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Authors

Golob, EJ
Pratt, H
Starr, A

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Preparatory slow potentials and event-related potentials in an auditory cued attention task

E.J. Golob^{a,b,*}, H. Pratt^{b,1}, A. Starr^{a,b}

^a*Institute for Brain Aging and Dementia, University of California, Irvine, CA 92697, USA*

^b*Department of Neurology, University of California, 154 Med Surge I, Irvine, CA 92697, USA*

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Abstract

Objectives: To examine reaction times and event-related potentials (ERPs) in an auditory cued attention task varying motor requirements, cue validity, and cue location.

Methods: Subjects ($n = 13$) listened to cue–target stimulus pairs. Verbal cues (monaural, binaural) indicated the ear to receive a target tone 1.5 s later. Cues correctly (valid) or incorrectly (invalid) predicted target ear, or were uninformative (neutral). In separate conditions subjects either responded by pressing one of two buttons, or did not respond to targets. ERPs for cues and targets (P50, N100, P200, late slow wave), and negative slow potentials between cues and targets were assessed.

Results: Target reaction times for valid cues were significantly shorter than for invalid cues, with intermediate values for neutral cues. When no motor response was required larger ERPs were seen to both cues and targets. Negative slow potentials had larger amplitudes before target presentation when subjects responded to targets; and were larger following neutral, vs. valid/invalid, cues. ERPs (N100, P200) to invalidly cued targets were significantly larger and a subsequent late slow wave was more positive, relative to validly cued targets.

Conclusions: Expectancy for targets begins shortly after cue presentation, and is affected by both motor requirements and the information content of the cue. ERP amplitudes to targets are modulated by the correspondence between cue information and actual target location. © 2002 Elsevier Science Ireland Ltd. All rights reserved.

Keywords: Selective attention; Readiness potential; Contingent negative variation; Processing negativity; N100

1. Introduction

Selective attention refers to the preferential processing of stimuli based on certain attributes, such as location, to the exclusion of other stimuli not sharing that attribute (Naatanen, 1990). Neurophysiological studies of attention in humans have employed event-related potentials (ERPs) to define when, and approximately where in the brain, attention-related neurophysiological changes are present. Studies of auditory selective attention show an enhanced, biphasic negative potential lasting from ~100 to 500 ms after stimulus presentation in response to tones delivered to the attended ear, relative to potentials from the same tones presented to the unattended ear (e.g. Hillyard et al., 1973; Woldorff and Hillyard, 1991; Woods, 1992; Teder-Salejari et al., 1999).

A limitation of this selective attention paradigm is that

behavioral measures cannot quantify the impact of attention because subjects only respond to targets in the attended ear. This limitation can be avoided in paradigms where a cue provides information, such as the location of an upcoming target (Posner, 1980). Cues can correctly predict target location (valid trials), incorrectly predict target location (invalid trials), or provide no information about target location (neutral trials). Cued attention tasks have the useful feature of behaviorally defining the costs and benefits of attention allocation because reaction times for valid, invalid, and neutral trials can be compared. Typically reaction time is shortest for valid trials, intermediate for neutral trials, and longest for invalid trials (Posner, 1980).

ERP studies of visual cued attention have demonstrated amplitude increases in early visual cortical components (P1, N1) for valid trials, relative to invalid trials (Eason et al., 1969; Mangun and Hillyard, 1991; Luck, 1995; Mangun, 1995). In an auditory cued attention experiment larger ERP amplitudes were seen for invalidly cued targets, relative to validly cued targets (Hugdahl and Nordby, 1994). A

* Corresponding author. Tel.: +1-949-824-2333; fax: +1-949-824-2132.
E-mail address: egolob@uci.edu (E.J. Golob).

¹ On sabbatical from the Technion, Israel Institute of Technology, Haifa, Israel.

late slow wave has also been observed that is more negative for validly cued targets (Schroger, 1993, 1994).

Pairs of cue and target stimuli have also been used to study neurophysiological changes associated with motor preparation and expectancy. In the contingent negative variation (CNV) paradigm subjects are sequentially presented two stimuli (S1 and S2), with S1 typically providing information about the upcoming S2 (Walter et al., 1964). A negative slow potential, (labeled the CNV), develops between S1 and S2. Amplitude of the CNV is sensitive to response requirements of the task, but the CNV is also present when subjects are not required to respond to S2 (Ruchkin et al., 1986). In studies of cued attention the presence of negative slow potentials between the cue and target has been noted but is typically not extensively studied (but see Harter et al., 1989; Wright et al., 1995).

The purpose of this study was to examine both ERP and slow potential changes in an auditory cued attention task. Three main variables were manipulated: (1) motor requirement (responding to target, no response to target), (2) cue location (central, peripheral), and (3) cue type (valid, invalid, neutral). Cue location was examined because, under certain conditions, peripheral cues induce prolonged reaction times to targets, a phenomenon called inhibition of return (Posner and Cohen, 1984; Klein, 2000). Potentials in response to the cue and targets, as well as slow potentials that developed during the interim period between cue and target presentation, were analyzed as a function of motor requirement, cue location, and cue type.

2. Subjects and methods

2.1. Subjects

Thirteen right-handed healthy normal volunteers (10 women and 3 men; mean age = 20.7, range 18–25) participated in this study. Subjects were students at the University of California, Irvine and received course credit for their participation. Experimental procedures were approved by the University of California, Irvine Institutional Review Board (Helsinki Committee), and all subjects signed an informed consent form.

