

# **Mechanisms of Visuospatial Attention: Evidence from Event-related Brain Potentials**

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A series of experiments are reviewed that studied mechanisms underlying visuospatial attention by measuring the influence of attentional selectivity on event-related brain potentials (ERPs). The results are interpreted within a theoretical framework developed by LaBerge (1995) and LaBerge and Brown (1989). Spatial attention can have an effect on occipital P1 and N1 components in trial-by-trial cueing situations, which indicate a spatially selective modulation of processing in the VI-IT pathway. However, this effect is strongly attenuated when unattended locations are potentially relevant, suggesting that early attentional modulations within the ventral stream are optional rather than obligatory. A distinct parietal negativity (Nd1) that is elicited in cued attention tasks is assumed to reflect the existence of a transient location expectation gradient within the posterior parietal cortex (PPC). This effect is not present in sustained attention situations. The fact that this effect is also observed with auditory stimuli suggests that this spatially selective PPC activity is modality-unspecific. Attentional selectivity in multi-stimulus arrays is reflected by the N2pc component, which may indicate location-specific processing modulations in the ventral pathway that are contingent upon an initial feature analysis.

## INTRODUCTION

Selective attention serves an important function in regulating the impact of external stimulation on behaviour. Attentional mechanisms are responsible for selecting which environmental objects and events come to control the discriminative performance of organisms when they are confronted with multiple

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potentially relevant stimuli. Attentional selectivity has often been interpreted to result from the fact that processing capacity is limited and that objects and events therefore have to compete for perceptual processing, identification and control of performance. Mechanisms of selective attention are thought to bias this competition in favour of information that is currently most important for adaptive behaviour (Desimone & Duncan, 1995).

Given this interpretation, selective attention may have several different functions, depending on the locus of competitive processes that are influenced by attention. Attention may serve to ensure that relevant sensory information is adequately processed (Broadbent, 1958), but may also be necessary for the selection and execution of specific responses (Allport, 1980). Because of this multiplicity of attentional functions, it is unlikely that the search for unitary mechanisms underlying selective attention will be successful. A more fruitful research strategy is to specify, as precisely as possible, different attentional functions and mechanisms and to relate these in turn to evidence from behavioural as well as neurobiological studies (Allport, 1993). This approach may eventually show that some of the controversial issues in the study of selective attention—including the debate over “early” versus “late” selection and the discussion about the special status of selection by spatial location—were based on simplified assumptions about general properties of attentional mechanisms that will come to be replaced by more specific characterizations of single attentional functions.

Studies of brain anatomy and function have played an increasingly important role in the investigation of selective attention, and the last decade has seen numerous studies in which attentional modulations on brain activity and effects of brain lesions on attentional functions were investigated. These studies have begun to reveal some of the mechanisms responsible for attentional selectivity by directly relating behavioural effects with underlying brain processes.

The focus of the present paper is the study of selective spatial attention with event-related brain potentials (ERPs). First, some general issues related to mechanisms underlying attentional selectivity will be discussed, focusing on a model originally proposed by LaBerge and Brown (1989) and further developed by LaBerge (1995), as this model will later serve as a conceptual framework for the interpretation of the ERP data. Then, a brief introduction to the methodology of ERP recordings will be given, and it will be argued that ERPs are a particularly suitable tool for investigating attentional functions and mechanisms. In the following sections, several ERP studies will be reported that investigated mechanisms of attentional selection by location in single-stimulus and multiple-stimulus arrays. The aim of this paper is to illustrate that ERP measures may provide a valuable source of information about the functional organization of attentional mechanisms.

## MECHANISMS OF ATTENTIONAL SELECTIVITY

One particularly prominent issue in the debate about the nature of attentional mechanisms concerns the locus of selectivity: Does attention operate at an early stage of perceptual processing—that is, before object identification and categorization—or at post-perceptual stages that follow the identification of objects? While initial studies of attention seemed to support the early selection view (Broadbent, 1958), late selection theories came to dominate the field inspired by numerous studies that found evidence of an automatic processing of unattended stimuli (Shiffrin & Schneider, 1977). Kahneman and Treisman (1984) suggested that this paradigm shift was due to the fact that the experimental situations investigated in the earlier studies (“filtering paradigms”) were typically more complex than the “selective set paradigms” employed in more recent research. They warned against direct inferences from the results obtained in studies of selective set to the nature of attentional mechanisms that operate in filtering situations. Early and late selection accounts are no longer viewed as mutually exclusive, and a number of theories have been put forward that combine assumptions from both the early and the late selection approach (Bundesen, 1990; Kahneman & Treisman, 1984; Lavie, 1995). Instead of searching for a single “locus of attentional selectivity”, it is now generally assumed that selection may occur at multiple loci within the information processing stream, and that the processes underlying these different selective processes may also differ from each other. Selection may proceed through a modulation of the activity of sensory neurons, can involve the selective facilitation or inhibition of neuronal responses in parietal or temporal cortex mediated by competitive processes, may affect the entry of specific information into a limited-capacity, short-term memory store, or could gate the admission of information to an executive control system (Allport, 1993).

