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Spatial cueing, sensory gating and selective response preparation: an ERP study on visuo-spatial orienting

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Summary Event-related brain potentials (ERPs) were recorded in a visuo-spatial attention task where the position of an imperative stimulus was indicated either validly or invalidly by a central arrow (trial-by-trial cueing). Subjects had to perform choice RT tasks with the response being dependent either on the identity of the target stimulus or on its position. When target identity was relevant for response selection, validly cued stimuli elicited amplitude enhancements of the early, sensory-evoked P1 and N1 components at lateral posterior sites. The N1 validity effect was limited to scalp sites ipsilateral to the visual field of stimulus presentation. Although these effects were found only when the sensory discrimination task was considerably difficult, they are in line with models assuming that modulations of sensory-perceptual processing ("sensory gating") are induced by spatial cueing. However, when target location was response-relevant, N1 amplitude enhancements were consistently elicited by invalidly cued letters.

CNV and LRP measures indicated that the arrow elicited response-related processing in the cue-target interval. Such processes occurred even when the cue contained no information about an upcoming response. Two consecutive lateralization phases were distinguishable in the LRP, with experimentally induced response assignments becoming effective only during the second phase.

Key words: Event-related potentials; Visuo-spatial attention; Contingent negative variation (CNV); Lateralized readiness potential (LRP)

Attention can be voluntarily directed to specific objects and locations within the visual field independently of overt eye movements. Stimuli at attended-to locations are detected with higher speed and accuracy as compared to stimuli presented outside the attentional focus (cf., Posner et al. 1978, 1980, 1982; Jonides 1981; Müller and Findlay 1987; Müller and Rabbit 1989). The question of which mechanisms may underly the orienting of visuo-spatial attention is still under dispute. On the one hand, visuo-spatial attention might directly influence perceptual processing, so that stimuli at attended locations are analyzed more rapidly or intensively. This hypothesis of an early, intraperceptual effect of spatial attention ("sensory gating") has been advocated by, among others, Posner (1980). On the other hand, the direction of attention in the visual field might influence subsequent, postperceptual, processing stages like response selection (cf., Sperling 1984).

In most behavioral studies on visuo-spatial orienting, trial-by-trial cueing paradigms were used, where a

symbolic precue (e.g., an arrow) informs subjects about the likely position of an upcoming imperative stimulus. Reactions to target stimuli occurring at validly indicated locations were found to be faster as compared to reactions to targets occurring at unprimed positions (cf., Posner et al. 1978, 1980, 1982). Furthermore, spatial cueing results in an increased detectability for validly cued stimuli (cf., Bashinski and Bacharach 1980; Downing 1988; Hawkins et al. 1990). These findings have been interpreted in terms of enhanced sensory processing received by stimuli at attended locations (cf., Posner 1980).

In most ERP studies on visuo-spatial attention, a sustained paradigm was used, where subjects were required to focus attention on one visual hemifield and to ignore events in the opposite hemifield. It was found that attended-to (valid) stimuli elicit enhanced P1 and N1 components as compared to stimuli that occur in the unattended hemifield (cf., Eason 1981; Harter et al. 1982; Hillyard and Münte 1984; Hillyard and Mangun 1987; Mangun and Hillyard 1988). Since the onset of these attention-related amplitude modulations is quite early (usually between 80 and 110 msec post stimulus) and neither scalp distributions nor onset latencies of the sensory-evoked P1 and N1 components

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seem to be altered (cf., Hillyard and Mangun 1987; Mangun and Hillyard 1988), these results have been interpreted similarly to the RT patterns reported above—as evidence for early intraperceptual “sensory gating” processes (cf., Mangun and Hillyard 1990 for an overview).

Although converging evidence seems to favor “sensory gating” as a mechanism underlying visuo-spatial attention, it must be noted that rather different paradigms have been employed in behavioral studies and ERP experiments, respectively. Only very few ERP studies have investigated effects of visuo-spatial orienting induced by trial-by-trial cueing. Mangun and Hillyard (1991; cf. also Mangun et al. 1987; Harter et al. 1989) found enhancements of P1 and N1 amplitudes at occipital scalp sites for validly as compared to invalidly cued targets. Since these effects were quite similar to ERP modulations found with the sustained attention paradigm, they suggested that functionally similar “sensory gating” mechanisms are active both in trial-by-trial cueing experiments and during sustained attention.

There are, however, some problems with this line of interpretation. The finding of a P1 validity effect obtained during trial-by-trial cueing conflicts with earlier results reported by Hillyard et al. (1985). In their experiments, subjects were required to attend to one hemifield that was indicated by a precue while short series of flashes were presented randomly in the left or right visual field. No P1 enhancement was visible in response to the first 4 stimuli presented at the relevant location. Contrary to the N1 effect, which was present for the very first attended-to flash within the series, the P1 validity effect took considerable time to develop. This failure to obtain an immediate P1 attention effect may be because a rather long cue-target interval (1.9 sec) was used.

Another difficulty has to do with the interpretation of the N1 validity effect. Mangun and Hillyard (1991) found N1 amplitude enhancements for attended locations only for a choice RT task, but not when subjects simply had to respond to the onset of a stimulus. Differential effects of spatial attention on P1 and N1 components have been reported before, suggesting that P1 and N1 modulations might reflect rather different aspects of visual processing (cf., Heinze et al. 1990; Luck et al. 1990). These authors tentatively propose that P1 enhancements elicited by spatial attention reflect a preset facilitation of information processing for specific locations (“sensory gain control”), while N1 enhancements indicate rapid processes of additional attentional focussing. Mangun and Hillyard (1991) suggest that P1 enhancements for validly cued stimuli observed both in the simple and in the choice reaction time task reflect the primary effect of visuo-spatial orienting. In the choice RT task, however, a further

focussing of attention (indicated by N1 amplitude modulations) might have been necessary to discriminate response-relevant features of the stimuli.

The present study was designed to test whether attention-related ERP modulations elicited within a trial-by-trial cueing paradigm are comparable to the effects reported for sustained-attention tasks and can be interpreted in line with the “sensory gating” hypothesis. In addition to studying the consequences on visual processing of attentional orienting induced by a symbolic precue, another aim of the present experiments was to investigate the influence of the cue on selective preparation processes in the cue-target interval. When precue direction and the type of reaction required by the upcoming imperative stimulus are probabilistically connected, specific expectation and response preparation processes might be elicited even before the imperative stimulus occurred. To test this, both the contingent negative variation (CNV) and the lateralized readiness potential (LRP) were measured in the cue-target interval. The LRP is a negative lateralization of a readiness potential over the contralateral motor cortex that indicates selective motor preparation and response initiation following an imperative stimulus (cf., Coles et al. 1988). When recorded in the interval between cue and target, the LRP may also be used to measure selective response preparation elicited by the cue (Coles 1989). The CNV is a slow negative ERP shift typically found with S1-S2 paradigms in the interval between warning and imperative stimulus. The proper functional interpretation of CNV is still under dispute (cf., Gaillard 1986). Whereas it is usually taken to be an indicator of response preparation processes, it has also been regarded as a measure of stimulus anticipation or selective attention.

In the experiments reported here, a Posner-like trial-by-trial cueing paradigm was employed. A central arrow indicated the probable location of an upcoming imperative letter stimulus. Two choice RT tasks differing in the stimulus attribute relevant for response selection were run: in one condition, reaction was dependent on letter identity, in the other, reaction was dependent on the location of the letter.

If the type of response is contingent upon letter location, the precue carries information about stimulus location as well as about the required response. In this condition, RT benefits from validly cued trials might therefore be due either to attentional focussing, or to selective response preparation during the cue-target interval, or to a combination of both factors. When reaction is dependent on stimulus identity, however, the precue is not informative with regard to the upcoming response. In this case, RT validity effects cannot be attributed to selective response preparation. If spatial attention were based on a selective gating of early visual information processing, one would expect RT

benefits for valid trials to be accompanied by selective amplitude enhancements of early sensory-evoked ERP components.