2.2. Experimental procedure

Silver-silver-chloride surface electroencephalogram (EEG) cup electrodes were applied over the scalp at F₃, F_z, F₄, C₃, C_z, C₄, P₃, P_z and P₄ sites placed according to the 10/20 system (Jasper, 1958). A ground electrode was placed on the right forehead, and a linked mastoid configuration was used for reference. Eye movements were monitored using differential recording of electrodes placed above and below the left eye. Electrode impedances were ≤ 5 k Ω , typically around 3 k Ω , and were periodically checked during the experiment. Subjects sat in a comfortable armchair in an acoustically isolated chamber and held a

pushbutton response box. Insert earphones were fitted to the left and right ears. Subjects were instructed to avoid eye-movements and blinking as much as possible, and to keep their gaze on a fixed point in front of them during task performance. Each experimental session lasted no longer than 2 h.

2.3. Experimental paradigm

Subjects listened to pairs of auditory stimuli, the first of which was a word cue ('left', 'right' or 'go'), and the second a target tone that was presented to either the left or right ear. The inter-stimulus interval between the cue and target was 1.5 s, and the inter-trial interval (target to following cue) was 2.0 s. Cues were presented at ~ 50 dB nHL, and lasted ~ 300 ms, and target tones (1000 Hz, 5 ms rise/fall time, 100 ms duration) were presented at 45 dB nHL. Subjects were instructed that the words 'right' and 'left' preceding each tone served as a cue to indicate which ear the subsequent target tone would be presented to. The word 'go' served as a neutral cue that could be used to time the occurrence of the target, but did not provide information about the ear the target would be presented to. The target tone was equally likely to be presented in the left or the right ear when the word 'go' was presented.

Subjects were told that in most trials the cue will accurately predict the ear receiving the target tone, but there will be some trials when the cue is incorrect. Cues accurately predicted the ear that the target tone would be presented to in 60% of the trials ('valid cues'). In 20% of the trials the cue incorrectly predicted which ear would receive the tone ('invalid cues'). Thus, cues were fairly reliable predictors of target location and the required response, and subjects were encouraged to use the cue to prepare for target presentation. Neutral cues were presented in 20% of the trials. Cue types were randomly distributed within a run, and 50% of the targets were presented to each ear.

The experiment used a within subject 2×2 design, with factors of response type (motor, non-motor) and cue location (central, peripheral), described subsequently. There were a total of 200 trials (120 valid, 40 invalid, 40 neutral trials) in each combination of response type and cue location conditions. For the non-motor condition subjects were instructed to note which ear the tone was presented to, and that no motor response was required to the target tone. In 10% of the trials subjects were presented the word 'where?' 2.0 s after target presentation. Subjects then pressed one of two buttons (arranged left and right on the keypad) using the thumb of the hand ipsilateral to the ear that received the target. All subjects performed the non-motor condition first to eliminate potential carryover effects from the motor condition to the non-motor condition. In the motor condition the same instructions were given, with the exception that subjects were instructed to press the left or right button after each tone, according to the

ear that the tone was presented to. Instructions stressed speed, provided the subject responded accurately.

In visual cued attention studies cues are presented at a central fixation point or in the peripheral visual field. To study the effects of cue location in the auditory modality binaural and monaural cues were presented. To maintain consistent terminology with visual cued attention studies, binaural and monaural cues were labeled ‘central’ and ‘peripheral’ cues, respectively. Central and peripheral descriptors can apply to auditory stimuli because binaural and monaural stimuli are perceived as originating from midline and lateral locations, respectively. In the peripheral condition the words ‘left’ and ‘right’ were presented to the left or right ear, respectively. In the central condition the words ‘left’ and ‘right’ were presented binaurally. The neutral cue (‘go’) was always presented binaurally. Presentation order of the central and peripheral conditions was counterbalanced across subjects.

2.4. ERP recording and measurement

EEG and electro-oculogram (EOG) were continuously recorded (DC–100 Hz, digitized at 500 Hz) and stored for off-line analysis. Continuous records were epoched beginning 100 ms before cue presentation until 2 s after target presentation (3.6 s total epoch), and averaged after vertical eye-movement correction (modified after Gratton et al., 1983). Potentials were averaged separately for each combination of response type and cue location levels. Within each combination of conditions sub-averages were made for valid, invalid, and neutral cue trials. In all, 12 (2 response type $\times$ 2 cue location $\times$ 3 cue type) 9-channel averages were constructed from each subject.

Reaction time to targets in the motor condition was calculated relative to stimulus onset. Accuracy in the motor condition was measured as the percent of correct responses to target tones, and in the non-motor condition as percent of correct responses to queries that occasionally followed target presentation.

For slow potential measurements the waveforms were digitally filtered (DC–3 Hz Butterworth, 12 dB/oct slopes). Slow potential amplitudes were quantified relative to a 100 ms baseline preceding the cue. The 1 s period beginning 500 ms after cue presentation until target presentation was divided into four 250 ms windows, and the mean amplitude of each window was measured.

Transient ERPs (P50, N100, P200) were bandpass filtered (1–16 Hz, Butterworth 12 dB/oct slopes). Peak amplitudes of the transient ERP components (P50, N100 and P200) to the cues and targets were measured relative to the average amplitude of the 100 ms baseline preceding the stimulus (cue or target). Latency was defined at the peak amplitude of the component relative to stimulus onset (cue or target). Amplitude and latency of P50 were defined at the point of maximum positivity between 20 and 100 ms post-stimulus. N100 amplitude and latency were defined at

the maximum negativity between 50 and 150 ms, and P200 amplitude and latency at the maximum positivity between 100 and 200 ms. For targets, late slow wave activity following the P200 was analyzed after lowpass filtering (DC–16 Hz) using two window measures to quantify mean voltage from 200–399 to 400–599 ms after target presentation. Grand-averaged waveforms did not reveal a consistent P300 component.