Related to the issue of early versus late selection is the question of whether spatial location plays a unique role in attentional selectivity, so that the selection of other stimulus attributes is contingent on the correct detection of their location (Nissen 1985; Tsal & Lavie, 1993). Evidence for a specific role of location arises from the fact that spatial cues are more effective in directing attention than non-spatial cues (Johnston & Dark, 1986). In fact, the superior selectivity when relevant and irrelevant objects are spatially separated has often been interpreted as evidence in favour of an early selection account (see Allport, 1993, for a critique of this assumption). While some theorists explicitly assume that spatial location plays a unique role in selective attention (LaBerge & Brown, 1989; Treisman & Gelade, 1980; Van der Heijden, 1993), others hold that there is no qualitative difference between location and other, non-spatial selection attributes (Bundesen, 1990; Desimone & Duncan, 1995; Duncan & Humphreys, 1989).

Given that there are multiple loci of attentional selectivity, and different mechanisms underlying these selective processes, it is crucial for models of selective attention developed by cognitive psychologists to take into account the functional architecture of the primate cortex and, more specifically, results from neurobiological studies investigating the impact of attentional factors on cortical activity. One such model has been proposed by LaBerge and Brown (1989; see also LaBerge, 1995). It was originally designed to describe attentional mechanisms underlying the identification of objects in multi-stimulus arrays, but can also be applied to single-stimulus events. The main aspects of this model will now be described in some detail, since they are employed in later sections to interpret several findings from event-related brain potential studies of selective attention.

According to this model, attentional selectivity is the result of an interaction between the two main visual processing pathways—the dorsal stream and the ventral stream (Ungerleider & Mishkin, 1982)—that is mediated by subcortical structures (the thalamus and the superior colliculus). The ventral pathway connects visual areas V1 and V2 with V3, V4 and the posterior and anterior areas of the inferotemporal (IT) cortex (areas TEO and TE). Its main function is the discrimination and identification of objects. The dorsal stream connects areas V1 and V2 to the posterior parietal cortex (PPC) and deals mainly with the spatial aspects of object perception. In the ventral stream, visual information is initially received and processed by areas V1 and V2, and is then sent via V4 to the IT cortex, where object identification takes place. Attentional selectivity is assumed to modulate the information flow in the pathways connecting V1 with IT. This modulation is mediated by thalamic circuits that are under the control of spatial information originating from the dorsal stream. When the location of a relevant object is precued, an attentional location expectation gradient is set up in the posterior parietal cortex. If the object is then presented at the expected location, this attentional gradient acts either directly or through the thalamus to increase the flow of information from this location in the pathways connecting V1 with IT, while simultaneously suppressing the information flow from other locations. As a result of this filtering operation, the IT cortex only receives and operates on feature information originating from a selected location. When the target object is presented at an uncued location, the expectation gradient set up by the cue will initially be in competition with the activation elicited by the target within the posterior parietal cortex, thus delaying the attentional selection of relevant information in the ventral processing stream.

In addition to these mechanisms, processing within the dorsal and ventral streams is also assumed to be controlled by prefrontal structures. The dorso-lateral prefrontal cortex (DLPFC) is involved in spatial memory and serves an important role in eliciting voluntary shifts of attention (e.g. in response to the task instructions “attend to objects presented in the leftmost position”). Accord-

ingly, the DLPFC has direct projections to the PPC, where prefrontal signals may set up an attentional gradient, which in turn influences processing in the ventral stream. The ventrolateral prefrontal cortex (VLPFC) is involved in memory for object features and may thus be important when attention is directed to non-spatial features (e.g. in response to the task instructions “attend to all squares regardless of their position”). The VLPFC is assumed to exert a modulatory influence on processing within the IT cortex.

The model developed by LaBerge and Brown (1989) and LaBerge (1995) explicitly assumes that location plays a unique role in attentional selectivity: The modulation of the pathways connecting V1 to IT is under the control of location information represented in PPC or DLPFC. Moreover, it can be viewed as an early-selection theory, since it assumes that attentional selectivity, as instantiated by a filtering process, operates before stimulus identification: that is, before objects are processed within IT cortex. It should be noted, however, that our present knowledge of functional architecture of the ventral stream does not allow a clear distinction between “early”, pre-categorical perceptual processing and processes related to the identification of an object. It is not obvious that there is a unique place within the V1–V2–V4–TEO–TE pathway where elementary feature analysis is terminated and object identification begins. Instead of trying to determine if the modulatory influence of spatial information on visual processing is “early” or “late”, a more fruitful research strategy would be to localize specific areas within the ventral pathway where neuronal activity is affected by attention.

