usually requires a relatively long period of sensory stimulation whereas dishabituation is a transient process. While the transient increase in amplitude of the P200 to non-targets immediately following the target would be in keeping with the time course of dishabituation, there was no evidence of a preceding habituation of P200 amplitude. The gradual decrement of P50 with stimulus sequence and its increase after the target might be considered as being compatible with habituation/dishabituation processes, if these P50 changes were to occur when subjects were not actively engaged in listening to and classifying the stimuli.

5. General conclusions

Averages sorted by the position of the non-targets relative to the target, in combination with a relatively long prestimulus period and long-time constant recordings, revealed dynamic changes in brain activity during the target detection task. The time course of these changes suggests the involvement of several different cognitive processes, differing in time of occurrence. The mobilization of attention, independent of response requirement, can account for the sequential changes of P50, P200/300 duration, and the late slow wave. Expectancy for making a motor response can explain the changes of the prestimulus negative shift (readiness-like potential or RP), N100, and P300.

Lastly, a transient process active immediately after the target independent of response requirement could account for the changes of P200. Knowledge of how these different cognitive processes interact would further our appreciation of the relationship of changes of auditory processing to response selection.

Acknowledgements

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