The influence of eye position on the present results is uncertain. Subjects were instructed to fixate on a picture in front of them, and were corrected if they looked to the side, but individual trials were not rejected if the subject broke fixation. Thus, it is possible that eye position could have affected brain potentials elicited by auditory stimuli (Groh et al., 2001).

2.5. Statistical analysis

Behavioral (performance accuracy and reaction times) and electrophysiological (ERP peak amplitudes, latencies, and mean amplitudes of slow potentials) measures were subjected to a General Linear Model analysis of variance (ANOVA) with Greenhouse–Geisser correction for violations of sphericity. Analyses tested the effects of response type (motor/non-motor), cue location (central/peripheral), cue type (valid/invalid/neutral), and electrode site. A time window factor that quantified mean amplitudes across various timeperiods was included for slow waves. Statistical results were reported using the degrees of freedom before Greenhouse–Geisser correction, and *P* values <0.05 were considered significant.

3. Results

3.1. Behavioral results

For the motor condition a 2 (cue location) $\times$ 3 (cue type) repeated measures ANOVA showed no significant effects of cue location or cue type on performance accuracy (Fig. 1A). Reaction time was significantly affected by cue type (valid/invalid/neutral) [$F(2, 24) = 5.6$; $P < 0.02$] (Fig. 1B), being shortest to targets following valid cues, intermediate with neutral cues, and longest for invalid cues. Measures of mean reaction times showed the same pattern of results, with a significant effect of cue type [$F(2, 24) = 6.5$; $P < 0.02$] (Miller, 1988).

Accuracy in response to the ‘where’ cue in the non-motor condition was comparable to the motor condition (central cue: 97.6% correct; peripheral cue: 95.6% correct). Because there were fewer opportunities to respond in the non-motor condition (10% trials), accuracy was collapsed across cue types. A paired comparison *t* test showed no significant differences in accuracy for central and peripheral cues in the non-motor condition.

Fig. 1. Mean accuracy (A) and median reaction time (B) measures of the cued attention task when a motor response was required across experimental conditions. Error bars denote one standard error. Values are displayed separately according to the cue type preceding the target (valid/neutral/invalid) and cue location (central/peripheral).

3.2. Event-related potentials

Grand average waveforms for the entire analysis period in the motor condition with central cues are presented in Fig. 2. Cues and targets elicited 3 main components (P50, N100, P200). Between the cue and target stimuli a negative slow potential developed that progressively increased in amplitude until target presentation. The transient ERPs were compatible with the well-established fronto-central scalp distributions of the P50–N100–P200 complex, therefore only potentials from the C_z electrode in response to cues and targets were analyzed.

3.2.1. ERPs to the cue

Grand average potentials to cues are presented in Figs. 3

Fig. 2. ERPs spanning the entire period from 100 ms before onset of a valid binaural (central) cue to 1 s following the target tone to which the subject was to respond by pressing a button (motor condition). Waveforms are the grand averages across all 13 subjects, at the 9 scalp locations studied (DC–16 Hz). Vertical lines indicate cue and target presentation.

and 4. A 2 (response type) $\times$ 2 (cue location) $\times$ 2 (cue type: valid, neutral) ANOVA was performed. Because from the subject's perspective valid and invalid cues are identical at cue presentation, ('valid' and 'invalid' are defined by the correspondence between cue information and subsequent target location), the effect of cue type included only valid and neutral cues.

Fig. 3. Comparison of grand average ERPs to cues in motor vs. non-motor conditions. N100 amplitudes were significantly larger in the non-motor vs. motor condition. P200 amplitudes showed a similar effect, but only for neutral cues. Tracings are shown from the C_z site.

Fig. 4. Grand average ERPs to valid and neutral cues in all combinations of experimental conditions (motor/non-motor and central/peripheral). Waveforms are shown from the C_z site.

Response type (motor/non-motor): Potentials as a function of response type are shown in Fig. 3. N100 amplitude was significantly [$F(1, 12) = 9.6$; $P < 0.01$] larger in the non-motor ($-7.7 \pm 0.6 \mu V$) vs. the motor ($-6.5 \pm 0.7 \mu V$) condition. P200 amplitude also showed a significant effect of response type [$F(1, 12) = 13.7$; $P < 0.01$], with larger amplitudes in the non-motor (7.8 ± 0.8) vs. motor (6.6 ± 0.8) condition. The difference in P200 amplitudes for neutral vs. valid cues was larger for non-motor, vs. motor, conditions, indicated by a significant response type $\times$ cue type interaction [$F(1, 12) = 16.0$; $P < 0.01$] (Fig. 3). P50 amplitude was not affected by response type, and follow-up analysis using only valid cues also showed a non-significant effect of response type.

Cue location (central/peripheral): Latencies of the P50 [$F(1, 12) = 6.5$; $P < 0.03$], N100 [$F(1, 12) = 11.2$; $P < 0.01$] and P200 [$F(1, 12) = 8.2$; $P < 0.02$] components were significantly affected by cue location (Figs. 3 and 4). P50 latency was ~ 8 ms shorter for central (63.4 ± 2.4) vs. peripheral (71.6 ± 3.0) cues. N100 latency was ~ 11 ms shorter for central vs. peripheral cues (132.3 ± 2.5 vs. 143.2 ± 3.2 ms, respectively), and P200 latency was ~ 9 ms shorter for central vs. peripheral cues (225.2 ± 3.5 vs. 234.4 ± 2.7 ms, respectively). There were no significant effects of cue location for P50, N100, or P200 amplitudes.