In later sections, several ERP studies are reported that studied the impact of selective spatial attention on information processing as indicated by a differential modulation of ERP waveforms elicited by stimuli at attended and unattended locations. The results of these studies will be discussed within the theoretical framework developed by LaBerge and Brown (1989) and LaBerge (1995), focusing on two central issues: (1) Is there evidence for an attentional modulation of information processing in the ventral stream and, if there is, does this modulation take place within the V1–IT pathway? (2) Can ERP measures provide information with respect to the presence of attentional location expectation gradients in the PPC cortex that are assumed to be set up in response to spatial precues? Before these experiments are discussed, the next section provides some general considerations about the ERP method and its utility for studying mechanisms of selective attention.

## ERP STUDIES OF VISUOSPATIAL ATTENTION

Event-related brain potentials (ERPs) reflect phasic modulations of brain activity that are time-locked to the onset of external or internal events. ERPs can be obtained by averaging the EEG activity measured in response to such events over a number of recording epochs. The result ERP waveforms consist

of positive- and negative-going deflections that are assumed to be generated at least partially by synchronous post-synaptic activities at the apical dendrites of pyramidal cells in cortical layer IV. These ERP deflections are labelled with respect to their polarity (positive or negative) and latency. In contrast to other measures of brain activity, such as single-cell recordings, ERPs provide a non-invasive method of monitoring brain events that take place during cognitive processing. They can thus be obtained with normal voluntary subjects under standard experimental conditions. Since ERPs provide a continuous on-line measure of cerebral activities, they can, in principle, be used as markers for specific stages of human information processing. To do this, the functional significance of ERP components has to be determined by studying how various experimental manipulations affect these components. Thus, one of the major aims in ERP research is to describe the relationship between ERP components and cognitive processes (see Coles, Gratton, & Fabiani, 1990, for a further discussion of this issue). Moreover, by localizing the cortical generators of ERP components that are markers for specific cognitive functions, ERPs can also provide information with respect to the functional architecture of the brain. It should be noted, however, that it is not possible to determine unequivocally the cerebral generators of ERP components exclusively on the basis of ERP scalp distributions. To discover which brain processes are responsible for ERP components, the ERP methodology has to be combined with other electrophysiological or neuroimaging techniques.

As a non-invasive continuous measure of the time course of cognitive processing that can also be obtained in the absence of overt response requirements, ERPs seem particularly suited for the study of attentional processes. In typical ERP studies of selective spatial attention, stimuli are presented at attended or at unattended locations, and ERP waveforms are computed for these different conditions. By comparing the ERPs elicited by attended-location and unattended-location stimuli, it is possible to determine when, and in what way, spatial attention comes to influence processing as reflected by the ERP waveforms. If specific ERP components are related to different cognitive operations, the presence or absence of systematic effects of selective attention on these components in different experimental circumstances may provide important information about the mechanisms underlying attentional selectivity. And by localizing the cerebral origin of the ERP components found to be sensitive to attentional manipulations, it is possible to identify those areas of the brain that subserve specific attentional functions.

## ERP EFFECTS OF VISUOSPATIAL ATTENTION IN THE VENTRAL PATHWAY

Visual information is first received by areas V1 and V2, where elementary feature information is represented and is then sent via V4 to IT cortex. In the

model described above (LaBerge, 1995), a spatially selective modulation of perceptual processing within the pathway connecting V1 to IT is caused by direct or indirect inputs from posterior parietal cortex, where expectancies about the location of relevant objects are represented by an attentional gradient that is set up in response to spatially informative precues. Such an influence of PPC signals on visual processing stages prior to IT may be responsible for behavioural effects of spatial precueing where single target stimuli are displayed in an otherwise empty field (Posner, Snyder, & Davidson, 1980). If such an influence does exist, one would expect to find evidence for it in the ERP waveforms elicited by stimuli at attended and unattended locations under conditions where the relevant location is specified in advance.

Most ERP studies on visuospatial attention have used a sustained attention paradigm. Instead of using precues, subjects are instructed at the beginning of each block to direct their attention to a specific location to detect target stimuli at that location (Eason 1981; Mangun & Hillyard, 1987). The typical outcome of such an experiment is shown in Fig. 1. In this unpublished study, letter stimuli (M and W) were presented with equal probability  $6^\circ$  to the left or right of the fixation. Subjects were instructed to respond to the letter W only when it was presented at the side specified prior to the start of each block (which was changed from left to right and back again between experimental blocks). A comparison of the ERPs elicited by attended- and unattended-location stimuli at occipital electrodes (collapsed over electrodes OL and OR, located halfway