Experiment 1

Methods

Subjects

Thirteen paid volunteers participated in the experiment. Three of them had to be excluded because of poor eye fixation control in the cue-target interval (see below). Thus 10 subjects (3 females), aged 21–45 years (mean age: 27.2 years) remained in the sample. All subjects were right-handed and had normal or corrected-to-normal vision.

Stimuli and apparatus

The subjects were seated in a dimly lit, electrically shielded and sound attenuated chamber, with response buttons under their left and right hands. A computer screen was placed 100 cm in front of the eyes and carefully positioned so that the stimuli (presented white-on-gray) occurred on the subject's horizontal straight-ahead line of sight. Each trial began with a 200 msec presentation of a centrally located arrow (subtending a visual angle of $1.5^\circ \times 0.6^\circ$) pointing either to the left or to the right side. 700 msec after cue offset, an uppercase letter (an M or W) appeared for 100 msec on the left or right side (6° horizontal distance from the screen center), subtending an angle of $1^\circ \times 1^\circ$. The intertrial interval between letter offset and onset of the next arrow was 2 sec.

Procedure

The experiment was divided into halves (described as experiments 1a and 1b below), each consisting of 12 blocks, resulting in a total of 24 experimental blocks. Each block consisted of 60 trials and had a duration of 2.5 min. Both letter stimuli appeared randomly and with equal probability on the left or right side and preceded by an arrow pointing either to the side where the letter appeared (validly cued letters) or to the opposite side (invalidly cued letters). Forty-four out of 60 trials (73.3%) per block were validly cued. In exp. 1a, subjects were required to respond with the left hand to the occurrence of the letter M and with the right hand when a W appeared on the screen (Response Cue: Letter Identity). During exp. 1b, response was conditional by the location of the letter: left letters required a left-hand reaction and conversely (Response Cue: Letter Location). The order of experimental halves was balanced across subjects. Subjects were instructed to respond as quickly and accurately as possible and to maintain central eye fixation during the

trials. To make subjects familiar with these specific task requirements, several training blocks were run at the beginning of the experiment.

Recording

The EEG was recorded with Ag-AgCl electrodes from F_z , C'_3 , C_z , C'_4 , P_z (according to the 10–20 system), from PL and PR (located halfway between P_z and the ear channel), and from OL and OR (located halfway between O_1 and T_5 , and O_2 and T_6 , respectively). All electrodes were referred to the right earlobe. The horizontal EOG was recorded bipolarly from electrodes at the outer canthi of both eyes, the vertical EOG from electrodes above and beside the right eye. Electrode impedance was kept below 5 k Ω . The amplifier bandpass was 0.10–70 Hz. EEG and EOG were sampled on-line every 7 msec and stored on disk. Reaction times were recorded for each trial.

Data analysis

The EEG and EOG were averaged off-line for epochs of 1800 msec, starting 100 msec prior to arrow onset, and ending 800 msec after letter onset. Trials with eyeblinks, horizontal eye movements, or overt response errors were excluded from analysis. After artifact removal, the computer-averaged horizontal EOG for each subject was scored for systematic deviations of eye position in the cue-target interval. If the maximal residual EOG deviation exceeded $+/- 1 \mu V$, the subject was disqualified.¹ The EEG was averaged separately for all combinations of task conditions (response cue: letter identity/letter position; validity: valid/invalid; visual field of presentation: left/right; stimulus identity: M/W), resulting in 16 average wave forms for each subject and electrode site. ERP effects in the cue-target interval and ERP effects following target onset were analyzed separately. For the RT data repeated measures ANOVAs were performed separately for exp. 1a and 1b for the following variables: cue validity, stimulus-response compatibility, and response side.

Analysis of ERPs in the cue-target interval (CNV, LRP)

CNV and LRP measures were computed relative to a 100 msec baseline interval prior to cue onset. The CNV amplitude was measured within 6 consecutive time windows of 100 msec duration (between 500 msec before and 100 msec after letter onset). The CNV elicited in exp. 1a and exp. 1b (averaged over all task

¹ This strict rejection procedure was employed because systematic eye movements in the arrows' direction were expected in the cue-target interval, so that validly cued letters would be projected closer to the fovea than invalid letters. This may result in ERP modulations that are totally unrelated to attentional orienting.

TABLE I

Latency windows (msec) for ERP components at different recording electrodes; experiments 1 and 2.

	P1	N1	P2	N2	P3
F _z , C _z , P _z	–	140–180	–	220–260	320–500
PL, PR	92–132	148–180	200–240	240–280	320–500
OL, OR	92–132	148–188	200–240	240–280	320–500

conditions and both arrow directions) was compared within each time window using *t* tests for repeated measures. To obtain the LRP, C₃'-C₄' difference potentials for trials with imperative stimuli occurring on the right side were subtracted from C₃'-C₄' difference potentials for trials with letters in the left visual field.² The LRPs to valid and invalid trials were compared within 8 time windows of 100 msec duration (beginning at cue offset and ending 100 msec after letter onset) using paired *t* tests.

Analysis of ERPs elicited by the imperative stimulus

All measures were taken relative to the mean voltage of the 100 msec interval preceding letter onset. Mean amplitudes and P3 peak amplitudes were computed over latency windows centered approximately on the components' peak latencies in the grand average (see Table I). Separate repeated measures analyses of variance were performed on these values for the following variables: electrode location, recording side (left vs. right), cue validity (valid vs. invalid), stimulus-response compatibility, and letter location (left vs. right). When appropriate, a Greenhouse-Geisser adjustment to the degrees of freedom was performed (indicated in the result section by GG).

Results

Behavioral performance

For both response assignment conditions, RTs to validly cued letters were significantly shorter than RTs to invalidly indicated letters. When letter identity served as response cue (exp. 1a), the mean RT for valid trials was 435 ± 13 msec, as compared to 453 ± 23 msec for invalid trials ($F(1, 9) = 15.93$; $P < 0.003$). In the case of letter position as response cue, mean valid and invalid RTs were 228 ± 9 and 275 ± 13 msec, respectively ($F(1, 9) = 77.55$; $P < 0.000$). In exp. 1a, RTs

² In exp. 1b, this procedure is equivalent to the standard LRP computation in which right reactions are subtracted from left reactions. In exp. 1a, however, stimuli and responses were spatially incompatible in half of the trials. Subtracting right-stimulus trials from left-stimulus trials thus leads to a "non-standard" LRP that is not informative with regard to selective response preparation following the imperative stimulus.

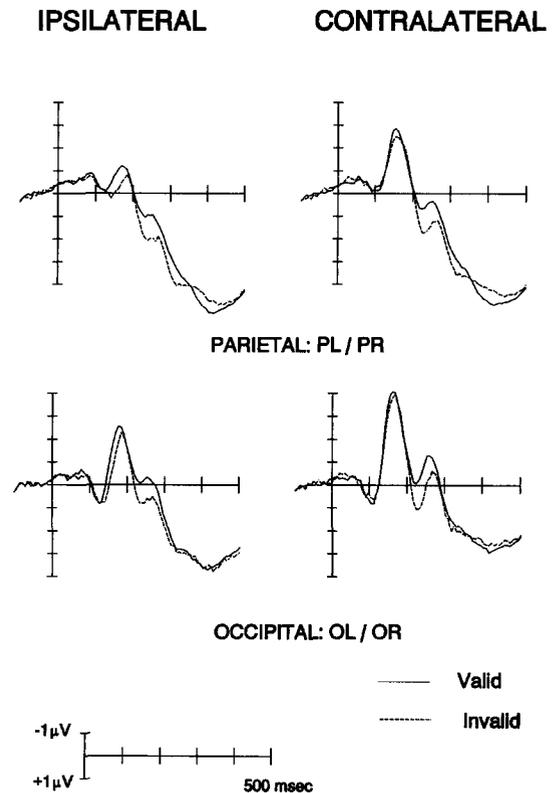


Fig. 1. Grand-averaged ERPs at parietal and occipital recording sites for validly and invalidly cued imperative stimuli, experiment 1a (Response Cue: Letter Identity). ERPs recorded from hemispheres ipsilateral and contralateral to the visual field of stimulation are presented separately.

in trials where the presentation side was compatible with the required response were faster as compared to incompatible trials (433 vs. 455 msec; $F(1, 9) = 28.29$; $P < 0.000$). Right-hand reactions were significantly faster than left-hand reactions both in exp. 1a and 1b (433 vs. 456 msec, and 246 vs. 257 msec, respectively). In exp. 1a, error rates for valid and invalid trials were not different (4.5% vs. 4.3%). In exp. 1b, response errors occurred more often in the case of invalid trials (0.9% vs. 4.8%; $t(1, 9) = -4.20$; $P < 0.002$).