Cue type (valid, neutral): Amplitudes of the N100 [$F(1, 12) = 9.3$; $P < 0.01$], and P200 [$F(1, 12) = 9.2$; $P < 0.01$] components were significantly affected by cue type. For both components amplitudes were larger for the neutral cue, relative to valid cues (Fig. 4). There was also a significant effect of cue type on P200 latency [$F(1, 12) = 5.3$; $P < 0.04$], with shorter P200 latencies for neutral cues (223.8 ± 3.3 ms), relative to valid (235.8 ± 4.1 ms) cues. There was also a significant cue type $\times$ cue location interaction [$F(1, 12) = 10.7$; $P < 0.01$], with larger P200 amplitude

Table 1
Event-related potentials to cues^a

Effect	Amplitude			Latency		
	P50	N100	P200	P50	N100	P200
Response type	ns	**	**	ns	ns	ns
Cue site	ns	ns	ns	*	**	*
Cue type	ns	**	**	ns	ns	*
Response type $\times$ cue type	ns	ns	**	ns	ns	ns
Cue type $\times$ cue site	ns	ns	**	ns	ns	ns

^a Notes. *, $P < 0.05$; **, $P < 0.01$; ns, not significant.

differences between neutral and valid cues for peripheral, vs. central, cue locations (Fig. 4).

For N100 latency there was a significant cue type $\times$ cue location interaction [$F(1, 12) = 6.3$; $P < 0.03$], with shorter latencies for valid, relative to neutral, cues at the central, but not peripheral, cue location (Fig. 4). P200 latency also had a significant cue type $\times$ cue location interaction [$F(1, 12) = 5.9$; $P < 0.04$], with shorter latencies for neutral, vs. valid, cues, but only for the peripheral cue location (Fig. 4).

Thus, there were 3 main sets of ERP findings for cues (Table 1). (1) N100 amplitudes were larger in the non-motor, relative to the motor condition, and larger for neutral, vs. valid, cues. (2) P200 amplitudes were significantly larger for non-motor, compared with motor, conditions, but only for neutral cues; and neutral cues had significantly larger amplitudes relative to valid cues, especially for peripheral cue locations. (3) P50, N100 and P200 latencies were shorter for central, vs. peripheral, cues. Relative to neutral cues, valid cues had shorter N100 latencies for the central

Fig. 5. Slow potentials between the cue and target sorted according to cue location (central/peripheral), cue type (valid/neutral), and response type (motor/non-motor). Waveforms are the grand averages at C_z . Black and white boxes indicate time periods for the 4, 250 ms window measures, starting at 1.0 s before target presentation.

Fig. 6. Slow potentials between cue and target as a function of response conditions (motor vs. non-motor) for central (left column) and peripheral (right column) conditions. Note that amplitude differences between response conditions begin between 500 and 250 ms before target presentation, with larger amplitudes for the motor condition. Black and white boxes indicate time periods for the 4, 250 ms window measures.

cue location, and longer P200 latencies at the peripheral cue location.

3.2.2. Negative slow potentials between cues and targets

Negative slow potentials between cues and targets developed after the cue-evoked P200 and peaked at target presentation (Figs. 5–7). There was greater negativity in the motor, vs. non-motor, condition beginning ~250–500 ms before target presentation (Fig. 6). The grand averaged midline potentials in Fig. 7 suggest an interaction between the effects of response type (motor, non-motor) and cue type (valid, neutral) because amplitude increases for neutral cues are apparent at all sites for the motor condition, but are limited to the frontal site in the non-motor condition. An ANOVA was conducted using the factors of cue location, response type, cue type (valid, neutral), time window (4, 250 ms windows), and electrode site (F_z , C_z , P_z). Significant main effects and notable interactions are described subsequently.

Response type (motor/non-motor): The main effect of response type did not attain significance ($P < 0.09$). There were significant response type $\times$ electrode site [$F(2, 24) = 6.3$; $P < 0.03$] and response type $\times$ time

window $\times$ electrode site interactions [$F(6, 72) = 7.2$; $P < 0.01$]. These results indicate greater negativity for the motor, vs. non-motor, condition ~250–500 ms before target presentation; a difference that was largest at the C_z site (see Fig. 6).

Cue location (central/peripheral): Slow potential amplitudes were significantly larger following central cues ($-2.7 \pm 0.4 \mu V$) vs. peripheral cues ($-1.9 \pm 0.4 \mu V$) [$F(1, 12) = 6.9$; $P < 0.03$]. Amplitude differences for central and peripheral cues were largest at frontal sites, indicated by a significant cue location $\times$ electrode site interaction [$F(2, 24) = 5.7$; $P < 0.03$].

Cue type (valid/neutral): There were significant interactions for cue type $\times$ time window [$F(3, 36) = 7.1$; $P < 0.01$] and cue type $\times$ electrode site [$F(2, 24) = 13.4$; $P < 0.001$]. Greater negativity was seen at frontal sites following neutral cues, relative to valid cues, and the difference between cue types varied somewhat across time windows (Fig. 7).

Time window (4, 250 ms windows preceding the target): Amplitudes of the negative slow potential were significantly different between time windows [$F(3, 36) = 54.7$; $P < 0.0001$], indicating the progressive increase in amplitude following cue presentation.

Fig. 7. Grand average slow potentials between the cue and target, sorted according to cue type (valid/neutral) and response type (motor/non-motor) at the midline electrodes. Black and white boxes indicate time periods for the 4, 250 ms window measures.

Fig. 8. Example of ERPs to targets at all electrode sites. N100 and P200 amplitudes were larger for invalid, relative to valid, targets, especially at anterior sites. A subsequent late slow wave that was maximal at parietal sites was more positive for invalid, relative to valid, targets. Potentials are from the peripheral motor conditions, but similar results were found in the other 3 combinations of response type and cue location factors. ERPs were low pass filtered (DC–16 Hz), and vertical lines indicate target onset.