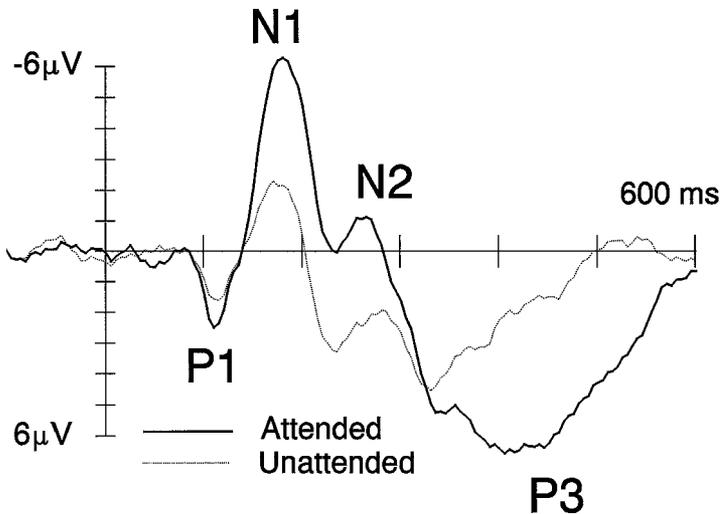


FIG. 1. Grand-averaged event-related brain potentials (ERPs) elicited by stimuli at attended locations (solid line) and unattended locations (dotted line) at lateral occipital sites (collapsed over electrodes OL and OR), in an experiment where subjects were instructed to keep their attention focused on the left or right side for an entire experimental block.

between O1 and T5, and O2 and T6, respectively) revealed systematic differences. Attention was found to modulate the P1, N1, N2 and P3 components, with larger amplitudes elicited by stimuli at attended locations. The earliest attentional effect was the amplitude modulation of the P1 component that started around 100 msec post-stimulus.

What conclusions can be drawn on the basis of this pattern of results? The enhancement of the N2 and P3 amplitudes are probably a result of the fact that 50% of the attended-location stimuli required a response, as N2 and P3 are known to be sensitive to the relevance of a stimulus for overt performance. In contrast, the earlier attentional modulations of the P1 and N1 components may be more directly related to mechanisms of spatial selectivity. The P1 and N1 components are often referred to as exogenous components, since they are triggered by visual stimuli independently of their psychological significance. Moreover, P1 and N1 are assumed to be sensory-specific, because they are elicited within different time windows, and with a different scalp distribution when non-visual stimuli are presented. This makes it likely that these components reflect early stages of visual-perceptual processes. In the context of the model discussed above, their attentional modulation may thus indicate a selective influence on processes that occur before the entry of visual information into IT cortex. Which visual areas within the V1–IT pathway are affected by attention? If it could be shown that the P1 component (where the earliest attentional amplitude modulations can be observed; see Fig. 1) is generated near to, or even within, striate cortex (V1), this would make a strong case in favour of an attentional modulation of elementary feature analysis.

Where is the cortical locus of the generator processes responsible for the P1 component? This was investigated in a study by Mangun, Hillyard, and Luck (1993), who instructed their subjects to attend to one out of four possible stimulus locations to detect infrequently presented targets at that location. To localize the attentional modulation of ERP components more precisely, current source density (CSD) analyses were conducted on the basis of ERP scalp distribution maps. The CSD maps were brought into register with the cortical gyri and sulci that were determined on the basis of each subject's individual MRI scan. With this technique, Mangun et al. (1993) located the P1 component over the ventrolateral prestriate occipital cortex; that is, outside V1, but presumably posterior to IT cortex. If P1 amplitude modulations constitute the earliest effects of visuospatial attention on ERP waveforms, and the P1 is generated in extrastriate areas, this would indicate that attention may not affect processes within the primary visual cortex. That would be in line with evidence from single-cell recordings that failed to find an attentional influence on the electrical activity of cells within striate cortex, but obtained strong modulatory effects for extrastriate cells (Desimone, 1993; but see Motter, 1993, for different results). With the help of ERP measurements, there is a direct way of finding out whether brain processes within striate cortex are modulated by spatial

attention. Since the human primary visual cortex is folded within the calcarine fissure, stimuli from the lower and upper visual fields are projected to separate, oppositely oriented cortical areas within the upper and lower banks of the calcarine fissure. An ERP component that is generated within striate cortex should therefore be strongly dependent upon the vertical location of a stimulus within the visual field. It should reverse polarity when ERPs elicited by stimuli from the upper and lower visual fields are compared. If an ERP component that showed this sort of polarity reversal was modulated by spatial attention, this would constitute a strong case in favour of attentional effects on processes within striate cortex.