ERPs elicited by the imperative stimulus

Experiment 1a. Grand-averaged ERPs elicited by validly and invalidly cued letters at lateral posterior sites are shown in Fig. 1. To simplify presentation, ERPs were collapsed across experimental conditions where the side of recording was ipsilateral or contralateral to the visual field of presentation. Neither for parietal nor for occipital sites could a P1 validity effect be observed. Similarly, there was no significant validity effect in the N1 range. However, a significant 3-way interaction (validity \times side of recording \times visual field of presentation; $F(1, 9) = 15.86$; $P < 0.003$, at parietal sites; $F(1, 9) = 16.36$; $P < 0.003$ at occipital sites) indicated that N1 amplitude enhancements for valid

trials tended to be located at ipsilateral scalp sites. Between 200 and 280 msec post stimulus, parietal and occipital ERPs to valid letters were more negative than ERPs for invalid trials. This is reflected in validity effects in the P2 and N2 latency ranges ($F(1, 9) = 18.79$; $P < 0.002$, and $F(1, 9) = 10.70$; $P < 0.010$, respectively). Enhanced N2 components to validly indicated imperative stimuli were also visible at midline scalp sites (F_z, C_z, P_z ; $F(1, 9) = 17.24$; $P < 0.002$, not shown in figures). There was no effect of cue validity on P3 amplitude.

Experiment 1b. Fig. 2 shows the grand-averaged posterior ERPs to valid and invalid trials for scalp sites ipsilateral and contralateral to the visual field of presentation, respectively. No influence of cue validity on P1 amplitude could be observed. Although cue validity did not have a significant main effect on N1 amplitude, a 3-way interaction (validity \times side of recording \times visual field of presentation; $F(1, 9) = 14.82$; $P < 0.004$, at parietal sites; $F(1, 9) = 9.59$; $P < 0.013$ at occipital sites) indicated that validity had a differential influence on N1 components ipsilateral and contralateral to the visual field of presentation: at contralateral recording sites, N1 mean amplitude was more negative for invalidly cued letters as compared to validly cued letters ($t(1, 9) = 2.27$; $P < 0.049$, at parietal sites; $t(1, 9) = 2.28$; $P < 0.049$ at occipital sites). At ipsilateral sites,

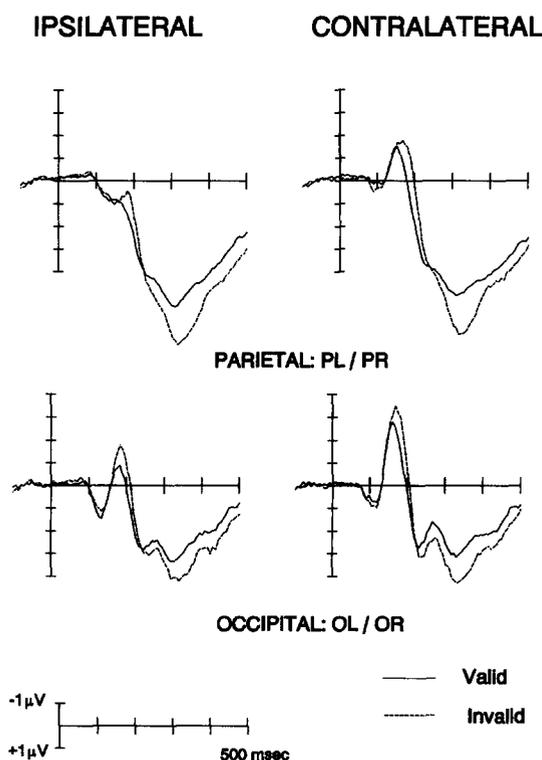


Fig. 2. Grand-averaged ERPs at parietal and occipital recording sites ipsilateral and contralateral to the visual field of presentation for validly and invalidly cued imperative stimuli, experiment 1b (Response Cue: Letter Position).

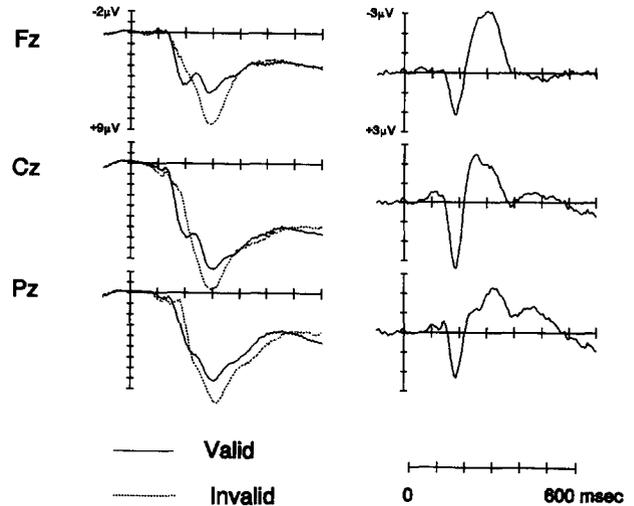


Fig. 3. Grand-averaged ERPs at F_z, C_z, P_z for validly and invalidly cued imperative stimuli (left side), and difference wave forms obtained by subtracting ERPs to invalid trials from ERPs to valid trials (right side), experiment 1b (Response Cue: Letter Position).

this difference was not significant. A similar negative enhancement for invalidly cued trials is also visible at midline recording sites (cf., Fig. 3). This effect was most pronounced between 160 and 210 msec post stimulus ($F(1, 9) = 12.06$; $P < 0.007$). No significant validity effect was obtained at PL/PR and OL/OR in the P2 and N2 latency range. However, validity had an effect on P3 amplitude—invalidly indicated letters elicited larger P3s than did valid trials. This effect was visible at lateral parieto-occipital sites ($F(1, 9) = 13.31$; $P < 0.005$) as well as at midline electrodes ($F(1, 9) = 6.11$; $P < 0.035$).

ERP modulations in the cue-target interval

CNV effects. To test whether the response assignment influenced CNV, CNV amplitudes elicited during exp. 1a were compared to amplitudes recorded during exp. 1b for each time window and electrode location (cf., Fig. 4). No significant difference was visible before 400 msec prior to letter onset. In the latency range from 400 to 0 msec before letter onset, CNV amplitudes elicited during exp. 1b were significantly enhanced as compared with exp. 1a at most electrode sites (except for F_z, C_3' , and OL). This effect was most pronounced at central and parietal recording sites and showed a marked right-hemisphere dominance.

LRP effects. The effect of cue direction on RP lateralization in the cue-target interval was measured by comparing lateralizations in valid and invalid trials separately for exp. 1a and 1b. As can be seen from Fig. 5, valid cues elicited a lateralization pattern that indicated preparation of that response side where the imperative stimulus would occur (that is, the side to which the arrow pointed). Invalid cues were also followed by preparation of the indicated side (the “wrong”

side with regard to the position of the imperative stimulus). This pattern was visible both for exp. 1a and exp. 1b. In exp. 1a, lateralization to valid and invalid cues differed significantly between 600 and 500 msec pre stimulus and again in the interval between 200 msec pre stimulus and 100 msec after letter onset. A similar biphasic pattern is visible for exp. 1b, with a first phase located between 600 and 500 msec pre stimulus, and the second phase ranging from 300 msec pre to 100 msec post stimulus (cf., Table II).