In summary, analysis of the slow waves between the cue and target showed greater negativity following neutral, vs. valid cues, and the magnitude varied across electrode sites and time windows. Negative slow potentials were larger in the motor, vs. non-motor, condition starting ~250–500 ms before target presentation.

3.2.3. ERPs to the target

An example of ERPs to targets is presented in Fig. 8 (peripheral motor conditions). The waveforms included a P50–N100–P200 complex and a late slow wave having an amplitude difference between valid and invalid targets beginning ~250 ms after stimulus presentation. The N100 and P200 components were larger for invalid cues, relative to valid cues, and the late slow wave in response to invalid targets was more positive than for validly cued targets.

3.2.3.1. ERPs: P50, N100, P200. ERP amplitudes and latencies were analyzed with 2 (cue location) $\times$ 2 (response type) $\times$ 3 (cue type) ANOVAs at the C_z site, with the following significant effects.

Response type (motor/non-motor): Grand average potentials to targets as a function of response type are shown in Fig. 9. N100 amplitudes were larger in the non-motor ($-7.1 \pm 0.7 \mu V$), vs. motor ($-6.2 \pm 0.6 \mu V$) condition [$F(1, 12) = 19.8$; $P < 0.001$] (Fig. 8). There was a significant effect of response type on P50 amplitude when only

valid cues were analyzed [$F(1, 12) = 25.7$; $P < 0.0001$]. There was also a significant effect of response type for P200 latency [$F(1, 12) = 14.9$; $P < 0.01$], with shorter latencies for the motor (179.0 ± 5.2 ms) vs. non-motor (189.7 ± 5.2 ms) condition.

Cue location (central/peripheral): P50 amplitudes were significantly larger for central ($1.8 \pm 0.3 \mu V$), vs. peripheral ($0.1 \pm 0.4 \mu V$) cues [$F(1, 12) = 20.7$; $P < 0.001$]. There was also a significant effect for P200 amplitude [$F(1, 12) = 18.2$; $P < 0.001$], which was larger for central than peripheral cues (7.7 ± 0.7 vs. $5.8 \pm 0.7 \mu V$, respectively). P200 latency was significantly longer for central (189.3 ± 4.9 ms) vs. peripheral (177.4 ± 3.5 ms) cues [$F(1, 12) = 8.9$; $P < 0.02$].

Cue type (valid, invalid, neutral): The P200 component was significantly affected by cue type [$F(2, 24) = 12.1$; $P < 0.001$], and the effect on N100 amplitude approached significance [$F(2, 24) = 3.2$; $P < 0.06$]. Both components had larger amplitudes to the invalid, relative to valid cues. Analysis of only valid and invalid cued targets showed a significant effect of cue type for N100 [$F(1, 12) = 6.9$; $P < 0.02$] and P200 [$F(1, 12) = 20.4$; $P < 0.001$] amplitudes (Fig. 10A). Potentials from the peripheral motor conditions are shown in Fig. 10B. Although P50 amplitude was larger to valid vs. invalid targets in Fig. 10B, there were no significant effects of cue type on P50 amplitude.

3.2.3.2. ERPs: late slow wave. Potentials from midline sites in each combination of response type and cue location are shown in Fig. 11. To initially characterize the late slow wave difference between valid and invalid targets a 2 (cue location) $\times$ 2 (response type) $\times$ 2 (cue type: valid, invalid) $\times$ 3 (electrode site: F_z , C_z , P_z) $\times$ 2 (time window: 200–399, 400–599 ms) ANOVA was conducted. There was a significant main effect for cue type [$F(1, 12) = 7.2$; $P < 0.02$], and a significant cue type $\times$ electrode site interaction [$F(2, 24) = 18.3$; $P < 0.001$]. Late slow wave amplitudes were more positive for invalid, compared to

Fig. 9. ERPs to targets following valid, invalid and neutral cues in the 4 experimental conditions (motor/non-motor and central/peripheral). Waveforms are the grand averages at C_z .

Fig. 10. (A) Average amplitudes, across the motor and non-motor experimental conditions, of N100 and P200 at C_z in response to targets presented after valid and invalid cues. N100 and P200 amplitudes were significantly larger in response to targets that followed an invalid cue. (B) Grand average ERPs at C_z to targets following valid and invalid peripheral cues in the non-motor experimental condition. Waveforms were bandpass filtered (1–16 Hz) to attenuate late slow wave activity.

valid targets, and the cue type $\times$ electrode site interaction indicated larger differences between valid and invalid targets at P_z, compared with C_z and F_z.

Because the late slow wave differences between valid and invalid targets were largest at P_z, detailed analysis was restricted to the P_z site. Amplitudes of the late slow wave for valid, invalid, and neutral targets are plotted in Fig. 12 for the 200–399 (A) and 400–599 ms (B) time windows. A 2 (response type) $\times$ 2 (cue location) $\times$ 3 (cue type: valid, invalid, neutral) $\times$ 2 (time window) ANOVA revealed the following effects.

Response type (motor/non-motor): There was a signifi-

cant main effect of response type [$F(1,12) = 14.4$; $P < 0.01$], with larger amplitudes for the motor condition, compared with the non-motor condition. This effect was likely due to the more negative pre-target baseline in the motor condition.

Cue location (central, peripheral): The effect of cue location was non-significant.

Cue type (valid, invalid, neutral): There was a significant effect for cue type [$F(2,24) = 11.1$; $P < 0.001$]. Results shown in Fig. 12 suggest that amplitudes for valid cues were smaller than for invalid cues, while the relationship between neutral targets and valid/invalid targets varied as a function of time window, and to a lesser degree cue location.