This was investigated in an experiment (Eimer, 1997) where stimuli were presented in a regular (clockwise or counterclockwise) order in one of the four visual quadrants (see Fig. 2a). Occasionally, stimuli were presented at irregular and, therefore, unexpected locations. The subjects' task was to respond to infrequently presented target stimuli. It was assumed that subjects would direct their attention in accordance with the regular order of stimulus presentation, and that stimuli at irregular positions would therefore be unattended. The reaction time (RT) results confirmed these predictions, with faster RTs to targets at regular (attended) compared with irregular (unattended) positions. ERPs were computed for expected- and unexpected-location stimuli separately for stimuli presented in the upper and lower visual fields. As pointed out before, an ERP component generated within striate cortex should reverse polarity in response to upper versus lower visual field stimuli. When the ERPs elicited by upper and lower visual field stimuli were compared, one component indeed showed a polarity reversal. This component (NP80) was maximal at midline parietal sites (electrode Pz), had a latency of about 70–80 msec (indicated in Fig. 2b by the arrow), and was positive for stimuli in the lower visual field, but negative for stimuli in the upper visual field. These properties are consistent with the assumption that the NP80 is generated within striate cortex. Further analyses revealed that this component was not affected by attention (see Mangun, 1995; for similar observations). At occipital electrodes, visuospatial attention again had a small but significant effect on the amplitudes of the P1 and N1 components, whereas the NP80 was not affected by attention at all (see Fig. 2c, for stimuli in the upper visual field).

Whereas the P1 is likely to be generated in the extrastriate ventro-lateral cortex, the exact location of the generator processes responsible for the occipital N1 component are unknown. One reason for this is that the N1 is rather broadly distributed over posterior as well as anterior regions of the scalp, indicating that it may result from the activity of several, spatially distinct generator regions. Recent evidence (Johannes, Münte, Heinze, & Mangun, 1995) has indicated that there are at least two functionally distinct posterior N1 components. A parietal N1 that is maximal around 170 msec after stimulus onset is followed by another N1 peaking around 200 msec with a distinct occipito-temporal

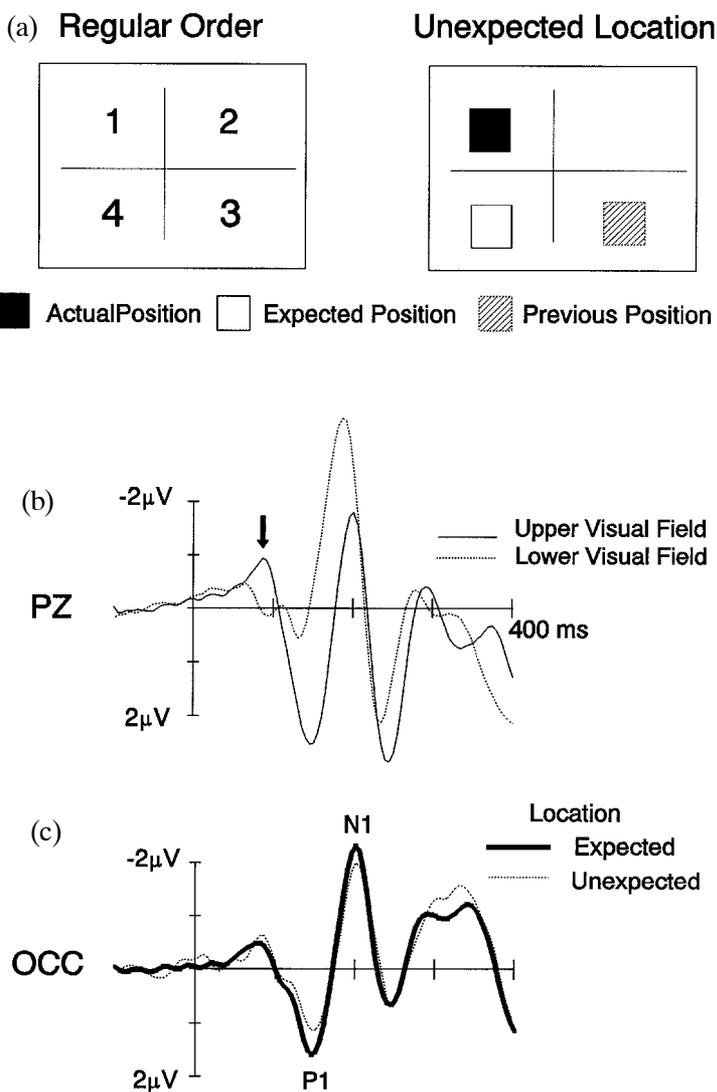


FIG. 2. (a) Illustration of an experiment where most stimuli were presented sequentially at predictable locations (clockwise: 1-2-3-4), and occasional stimuli were presented at unexpected (unattended) locations. (b) Grand-averaged ERPs elicited at electrode Pz by stimuli in the upper half (solid line) and lower half (dotted line) of the visual field. The arrow indicates the presence of a component (NP80) that inverses polarity for upper as compared with lower field stimuli. (c) Grand-averaged ERPs elicited at occipital electrodes (collapsed over OL and OR) by expected-location (solid line) and unexpected-location stimuli (dotted line) in the upper visual field.

distribution. Mangun (1995) has tentatively argued that the occipital P1 and N1 components reflect processing within the ventral pathway, whereas the parietal N1 component is related to processing within the dorsal stream. If the parietal N1 and the occipital N1 components reflect activity within separate pathways, it is likely that attentional modulations of these components indicate functionally different selective processes. This will be discussed further below.