Discussion of experiment 1

One aim of experiment 1 was to study whether selective response expectation and preparation processes are elicited in the cue-target interval. It was found that the CNV was influenced by the amount of response-related information conveyed by the precue. When it indicated the coming response with about 75% probability, CNV amplitude was enhanced in comparison to exp. 1a, where the arrow informed only about the position, but not about response assignment of an imperative stimulus. Given that this effect is not due to the difference in task difficulty between the two experimental halves, it may be taken as evidence for the assumption that the CNV is closely related to specific response preparation in the S1-S2 interval.

A more direct measure of the amount and direction of response preparation in the cue-target interval is the lateralization of negativity measured above the left and right motor cortices (LRP). It was found that arrow

direction influenced lateralization systematically. In exp. 1b, a pronounced biphasic lateralization reflected response preparation for the side indicated by the precue. Since on approximately 75% of all trials, arrow direction signaled the correct response side, this lateralization tendency was to be expected. However, a qualitatively similar, albeit smaller, lateralization pattern was present in exp. 1a, where response side was not contingent upon arrow direction. It seems that specific response preparation processes can be induced by a spatial cue even when there is no objective connection between cue and response location.

The most striking finding of exp. 1 was that, in spite of highly significant RT benefits for validly cued trials, no electrophysiological evidence for early "sensory gating" of attended-to stimuli could be found. Neither P1 nor N1 component showed significant enhancement in response to validly cued targets. Since the RT pattern obtained in exp. 1a cannot be explained by reference to pre-target response preparation processes (which might have contributed to the RT benefit for valid trials in exp. 1b), it is most likely to be due to differential processing of valid and invalid stimuli. A reliable effect of cue validity found in exp. 1a was an enhanced negativity for validly cued trials in the P2 and N2 range. Since this effect had an onset latency of more than 200 msec, it cannot be regarded as an indicator of "sensory gating." Whether this negative shift for valid trials should be interpreted as a sign of enhanced post-sensory processing of attended-to stimuli is yet an open question. It is possible that the task of discrimi-

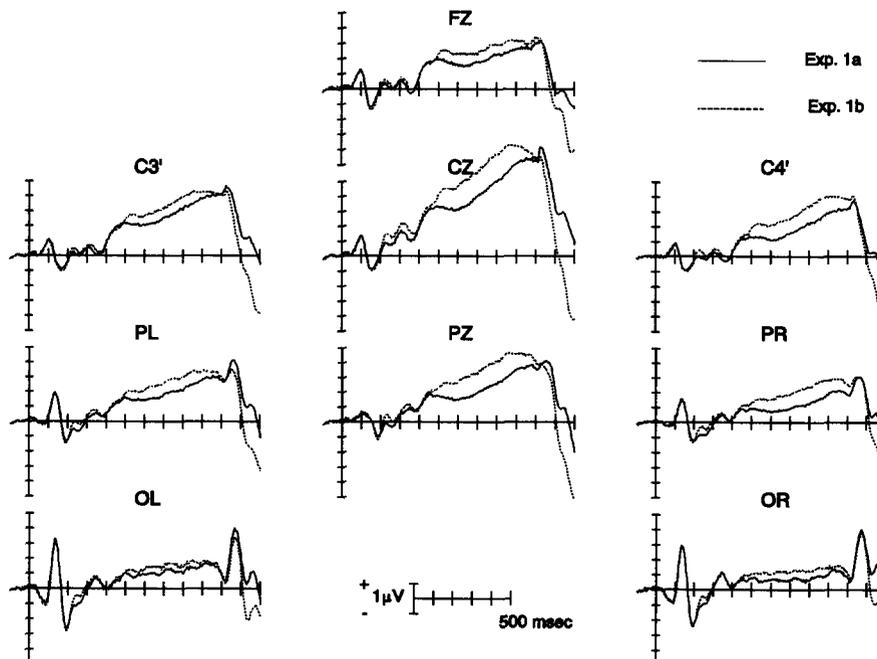


Fig. 4. Grand-averaged wave forms showing the CNV development in exp. 1a (Response Cue: Letter Identity) and exp. 1b (Response Cue: Letter Position) in the cue-target interval (relative to a 100 msec baseline prior to the onset of the cue stimulus).

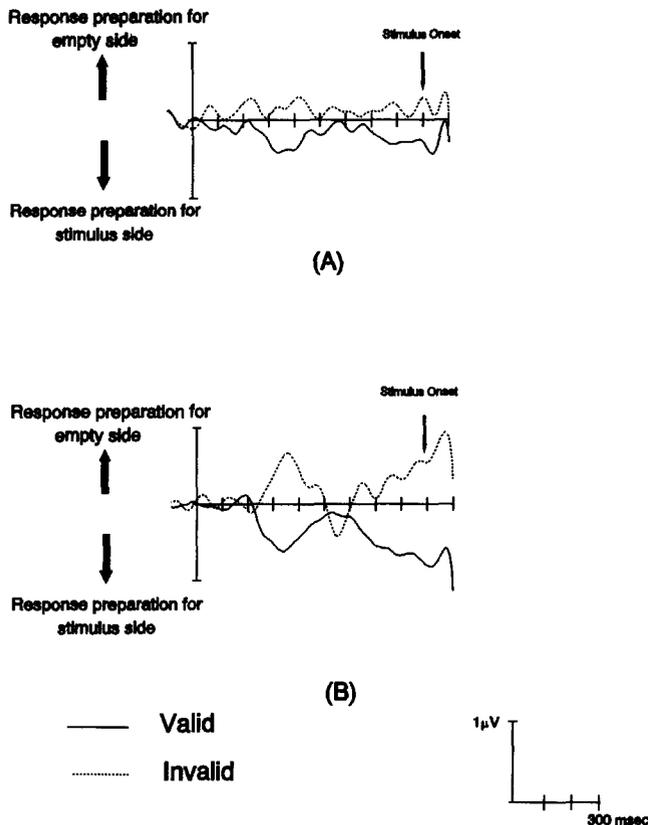


Fig. 5. Lateralized readiness potential in the cue-target interval. A: exp. 1a (Response Cue: Letter Identity). B: exp. 1b (Response Cue: Letter Position). Downward-going deflections reflect a negative lateralization measured over motor areas contralateral to the visual field of the imperative stimulus, indicating a tendency to prepare for a response at the stimulus side. Upward-going deflections indicate response preparation for the empty side. (Wave forms are low-pass filtered with a cut-off frequency of 12 Hz and 24 dB/oct roll-off.)

nating between two letters presented well above threshold was not difficult enough for subjects to direct their attention fully to the visual field indicated by the precue. If this were true, a somewhat more demanding discrimination task would be more likely to produce

TABLE II

Differences in lateralized readiness potential (LRP) amplitudes (μV) between valid and invalid trials for experiments 1a and 2a (Response Cue: Letter Identity) and experiments 1b and 2b (Response Cue: Letter Position) within consecutive time windows (intervals given in msec prior to letter onset).

Window latency (msec)	Exp. 1a	Exp. 1b	Exp. 2a	Exp. 2b
700–600	0.298	0.427	0.758 *	0.662 *
600–500	0.600 *	1.127 **	0.967 **	0.993 **
500–400	0.342	0.487	0.587 *	0.524
400–300	0.190	-0.099	0.336	-0.080
300–200	0.238	0.575 *	0.618 *	0.041
200–100	0.434 *	0.947 *	0.811 **	-0.051
100–0	0.410 *	1.201 **	0.426	-0.322
0–(-100)	0.456 *	1.492 **	0.512 *	-0.375

* $P < 0.05$; ** $P < 0.01$.

ERP modulations indicating preferential sensory processing of the attended side.

A second striking finding was the “inverse N1 validity effect” obtained in exp. 1b. Invalid trials elicited a larger N1 at posterior contralateral sites than did valid trials. Enhanced negativities for invalidly cued targets were also visible in midline records within the same latency range (cf., Fig. 3). These unexpected findings might be due either to an overlap with motor potentials or to differences in CNV resolution times for valid and invalid trials, respectively. Since RTs were about 60 msec faster in valid than in invalid trials, it is not implausible to assume that motor potentials or the onset of CNV resolution were partially overlapping with the development of the N1 component during valid trials, resulting in an artificial decrease of N1 amplitude. If this were true, the “inverse N1 effect” should disappear under experimental conditions where RTs are prolonged as compared to exp. 1b. Under these circumstances, motor potentials and CNV resolution should be delayed, thereby leaving the N1 component to valid trials unaffected.