To directly compare differences between cue types, 3 separate 2 (response type) $\times$ 2 (cue location) $\times$ 2 (cue type) $\times$ 2 (time window) ANOVAs were conducted. Each ANOVA used two of the 3 cue types (valid vs. invalid, valid vs. neutral, neutral vs. invalid). There was a significant effect of cue type for the valid vs. invalid [$F(1,12) = 25.4$; $P < 0.001$] and valid vs. neutral [$F(1,12) = 7.7$; $P < 0.02$] ANOVAs, with smaller amplitudes to valid targets in each comparison. For the neutral vs. invalid comparison the effect of cue type was non-significant ($P < 0.08$), but there was a significant cue type $\times$ time window interaction [$F(1,12) = 5.1$; $P < 0.05$] indicating smaller amplitudes to neutral cues in the 400–600 ms, but not the 200–400 ms, time window.

In summary, compared with validly cued targets, invalid targets elicited larger N100 and P200 amplitudes, and a more positive late slow wave between 200 and 600 ms (Table 2). P50 and N100 amplitudes were larger in the non-motor, vs. motor, condition. A summary of the ERP results for cues and targets as a function of response type (motor, non-motor), cue location (central, peripheral), and cue type (valid, invalid, neutral) is shown in Table 3.

4. Discussion

In this study behavioral and neurophysiological measures were used to study the effects of attentional cueing. The behavioral results using auditory stimuli were consistent with previous cued attention studies in the visual modality (e.g. Posner, 1980). Reaction time benefits were observed for validly cued targets, and reaction time costs were observed for invalidly cued targets. The main ERP findings were: (1) when subjects were not required to make a motor response to targets larger ERPs were seen to both cues (N100, P200) and targets (P50, N100), relative to when subjects responded to targets, (2) negative slow potentials between the cue and target had larger amplitudes beginning ~500–250 ms before target presentation when subjects responded to targets, vs. when subjects did not respond to targets, (3) larger negative slow potentials were observed following uninformative neutral cues, relative to cues that

Fig. 11. Potentials to targets at midline sites for all combinations of response type and cue type conditions. Late slow waves showing a difference between valid and invalid cues were largest at P_z , but in the peripheral motor condition were also apparent at C_z . Potentials returned to the pre-trial baseline by ~ 800 ms, indicated by a stable positive potential because the 100 ms pre-stimulus baseline was at the end of the negative slow potentials that developed before target presentation. Timeperiods of the window measures are illustrated by the black (200–399 ms) and white (400–599 ms) boxes under the P_z tracings. Potentials were low pass filtered (DC–16 Hz), and vertical line indicates target presentation.

predicted the ear that would receive the target tone, and (4) larger N100 and P200 amplitudes and a more positive late slow wave were evoked by targets following invalid cues, relative to targets following valid cues.

4.1. ERPs and cue information

4.1.1. Potentials to the cue

Cues were words presented either monaurally (peripheral valid and invalid cues) or binaurally (all neutral cues, central valid and invalid cues). Psychophysical studies show that binaural presentation results in up to a 3 dB difference in subjective loudness compared to monaural presentation of the same stimulus (Licklider, 1951), which could relate to shorter ERP latencies for central vs. peripheral cues (McPherson and Starr, 1993). Binaural stimuli did not significantly increase P50, N100, or P200 amplitudes, a result compatible with previous studies of the N100 that show either non-significant changes, small increases, or small decreases for binaural vs. monaural stimuli (Davis and Zerlin, 1966; Picton et al., 1978; McPherson and Starr, 1993; Lavikainen et al., 1997). Larger N100 and P200 amplitudes for neutral cues, compared with valid

cues, may be related to differences in the cue's ability to predict target location because the effect was also seen in the central condition, where all cues were binaural. However, the possibility that physical differences in cue stimuli (the word 'go' vs. 'right' and 'left') might contribute to larger amplitudes to neutral cues cannot be ruled out.

4.1.2. Potentials between cue and target

Negative slow potentials following neutral cues were significantly larger than for valid cues, a result compatible with bilateral motor preparation when cue location, and consequently the responding hand, was not predicted by the neutral cue (Cui and Deecke, 1999). A small difference was also seen as a function of cue location, with significantly larger negative slow potential amplitudes following central cues, compared with peripheral cues, but the interpretation of the effect is unclear.

4.1.3. Potentials to the target

The current results suggest at least two types of attentional modulation, as indicated by ERPs to targets. The initial process is reflected by the N100 and P200, with greater amplitudes for invalid, vs. valid, targets. The N100

Fig. 12. Plot of late slow wave amplitudes to targets as a function of cue type between 200–399 ms (A) and 400–599 ms (B) after target presentation. In all conditions and windows late slow waves to invalid targets were more positive than valid targets. From 200 to 399 ms targets following neutral cues had amplitudes comparable to invalids, and from 400 to 59 ms neutral targets had amplitudes similar to valid targets.

and P200 differences suggest that neural activity in auditory cortex is modulated as a function of attentional cueing because generators of the N100 and P200 components

Table 2
Event-related potentials to targets^a

Effect	Amplitude				Latency		
	P50	N100	P200	LSW ^b	P50	N100	P200
Response type ^c	**	***	ns	**	ns	ns	**
Cue site	***	ns	***	ns	ns	ns	*
Cue type ^d	ns	*	***	***	n/a	n/a	n/a

^a Notes. Abbreviations: LSW, late slow wave; n/a, not applicable. *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; ns, not significant.

^b Late slow wave results are shown from analysis at P_z site only.

^c Response type effect for P50 amplitude included only valid trials.