It should be noted that attentional modulations of the occipital P1 component were not found in ERP studies where attention was directed to a non-spatial feature like stimulus colour (Wijers et al., 1989). Non-spatial selective attention usually results in a negative enhancement of the ERPs elicited by stimuli with to-be-attended features that starts more than 150 msec post-stimulus, and therefore does not affect the amplitude of the P1 component. Hillyard and Münte (1984) found that these ERP effects of attention directed to colour were larger for stimuli at attended locations than for stimuli at unattended locations, and argued that the selective processing of colour may even be contingent upon the prior selection of stimuli on the basis of their location. This seems to support the assumption that the location of objects plays a unique role in attentional selectivity (see above). However, in another condition of Hillyard and Münte, (1984) experiment, where both possible stimulus locations were in close proximity, ERP effects of colour selection preceded the effects of spatial selectivity, indicating that the latency of the attentional ERP effects may depend not only on the type of stimulus attribute relevant for attentional selection, but also on the relative discriminabilities of these attributes.

The ERP studies reported so far provide evidence that processes in the primary visual cortex are not modulated by spatial attention, but that attention affects processing in extrastriate visual areas involved in the processing of object features (like orientation, form, colour, and movement direction). These results can thus be interpreted as evidence for the assumption that processes within the pathway linking V1 to IT can be selectively influenced by expectations about the location of relevant stimulus information. In the next section, I discuss whether this sort of influence is an inevitable consequence of spatial precueing or the result of an optional processing strategy.

### OPTIONAL AND OBLIGATORY ATTENTIONAL INFLUENCES ON PERCEPTUAL PROCESSING

Most ERP studies on visuospatial attention have employed a sustained attention paradigm where subjects are instructed to keep their attention focused on a specific location for a longer period of time. Experiments in which behavioural parameters (response speed or accuracy) are measured are usually conducted under rather different circumstances. Here, the to-be-attended location is indicated by a precue at the beginning of each trial, and attention has to be shifted between locations in successive trials (Posner et al., 1980). The sustained

attention paradigm differs from trial-by-trial cueing studies not only in what may be called “attentional allocation dynamics” (sustained versus transient), but also with respect to the relevance of stimuli presented at unattended locations. In ERP experiments that use a sustained attention paradigm, overt responses are only required to infrequent targets at attended locations, but not to stimuli presented at unattended locations. Trial-by-trial cueing studies are usually conducted to investigate performance differences in response to stimuli at attended and unattended locations, and responses are therefore required to attended as well as to unattended stimuli.

Transient and sustained attentional allocation dynamics may elicit different selective mechanisms, as will be discussed later. However, differences in the response relevance of stimuli presented at unattended locations may also affect attentional processes. When stimuli at unattended locations are always irrelevant and can therefore be completely ignored, enhanced occipital P1 and N1 amplitudes have been observed for stimuli at attended locations (cf. Fig. 1), presumably indicating a spatially selective modulation of processing in the V1–IT pathway. One may ask whether this sort of effect is inevitably elicited whenever specific expectations about the location of relevant stimulation are induced. Biasing the sensory input to IT cortex in favour of information presented at one attended location might be a reasonable strategy when all other locations are irrelevant for response selection, but may actually result in overall performance decrements when relevant information is presented at unexpected locations on a certain percentage of trials. This potential problem could be overcome if such modulatory influences of positional expectancies on visual processing in the V1–IT pathway were optional rather than obligatory.

Although the distinction between obligatory and optional selective influences on information processing may be important for models of attentional mechanisms, it has often been ignored (Allport, 1993). To determine whether the attentional modulation of occipital P1 and N1 components is affected by the response relevance of stimuli at unattended locations, a trial-by-trial cueing experiment was conducted where this factor was varied (see Eimer, 1994b, experiment 2). Each trial started with a 200 msec presentation of a central precue (an arrow pointing to the left or right side). Then, 700 msec after cue offset, a target stimulus (the letter M or W) was presented for 100 msec  $6^\circ$  to the left or right of fixation. Seventy-five percent of the trials were valid; that is, the target was presented at the side indicated by the cue. In the remaining 25% invalid trials, the target was presented contralateral to the cued location. In one part of the experiment, subjects were instructed to respond to all target stimuli (the letter M required a left-hand reaction, and the letter W a right-hand response) irrespective of whether they were presented at cued or uncued locations. In the other part, the task was to respond to validly cued targets only, and to withhold response when a target was presented at the uncued locations.