Experiment 2

Experiment 2 was designed to test further the findings of exp. 1. Since discrimination difficulty was suspected to be a critical factor for ERP “sensory gating” effects, the discrimination task was made slightly more difficult by introducing a third letter stimulus. One letter was declared as Nogo stimulus, whereas the other two signaled left and right responses, respectively, so that subjects were required to make a 3-way discrimination (exp. 2a).

Another question left open by exp. 1 was whether the “inverse N1 effect,” observed when letter position served as response cue in exp. 1b, was an artifact of differential CNV resolution times for valid and invalid trials. This assumption was tested in exp. 2b, where the subject’s task was to give a right response to letters on the left side, and vice versa. Under these conditions, reaction times were expected to be considerably longer than in exp. 1b, where stimulus-response couplings were compatible. Motor potentials and CNV resolution onset should be delayed accordingly and thereby not affect the development of the N1 component for valid trials. If differential CNV resolution was the main cause for the “inverse N1 validity effect,” no such effect should be observable in exp. 2b.

Methods

Subjects

Thirteen paid volunteers participated in the experiment. One of them had to be excluded because of poor

eye fixation control in the cue-target interval. Thus 12 subjects (7 females), aged 21–39 years (mean age: 26.8 years), remained in the sample. All subjects were right-handed and had normal or corrected-to-normal vision.

Stimuli and apparatus

Stimuli and apparatus were identical to those in exp. 1, except that during one experimental half (exp. 2a), an additional letter stimulus (a capital N) was included.

Procedure

Two experimental halves (exp. 2a and 2b) were run. The overall procedure was identical to exp. 1, except that response instructions were different. In exp. 2a, subjects were instructed to press the left button when the letter M was presented and respond with the right hand when a the letter N appeared (Response Cue: Letter Identity). When the letter W was presented, subjects were instructed not to respond at all (Nogo stimulus). 16 out of 60 trials (12 valid and 4 invalid trials) per block were Nogo trials. In exp. 2b, stimuli were identical to exp. 1b, but subjects were required to respond with the left hand when a letter (either M or W) was presented on the right side, and with the right hand when the letter appeared on the left (Response Cue: Letter Location). Cue validity was kept at 73.3% for both exp. 2a and 2b. The order of experimental halves was balanced across subjects.

Recording and data analysis

These procedures were identical to those described above for exp. 1. In exp. 2a, Nogo trials were not analyzed, so that only ERPs to response-relevant (Go) stimuli will be discussed in the next sections. To test whether the “inverse N1 effect” found in exp. 1b is due to an overlap with motor potentials and CNV resolution in trials with short RTs, sub-averages based RT quartiles for valid and invalid trials were formed for exp. 2b.

Results

Behavioral performance

For both response assignments, RTs to validly cued letters were significantly shorter than RTs to invalidly indicated letters. When letter identity served as response cue (exp. 2a), mean RT for valid trials was 511 ± 15 msec, as compared to 530 ± 25 msec for invalid trials ($F(1, 11) = 23.01$; $P < 0.001$). In the case of letter position as response cue (exp. 2b), the mean RT was 312 ± 12 and 369 ± 19 msec, respectively ($F(1, 11) = 31.05$; $P < 0.000$). Contrary to exp. 1, neither stimulus-response compatibility effects (in exp. 2a) nor significant advantages for right-hand responses could be observed. In exp. 2a, error rates for valid and

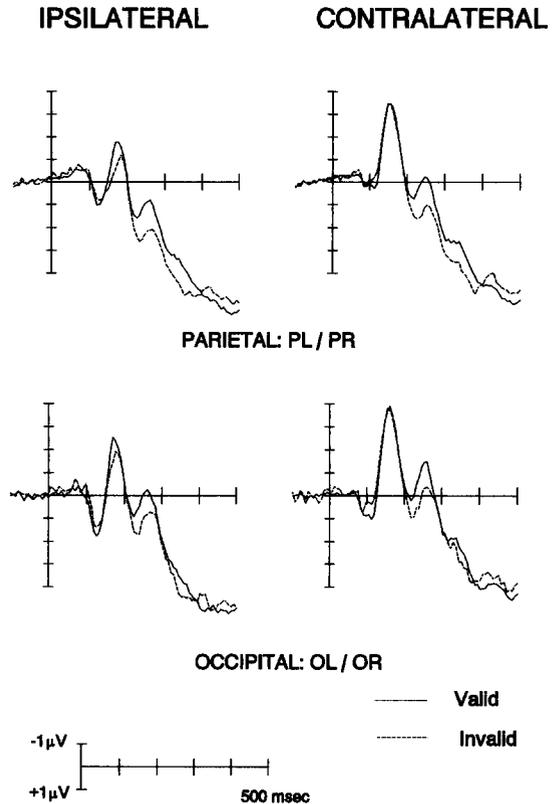


Fig. 6. Grand-averaged ERPs at parietal and occipital recording sites ipsilateral and contralateral to the visual field of presentation for validly and invalidly cued imperative stimuli, experiment 2a (Response Cue: Letter Identity).

invalid trials were not significantly different (2.7% vs. 3.0%). In exp. 2b, response errors occurred more often in the case of invalid trials (4.7% vs. 1.6%; $t(1, 11) = -3.03$; $P < 0.011$).

ERPs elicited by the imperative stimulus

Experiment 2a. Grand-averaged ERPs elicited by validly and invalidly cued imperative letter stimuli at ipsilateral and contralateral posterior sites are shown in Fig. 6. A significant P1 validity effect emerged at occipital sites ($F(1, 11) = 6.32$; $P < 0.029$) both for ipsilateral and contralateral locations. N1 amplitude was enhanced for validly indicated letters at parietal sites ($F(1, 11) = 5.21$; $P < 0.043$), but this effect failed to reach significance at occipital electrodes ($F(1, 11) = 4.41$; $P < 0.060$). However, a highly significant 3-way interaction (validity \times side of recording \times visual field of presentation; $F(1, 11) = 23.61$; $P < 0.001$, at parietal sites; $F(1, 11) = 6.23$; $P < 0.030$ at occipital sites), indicated that the N1 validity effect was considerably larger at ipsilateral scalp sites. At ipsilateral parietal and occipital sites, N1 mean amplitude was significantly more negative for validly cued letters ($t(1, 11) = -3.92$; $P < 0.002$, at PL/PR; $t(1, 11) = -3.21$; $P < 0.008$, at OL/OR), whereas there was no validity

effect at contralateral recording sites. Beyond 200 msec post stimulus, parietal and occipital ERPs to valid trials displayed a pronounced negative shift when compared to ERPs for invalid trials. This is reflected in a validity effect in the P2 and N2 latency range ($F(1, 11) = 20.32$; $P < 0.001$, and $F(1, 11) = 15.95$; $P < 0.002$, respectively). Enhanced negativities to valid trials were also present at midline scalp sites (F_z , C_z , P_z ; $F(1, 11) = 19.67$; $P < 0.001$, not shown in figures). Invalidly cued stimuli elicited a larger P3 amplitude than valid letters at midline electrode locations. However, as indicated by an interaction between validity and electrode location ($F(2, 22) = 7.93$; $P < 0.006$, GG), this effect was present only at F_z and C_z , but not at P_z .