^d Cue type effects were from analysis of only valid and invalid targets.

have been identified within primary and secondary auditory cortical areas (e.g. Scherg and Von Cramon, 1986; Knight et al., 1988; Woldorff et al., 1993; Liegeois-Chauvel et al., 1994; Siedenberg et al., 1996; Picton et al., 1999). Then, beginning ~200–250 ms and lasting until ~600 ms the late slow wave to invalidly cued targets is more positive, relative to validly cued targets. Greater P200 amplitudes may be a genuine enhancement of P200 amplitude, independent of the late slow wave, or may reflect the beginning of the late slow wave that coincides with the P200. The late slow wave difference between validly and invalidly cued targets may be a more positive late slow wave in response to invalidly cued targets, and/or a more negative late slow wave to the validly cued targets.

A previous visual cued attention study demonstrated the costs and benefits of cueing by comparing potentials to targets after valid, invalid, and neutral cues (Luck et al., 1994). The timecourse of ERPs showed an initial cost (invalid $\neq$ valid = neutral), reflected by smaller P1 amplitudes to invalid targets, relative to valid and neutral targets which had equivalent amplitudes. Attentional benefits (valid $\neq$ invalid = neutral) were then indicated by the subsequent N1 which was larger for valid targets, relative to invalid and neutral targets which had approximately equal amplitudes. The present results using auditory stimuli were consistent with a similar pattern of costs, indicated by N100/P200, followed by benefits (late slow wave). Larger N100 and P200 amplitudes for invalid, vs. valid, targets were followed by the early (200–399 ms) portion of the late slow wave which was more negative for valid targets, compared to invalid and neutral targets. The late slow wave measured from 400 to 599 ms may reflect additional processing of targets because, on average, the subject had already responded to the target during this timeperiod. N100 and P200 amplitudes to neutral targets did not show a consistent pattern among combinations of response type and cue location conditions, a result that may reflect a low S/N ratio for invalid and neutral targets, relative to the effect size for valid vs. invalid targets. Thus, the present results are consistent with the idea that N100 and P200 amplitudes may reflect attentional costs (invalid $\neq$ valid = neutral). The results from the late slow wave were more clear. From 200 to 399 ms amplitudes to neutral targets were more positive than valid targets and similar to invalid targets, a result that suggests differential processing of valid targets. However, we recognize that more data are needed to support the possibility that ERPs reflect attentional costs and benefits in auditory cued attention. The issue of N100 and P200 amplitudes for neutral, relative to valid and invalid targets, is unclear, and alternative interpretations of late slow wave activity, such as the presence of a positive wave for invalid and neutral targets that lasts longer for invalid targets, have not been ruled out.

4.1.4. Comparison of auditory cued and selective attention

ERPs in auditory selective attention experiments show a

Table 3
Summary of event-related potential results^a

	Component	Cue ERPs			Target ERPs		
		Response type	Cue site	Cue type (valid, neutral)	Response type	Cue site	Cue type (valid, invalid)
Amplitude	P50 ^b	ns/ns	ns	ns	NM > M	C > P	ns
	N100 ^c	NM > M	ns	N > V	NM > M	ns	I > V
	P200 ^c	NM > M	ns	N > V	ns	C > P	I > V
	Late slow wave ^d	n/a	n/a	n/a	M > NM	ns	I > V
Latency	P50	ns	C < P	ns	ns	ns	ns
	N100	ns	C < P	ns	ns	ns	ns
	P200	ns	C < P	N < V	M > NM	ns	ns

^a Notes. Abbreviations: Response type (M, motor; NM, non-motor), cue site (C, central; P, peripheral), cue type (V, valid; I, invalid; N, neutral), ns, not significant.

^b The effect of response type for P50 amplitudes showed a significant effect for valid stimuli.

^c The effect of cue type for N100 and P200 to targets was tested using all cue types, and only valid vs. invalid cues (all/valid vs. invalid).

^d Amplitudes of invalid targets were greater than valid targets in terms of being more positive than valid targets. It is unclear if the late slow wave is best characterized as a positivity to invalids, a negativity to invalids, or both.

sustained processing negativity for stimuli presented to the attended, relative to the ignored, ear that begins at ~100 ms after stimulus presentation, continues until ~500 ms, shows a fronto-central scalp distribution, and typically results in larger N100 amplitudes to attended stimuli (e.g. Hillyard et al., 1973; Naatanen, 1990; Woldorff and Hillyard, 1991). Assuming a processing negativity would develop for stimuli at the cued ear, one might have expected larger N100 and smaller P200 amplitudes to valid targets. Instead, both N100 and P200 amplitudes were larger for invalid targets, even when DC filter settings were used to allow full expression of the late slow wave (Fig. 11).

There are several differences between the processing negativity and the late slow wave observed in the present study. First, the processing negativity in selective attention can begin <100 ms after stimulus presentation (Naatanen, 1990), in contrast to the late slow wave in the current study which began ~250 ms after target presentation. In addition, the processing negativity requires ~30–45 s of stimulus presentation with attention focused towards stimuli presented to one ear before a difference between attended and ignored stimuli is observed (Donald and Young, 1982), while in cued attention studies the attended (i.e. cued) ear randomly varies on a trial-by-trial basis every few seconds. Finally, the late slow wave in the present study was maximal at parietal sites; while the processing negativity, especially the late processing negativity, has a fronto-central scalp distribution (Naatanen, 1990). Taken together, these considerations suggest that the late slow wave difference between valid and invalid targets observed in the current study and previous auditory cued attention studies (e.g. Schroger, 1993) is distinct from the processing negativity observed in selective attention studies.

The above analysis of ERP findings in terms of attentional costs and benefits may also be relevant to understanding the differences between ERP results (N100, late slow wave) in auditory selective attention and cued attention tasks. During selective attention subjects attend to a single sensory channel

(such as one ear), to the exclusion of the other channel, while in cueing tasks attention to one channel is encouraged by the cue, but the other channel is still relevant for accurate performance and must be monitored as well. Thus, by design, the selective attention task has no attentional costs because only one channel is relevant for task performance. In the absence of attentional costs, sustained potentials associated with attention may develop earlier and have different properties in selective attention tasks.