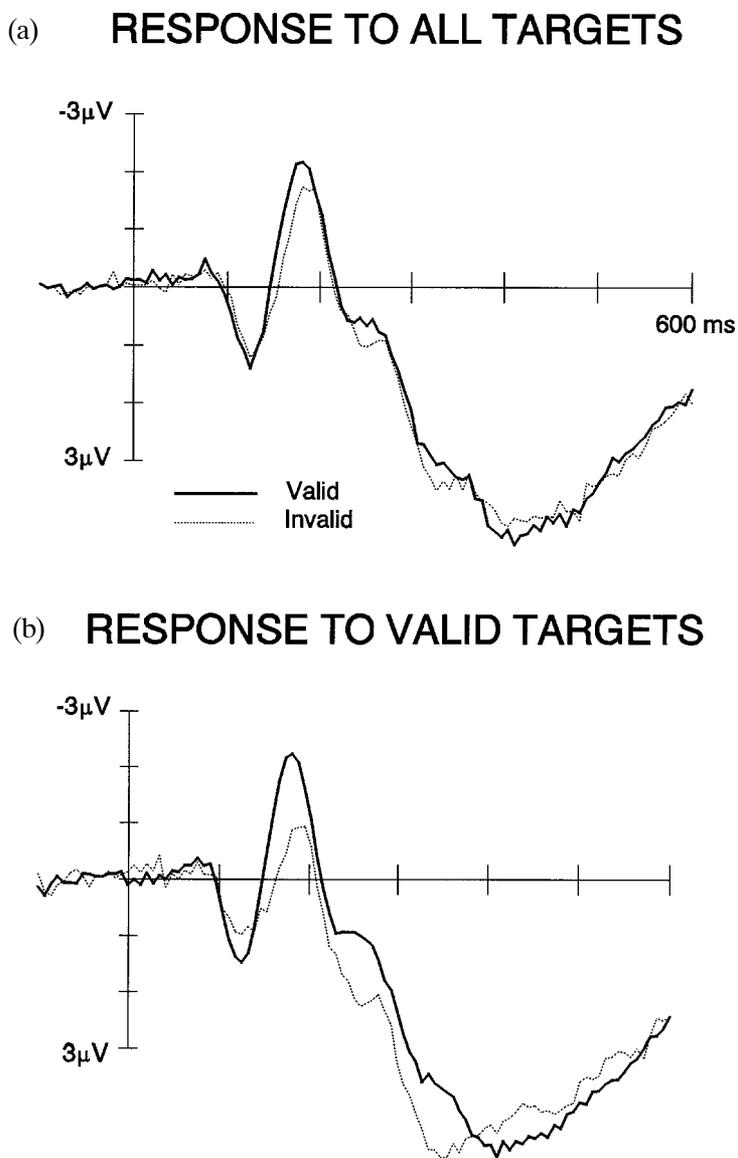


FIG. 3. Grand-averaged ERPs elicited at occipital electrodes ipsilateral to the location of the target stimulus in a trial-by-trial cueing experiment by valid trials (solid lines) and invalid trials (dotted lines). (a) ERPs elicited in a condition where responses were required in valid and in invalid trials. (b) ERPs elicited in a condition where responses were required in valid trials only.

The ERP waveforms elicited by validly and invalidly cued targets at occipital electrodes ipsilateral to the position of the target in these two conditions are shown in Fig. 3. When all targets were relevant, no statistically reliable attentional modulations of P1 and N1 amplitudes were elicited, even though overt performance showed faster RTs in valid than in invalid trials. In contrast, when only validly cued stimuli required a response, the P1 and N1 amplitudes were clearly affected by cue validity (see Fig. 3b). These ERP results suggest that the spatially selective modulation of perceptual processing, as indicated by the attentional effects on P1 and N1 amplitudes, is not completely obligatory, but may be influenced by the response relevance of unattended-location stimuli. A spatially selective bias for processing within the V1–IT pathway is elicited by advance information about stimulus location when stimuli at uncued locations do not require a response and can therefore be completely ignored, but not (or to a lesser degree) when uncued locations are potentially relevant (Eimer, 1993; see also Mangun & Hillyard, 1991).