Experiment 2b. Fig. 7 shows grand-averaged posterior ERPs to valid and invalid trials for scalp sites ipsilateral and contralateral to the visual field of presentation. At occipital sites the validity effect on P1 amplitude failed to reach significance ($F(1, 11) = 4.13$; $P < 0.067$). It reached significance, however, for parietal recording sites ($F(1, 11) = 6.00$; $P < 0.032$). Although cue validity did not yield a significant main effect on N1 mean amplitude, there was a validity effect at sites contralateral to the field of stimulus presentation. At contralateral electrodes, N1 mean amplitude was enhanced for invalid trials ($t(1, 11) = 3.37$;

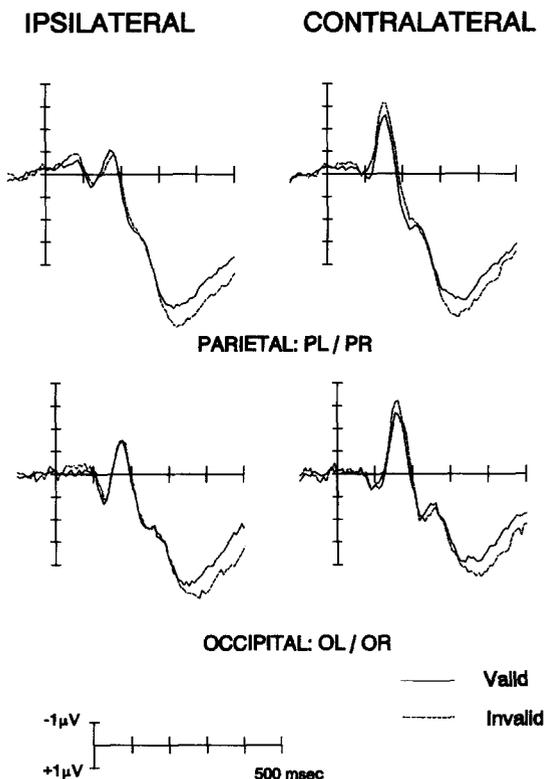


Fig. 7. Grand-averaged ERPs at parietal and occipital recording sites ipsilateral and contralateral to the visual field of presentation for validly and invalidly cued imperative stimuli, experiment 2b (Response Cue: Letter Position).

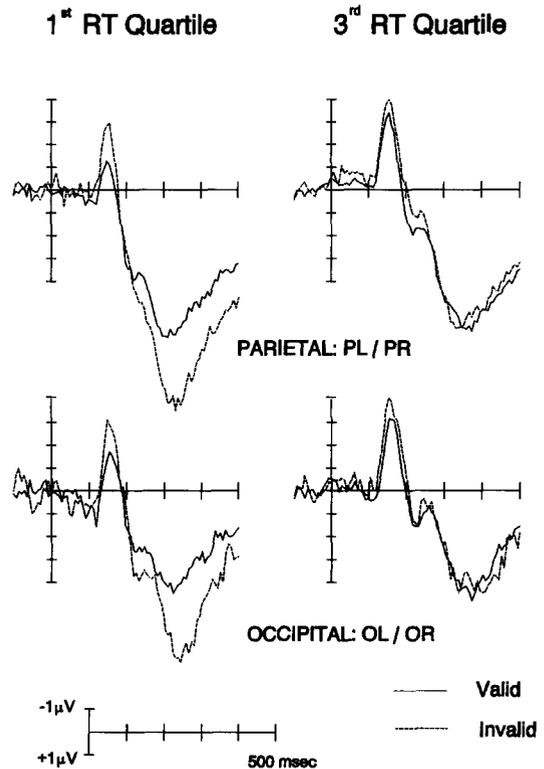


Fig. 8. Sub-averaged ERPs based on RT quartiles at parietal and occipital recording sites contralateral to the visual field of stimulation for validly and invalidly cued imperative stimuli, experiment 2b (Response Cue: Letter Position). Left side: 1st RT quartile. Right side: 3rd RT quartile.

$P < 0.006$, at parietal sites; $t(1, 11) = 3.20$; $P < 0.008$ at occipital sites). No significant difference was found at ipsilateral sites. As revealed by the sub-averages formed on the basis of RT quartiles, this “inverse N1 effect” was found not only with trials with short RTs, but also for the 2nd and 3rd RT quartile (cf., Fig. 8). A negative enhancement for invalidly cued trials was also visible at midline recording sites between 160 and 210 msec post stimulus ($F(1, 11) = 19.06$; $P < 0.001$). Invalidly indicated letters elicited a larger P3 than did valid trials. This effect was visible at lateral parieto-occipital sites ($F(1, 11) = 16.25$; $P < 0.002$) as well as at midline electrodes ($F(1, 11) = 18.76$; $P < 0.001$).

ERPs in the cue-target interval

CNV effects. CNV amplitudes elicited in the cue-target interval of exp. 2a were compared to the CNV recorded during exp. 2b for each electrode location (cf., Fig. 9). Amplitude differences between the two response assignment conditions could be observed at most recording sites, starting 400 msec prior to the imperative stimulus and extending beyond letter onset. Larger CNV amplitudes were elicited during exp. 2b. This effect was most pronounced at central recording sites, but without clear hemispheric dominance.

LRP effects. Lateralization in validly cued trials was compared to the lateralization in invalid trials during the cue-target interval for exp. 2a and 2b (cf., Fig. 10 and Table II). In exp. 2a, a biphasic lateralization pattern (with a first phase extending from 700 to 400 msec pre stimulus, and the second phase from 300 msec before to 100 msec after letter onset) indicated preparation of the response side pointed to by the arrow cue. The same tendency was visible during the first lateralization phase of exp. 2b (between 700 and 500 msec pre stimulus). During the later part of the cue-target interval, however, this lateralization disappeared, giving way for a reverse LRP pattern at the time of letter onset, where a tendency to prepare for the response contralateral to the arrows' direction was visible. However, this latter effect failed to reach statistical significance.

Discussion of experiment 2

Some questions raised by experiment 1 received at least a tentative answer from experiment 2. Increasing discrimination difficulty seems to have affected early attention-related ERP modulations. In contrast to exp. 1a, where no ERP signs of "sensory gating" were found, there was an early sensory-specific validity effect in exp. 2a. Most notably, P1 amplitude was enhanced for validly as compared to invalidly cued targets. Cue validity also affected the N1 component at lateral posterior sites in exp. 2a; that is, N1 was more negative for valid trials. The N1 validity effect was found to have an ipsilateral distribution and was not

visible at recording sites contralateral to the visual field of presentation.

In exp. 2b, RTs to validly cued letters were delayed about 60 msec as compared to exp. 1b due to the stimulus-response incompatibility. Motor potentials and the onset of CNV resolution should also be delayed and therefore no longer overlap with the N1 component in valid trials. However, the "inverse N1 validity effect" observed in exp. 1b was still present. As can be seen from the sub-averages based on RT quartiles (cf., Fig. 8), this effect was largest for trials with short RTs, but was present also for longer-latency responses. It is thus rather unlikely that overlap with motor potentials or differential CNV resolution times for valid and invalid trials are the only factors responsible for the "inverse N1 effect."

With regard to the CNV elicited in the cue-target interval and its interpretation as a sign of selective response preparation, exp. 2 confirmed the findings of exp. 1. CNV amplitude was found to be larger in response to partially informative cues (exp. 2b) as compared to precues that contained no information about the future response. This CNV effect had a longer duration and was more broadly distributed than in exp. 1. One explanation for this is the inclusion of Nogo trials in exp. 2a, which reduced the overall response probability and thereby presumably also the amount of CNV produced in the cue-target interval.