It is notable that in both the motor and non-motor conditions a negative slow wave developed between the cue and target, and ERP amplitudes (N100, P200, LSW) to valid and invalid targets were significantly different. In principle, subjects did not need to use the cue information to anticipate target location in the non-motor condition, because there was ample time to encode and remember the target's location before the occasional response query was presented. Thus, it appears that processes that, presumably, mediate performance in the motor condition may have been engaged in the non-motor condition.

4.2. Effects of response requirements

4.2.1. Potentials to the cue and target

For target stimuli N100 and P50 amplitudes were larger in the non-motor condition, compared with the motor condition. Amplitude reductions for targets in the motor condition are consistent with previously observed attenuations in auditory ERP amplitudes prior to voluntary movements (Hazemann et al., 1975; Tapia et al., 1987). For both cues and targets it is unlikely that amplitude differences between motor and non-motor conditions were due to the influence of the negative slow potentials because bandpass filtering attenuated the slow potentials, and amplitude increases were observed for both negative (N100) and positive (P50, P200) components.

In response to cues the N100 and P200 were also larger in the non-motor, vs. motor, condition. The finding of smaller

ERP amplitudes to cues in the motor, vs. non-motor, condition is difficult to ascribe to attenuations due to voluntary movement because at least 1.5 s elapsed between cue presentation and movement in response to targets in the motor condition. Thus, modulations of cue ERP amplitudes in motor, vs. non-motor, conditions may indicate differences associated with motor system function that are present even during periods in the trial when a motor response is not immediately required, such as during cue presentation.

We speculate that reductions in cue ERP amplitudes in the motor condition, relative to the non-motor condition, may reflect modulation of auditory cortical activity as a function of motor preparation because the cue not only specifies target location but also the appropriate response to the target. Modulation of cue ERPs may be an initial indicator of premotor and prefrontal activity that continues during the interval between cue and target, and may contribute to the negative slow potentials recorded at the scalp. Consistent with this idea, studies suggest that premotor and prefrontal regions are important generator sites of the negative slow potential that develops between S1 and S2 in CNV tasks (e.g. Basile et al., 1994; Hultin et al., 1996; Hamano et al., 1997), and neurons in the premotor cortex can respond to cues providing information about an

upcoming movement (Wise et al., 1983; Crammond and Kalaska, 2000).

4.2.2. Potentials between cue and target

Two major types of negative slow potentials related to motor preparation and stimulus expectancy have been described: the readiness potential (RP) and the CNV. The RP begins ~1 s before subjects perform a self-initiated movement, and is most prominent over fronto-central electrode sites contralateral to the responding hand (Deecke et al., 1969; Shibasaki and Rothwell, 1999). The CNV (or late-CNV, E-wave component) has a frontal–central scalp prominence, and develops before an expected stimulus that does not necessarily require a motor response (Walter et al., 1964; Ruchkin et al., 1986).

Motor preparation, similar to the RP, may contribute to the negative slow potential because there was a significant effect of response type (motor/non-motor), with larger amplitudes in the motor, relative to the non-motor, condition. Consistent with this notion, a previous study showed that a lateralized readiness potential developed following cues predicting the hand that would respond to the upcoming target (Gratton et al., 1990). Although negative slow potential amplitudes were modulated by motor requirements, the negative slow poten-

Cognitive Processes and Experimental Results			
Trial	Cue	Retention Period	Target
Process	Working Memory • Motor Preparation (A)	Presetting • Stimulus Expectancy (C) • Motor Preparation (B) (D)	Attention Allocation • Costs? (E) • Benefits (F) Response Execution (G)
Results	(A) N100/P200 Non-motor > Motor	(B) Slow Wave: Neutral > Valid	(E) N100/P200 Invalid > Valid
		(C) Slow Wave: (1000–250 ms) Motor = Non-motor	(F) LSW Valid vs. Invalid & Neutral
		(D) Slow Wave: (250–0 ms) Motor > Non-motor	(G) P50/N100 Non-motor > Motor

Fig. 13. Possible cognitive processes engaged during cued attention. Top panels indicate the 3 phases of a trial (cue presentation, retention period, target presentation). Circled letters indicate correspondence between putative cognitive processes (middle panels) and experimental results (bottom panels). ERP results are indicated for cue and target phases, and negative slow wave results are indicated for the retention period. A question mark is shown for attentional cueing 'costs' because the results are consistent with an association between N100 amplitude and costs, but other explanations have not been ruled out (see text). LSW = late slow wave.

tial was observed at all electrode sites in the non-motor condition. This suggests that the negative slow potential, particularly in the non-motor condition, has features similar to the CNV, and may be associated with expectancy for the upcoming target stimulus (Ruchkin et al., 1986; Brunia, 1999).

4.3. Attention and motor preparation

In the present study subjects received information about where targets were likely to be presented, and also information about what response is likely to be needed after target presentation. Utilization of both stimulus- and response-related information could facilitate reaction times to valid trials, and would likely impede the generation of rapid responses to targets in invalid trials. A general summary of processes that may be operative during cued attention trial is shown in Fig. 13. The ERP results suggest that motor preparation and/or expectancy for target appearance begins after cue presentation (evidenced by differences in ERPs to the cue and negative slow potentials), while modulation of the sensory response to expected (or unexpected) targets is observed in ERPs to targets. This modulation may take the form of initial processes associated with the costs of incorrect cueing, followed by benefits of correct cueing. These observations are consistent with the general idea that attentional selectivity is intimately associated with selection of stimuli and selection for action (Brunia, 1999).

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