Somewhat surprising results were found with the LRP measures. In exp. 2a, the findings from exp. 1a were confirmed: although the precue contained no information about the response to be performed after

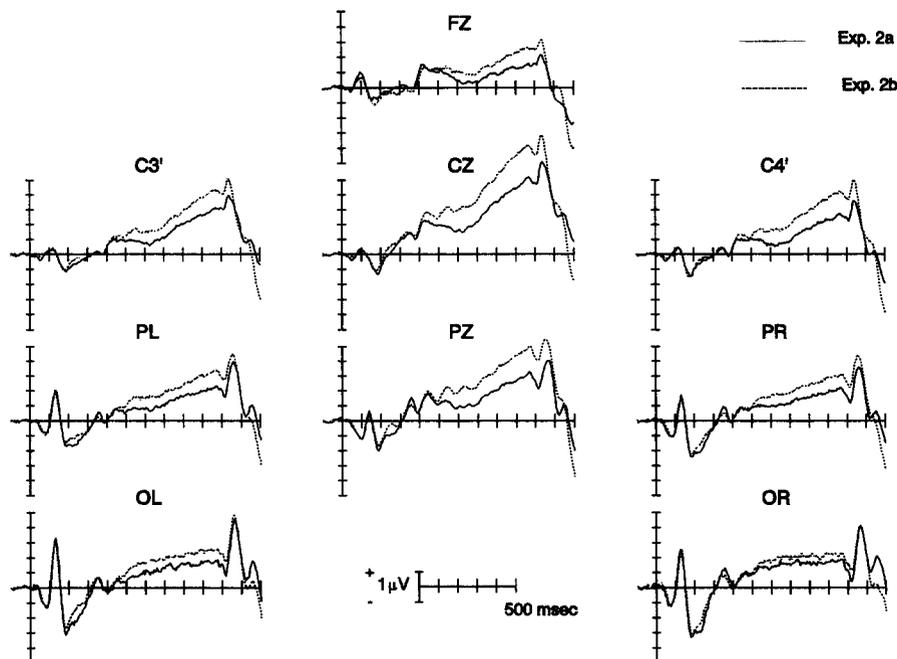


Fig. 9. Grand-average wave forms showing the CNV development in exp. 2a (Response Cue: Letter Identity) and exp. 2b (Response Cue: Letter Position) in the cue-target interval (relative to a 100 msec baseline prior to the onset of the cue stimulus).

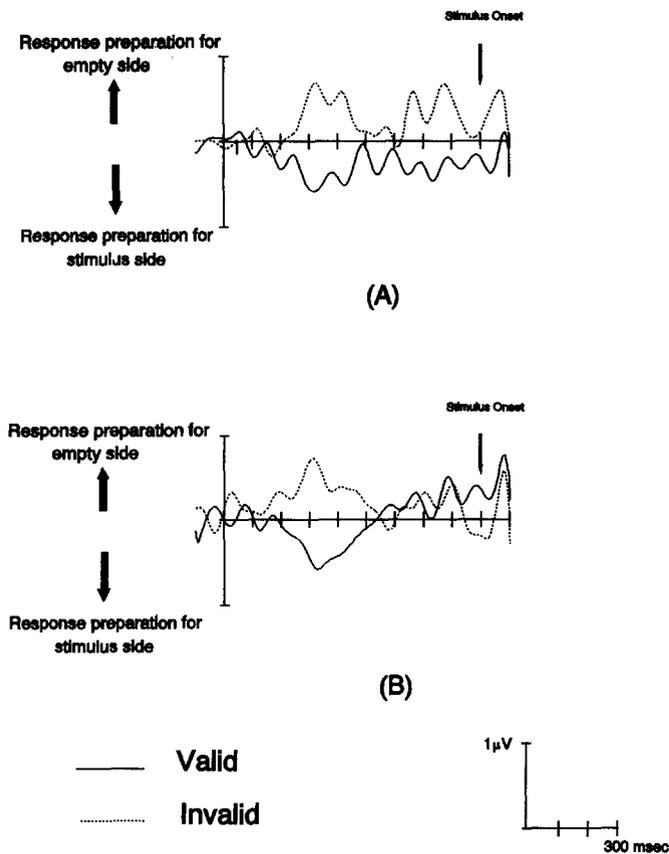


Fig. 10. Lateralized readiness potential in the cue-target interval. A: exp. 2a (Response Cue: Letter Identity). B: exp. 2b (Response Cue: Letter Position). Downward-going deflections reflect a negative lateralization measured over motor areas contralateral to the visual field of the imperative stimulus, indicating a tendency to prepare a response on the stimulus side. Upward-going deflections indicate response preparation for the empty side. (Wave forms are low-pass filtered with a cut-off frequency of 12 Hz and 24 dB/oct roll-off.)

the imperative stimulus, subject's lateralization patterns revealed a tendency to prepare the response side that was indicated by the arrow. Again, a biphasic lateralization pattern was visible. In exp. 2b, the required response was always contralateral to the visual stimulus field (and therefore contralateral to the arrow's direction in about 75% of all trials). However, the first phase of the LRP was virtually identical to the LRP pattern obtained for exp. 1b (cf., Figs. 4 and 8). It indicated preparation for a response that, given the different instructions, was likely to be the "wrong" one. Shortly before the onset of the imperative stimulus, however, this pattern reversed, revealing a (non-significant) preparation for a response contralateral to the arrow's direction. It may be concluded that the first phase of response preparation as manifested by LRP measures is immediately driven by the spatial properties of the precue, and not by specific task demands. With a conflicting response instruction (as in exp. 2b), this initial preparation tendency might be reversed even before the imperative stimulus was presented.

General discussion

When studying the orienting of visual attention within a trial-by-trial cueing paradigm, at least two consecutive processes have to be distinguished. First, a spatial cue is identified and used to orient attention within the cue-target interval. After target onset, visual processing is selectively modulated according to the position of the target relative to the attentional focus. According to the "sensory gating" hypothesis, the primary "attentional tuning" process in the cue-target interval might be based on a selective modulation of visual pathways for specific retinal locations (cf., Harter and Aine 1984). Electrophysiological evidence for this hypothetical process has been reported by Harter et al. (1989), who found a lateralized posterior negativity in the cue-target interval that was attributed to the active orienting of attention.

In the present study, processes within the cue-target interval have been studied that are not directly related to attentional orienting. Some evidence has been found that spatial precues are used for response preparation. If precues carry response-relevant information, CNV amplitude is enhanced as compared to the CNV elicited by non-informative cues. However, specific response tendencies seem to be evoked not only by informative cues, but also when both alternative responses are equally likely. As indicated by LRP measures, the spatial properties of the precue seem to exert a strong influence on initial lateralization regardless of specific response instructions. This was most evident when the arrow pointed to the side opposite to the likely response, where the initial lateralization indicated preparation of the presumably false response. It may tentatively be assumed that the two lateralization phases that were distinguishable in the cue-target interval are functionally different. In the first phase, the spatial properties of the cue are dominant, whereas the LRP in the second phase seems to be influenced mainly by specific response expectancies.³

According to the "sensory gating" hypothesis, targets presented in the focus of attention receive preferential perceptual processing which is manifested in enhanced P1- and N1 components for validly cued letters. In the experiments reported above, such validity effects were found to be highly dependent on spe-

³ This interpretation of lateralized negativities in the cue-target interval differs from that offered by Harter et al. (1989), who found a lateralized negativity between cue and target at posterior sites and interpreted it as a sign for the active direction of attention. In contrast to these findings, post-hoc comparisons of the lateralization at central sites with those over lateral parietal and occipital electrode pairs revealed that it was either maximal at C₃-C₄ (in exp. 1a, 1b and 2a) or equally distributed over central and parietal electrodes (in exp. 2b).

cific task characteristics. A reliable posterior P1 validity effect was found only when the feature discrimination task preceding response decision was rather difficult (exp. 2a). The N1 component tended to be enhanced for validly cued trials when letter identity was relevant for response selection. This effect was found to be localized over the scalp ipsilateral to the visual field of presentation in both exp. 1a and exp. 2a, confirming similar results obtained within a trial-by-trial cueing paradigm reported by Mangun and Hillyard (1991). However, these findings stand in contrast to ERP studies employing a sustained attention paradigm, where attended-to stimuli usually elicit contralaterally focussed N1 enhancements. With respect to these differences in scalp localization, it seems doubtful whether the N1 validity effects obtained with trial-by-trial cueing and during sustained attention reflect functionally similar underlying mechanisms.

An important difference between trial-by-trial cueing and sustained attention paradigms is the fact that, in the latter case, stimuli in the to-be-ignored visual field are not response-relevant, while invalidly cued stimuli always require a response in the Posner paradigm. Thus sustained attention tasks may allow for a complete focussing of attention at the relevant side, while a similar attentional policy might lead to considerable performance deficits in the trial-by-trial cueing situation. This difference might be responsible for the fact that sensory-specific ERP effects of visuo-spatial attention are quite small for the trial-by-trial cueing paradigm, especially when compared to P1 and N1 modulations found with sustained attention tasks.

Another quite surprising finding whose functional interpretation is far from clear is the "inverse N1 validity effect" obtained when letter location was relevant for response selection. As the initial hypothesis of differential CNV resolution times for valid and invalid trials as the main cause for this effect could not be confirmed in exp. 2b, alternative explanations have to be considered. It might tentatively be assumed that whenever the importance of the spatial localization of imperative stimuli is stressed (e.g., when letter location serves as response cue), the precue leads to specific expectations with regard to stimulus position. Disconfirmation of such expectations might be manifested in the ERP as a "mismatch negativity"-like negative deflection for invalid trials. This assumption is in line with the finding that negative enhancements for invalid trials were not confined to occipital and parietal electrodes, but could also be observed over midline scalp sites. It is thus conceivable that the N1 component is selectively influenced by two counteracting experimental factors. Valid trials might have elicited enhanced N1 amplitudes at ipsilateral sites (most notably in the "Response Cue: Letter Identity" condition), whereas "expectation mismatch" negativities were elicited by

invalidly cued letters (presumably more strongly in the "Response Cue: Letter Position" condition). This hypothesis could explain both the rather small N1 validity effects observed in the present experiments (because an enhanced negativity in the N1 range was elicited by invalid trials as well) and the contralaterality of the "inverse N1 effect" (because the N1 validity effect was much smaller at contralateral recording sites). However, as the existence of MMN-like negativities in the visual modality is a matter of recent discussion (cf., Alho et al. 1992; Woods et al. 1992), further research is necessary to establish the proper functional interpretation of the differential N1 modulations observed in the present experiments.

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References

- Alho, K., Woods, D.L. and Algazi, A. Intermodal selective attention. I. Effects of attentional load on processing of auditory and visual stimuli in central space. *Electroenceph. clin. Neurophysiol.*, 1992, 82: 356–368.
- Bashinski, H.S. and Bacharach, V.R. Enhancement of perceptual sensitivity as the result of selectively attending to spatial locations. *Percept. Psychophys.*, 1980, 28: 241–248.
- Coles, M.G.H. Modern mind-brain reading: psychophysiology, physiology, and cognition. *Psychophysiology*, 1989, 26: 251–269.
- Coles, M.G.H., Gratton, G. and Donchin, E. Detecting early communication: using measures of movement-related potentials to illuminate human information processing. *Biol. Psychol.*, 1988, 26: 69–89.
- Downing, C.J. Expectancy and visual-spatial attention: effects on perceptual quality. *J. Exp. Psychol.: Hum. Percept. Perform.*, 1988, 14: 188–202.
- Eason, R.G. Visual evoked potentials correlates of early neural filtering during selective attention. *Bull. Psychon. Soc.*, 1981, 18: 203–206.
- Gaillard, A.W.K. The CNV as an index of response preparation. In: W.C. McCallum, R. Zappoli and F. Denoth (Eds.), *Cerebral Psychophysiology: Studies in Event-Related Potentials*. Elsevier, Amsterdam, 1986: 196–206.
- Harter, M.R. and Aine, C.J. Brain mechanisms of visual selective attention. In: R. Parasuraman and D.R. Davies (Eds.), *Varieties of Attention*. Academic Press, London, 1984: 293–321.
- Harter, M.R., Aine, C. and Schroeder, C. Hemispheric differences in the neural processing of stimulus location and type: effects of selective attention on visual evoked potentials. *Neuropsychologia*, 1982, 20: 421–438.
- Harter, M.R., Miller, S.L., Price, N.J., LaLonde, M.E. and Keyes, A.L. Neural processes involved in directing attention. *J. Cogn. Neurosci.*, 1989, 1: 223–237.
- Hawkins, H.L., Hillyard, S.A., Luck, S.J., Mouloua, M., Downing, C.J. and Woodward, D.P. Visual attention modulates signal detectability. *J. Exp. Psychol.: Hum. Percept. Perform.*, 1990, 16: 802–811.

- Heinze, H.J., Luck, S.J., Mangun, G.R. and Hillyard, S.A. Visual event-related potentials index focussed attention within bilateral stimulus arrays. I. Evidence for early selection. *Electroenceph. clin. Neurophysiol.*, 1990, 75: 511–527.
- Hillyard, S.A. and Mangun, G.R. Sensory gating as a physiological mechanism for visual selective attention. In: R. Johnson, Jr., R. Parasuraman and J.W. Rohrbaugh (Eds.), *Current Trends in Event-Related Potential Research*. Elsevier, Amsterdam, 1987: 61–67.
- Hillyard, S.A. and Münte, T.F. Selective attention to color and location: an analysis with event-related brain potentials. *Percept. Psychophys.*, 1984, 36: 185–198.
- Hillyard, S.A., Münte, T.F. and Neville, H.J. Visual-spatial attention, orienting and brain physiology. In: M.I. Posner and O.S. Marin (Eds.), *Mechanisms of Attention: Attention and Performance XI*. Erlbaum, Hillsdale, NJ, 1985: 63–84.
- Jonides, J. Voluntary versus automatic control over the mind's eye's movement. In: J.B. Long and A.D. Baddeley (Eds.), *Attention and Performance*, Vol. IX. Erlbaum, Hillsdale, NJ, 1981: 187–203.
- Luck, S.J., Heinze, H.J., Mangun, G.R. and Hillyard, S.A. Visual event-related potentials index focused attention within bilateral stimulus arrays. II. Functional dissociation of P1 and N1 components. *Electroenceph. clin. Neurophysiol.*, 1990, 75: 528–542.
- Mangun, G.R. and Hillyard, S.A. Spatial gradients of visual attention: behavioral and electrophysiological evidence. *Electroenceph. clin. Neurophysiol.*, 1988, 70: 417–428.
- Mangun, G.R. and Hillyard, S.A. Electrophysiological studies of visual selective attention in humans. In: A. Scheibel and A. Wechsler (Eds.), *The Neurobiological Foundations of Higher Cognitive Function*. Guilford Press, New York, 1990: 271–294.
- Mangun, G.R. and Hillyard, S.A. Modulations of sensory-evoked brain potentials indicate changes in perceptual processing during visual-spatial priming. *J. Exp. Psychol.: Hum. Percept. Perform.*, 1991, 17: 1057–1074.
- Mangun, G.R., Hansen, J.C. and Hillyard, S.A. The spatial orienting of visual attention: sensory facilitation or response bias? In: R. Johnson, Jr., R. Parasuraman and J.W. Rohrbaugh (Eds.), *Current Trends in Event-Related Potential Research*. Elsevier, Amsterdam, 1987: 118–124.
- Müller, H.J. and Findlay, J.M. Sensitivity and criterion effects in the spatial cueing of visual attention. *Percept. Psychophys.*, 1987, 42: 383–399.
- Müller, H.J. and Rabbit, P.M.A. Reflexive and voluntary orienting of visual attention: time course of activation and resistance to interruption. *J. Exp. Psychol.: Hum. Percept. Perform.*, 1989, 15: 315–330.
- Posner, M.I. Orienting of attention. *Quart. J. Exp. Psychol.*, 1980, 32: 3–25.
- Posner, M.I., Nissen, M.J. and Ogden, W.C. Attended and unattended processing modes: the role of set for spatial location. In: H.L. Pick and E.J. Saltzman (Eds.), *Modes of Perceiving and Processing Information*. Erlbaum, Hillsdale, NJ, 1978: 137–157.
- Posner, M.I., Snyder, C.R.R. and Davidson, B.J. Attention and the detection of signals. *J. Exp. Psychol.: Gen.*, 1980, 109: 160–174.
- Posner, M.I., Cohen, Y. and Rafal, R.D. Neural systems control of spatial orienting. *Proc. Roy. Soc. Lond. B*, 1982, 298: 187–198.
- Sperling, G. A unified theory of attention and signal detection. In: R. Parasuraman and D.R. Davies (Eds.), *Varieties of Attention*. Academic Press, Orlando, FL, 1984: 103–181.
- Woods, D.L., Alho, K. and Algazi, A. Intermodal selective attention. I. Effects on event-related potentials on lateralized auditory and visual stimuli. *Electroenceph. clin. Neurophysiol.*, 1992, 82: 341–355.