#### ATTENTIONAL GRADIENTS IN THE POSTERIOR PARIETAL CORTEX

A notable result of the experiment reported in the last section was the presence of attentional effects on overt performance in the absence of a reliable attentional modulation of exogenous ERP components (Fig. 3a). While the former result indicates that the cue was effective in directing spatial attention, the latter result suggests that perceptual processing in the V1–IT pathway was not significantly affected. In the framework of LaBerge and Brown's (1989) model, one may assume that no location expectation gradient is elicited in PPC in response to cues when uncued locations are potentially relevant, and therefore no modulatory influence on ventral stream processing is exerted by PPC signals. However, such an account cannot explain why overt performance was superior in response to validly cued (attended) stimuli. Alternatively, it is possible that an attentional gradient was set up in PPC areas by the cue but that this gradient affected processing within the ventral stream only at a later stage. Are there any observations to be made in the ERP waveforms obtained in the above experiment with respect to the presence of specific location expectations within posterior parietal cortex?

This was investigated by comparing the ERPs elicited in valid and invalid trials at the midline electrodes Fz, Cz and Pz in the experimental condition described above, where responses were required in both the valid and invalid trials. Figure 4 shows these ERPs together with the difference waves obtained by subtracting the ERPs for invalid trials from the ERPs for valid trials (right side). Valid trials elicited an enlarged negativity compared with invalid trials, with a first peak (Nd1) around 160 msec post-stimulus that was maximal at parietal sites (electrode Pz), and a second, more broadly distributed negativity

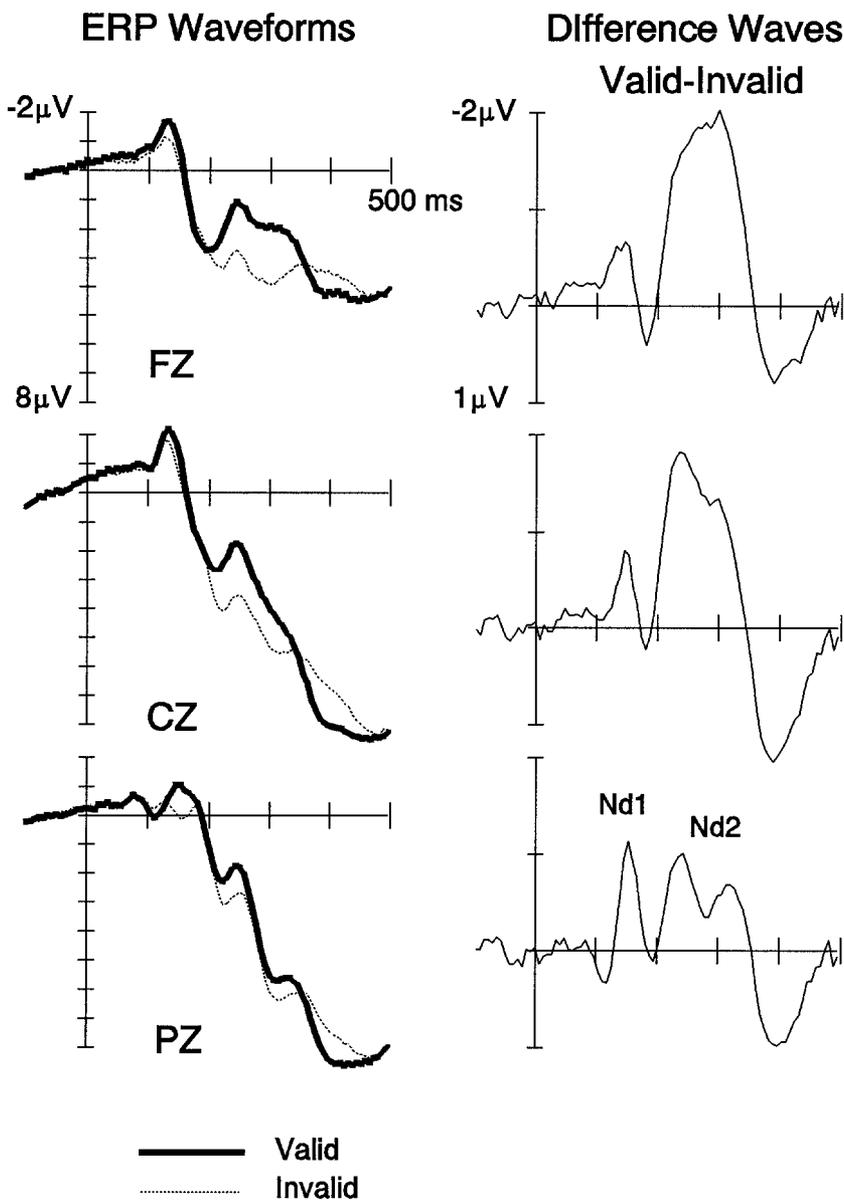


FIG. 4. (Left) Grand-averaged ERPs elicited at midline electrodes Fz, Cz and Pz in a trial-by-trial cueing experiment for valid trials (solid lines) and invalid trials (dotted lines) in a condition where responses were required in valid as well as in invalid trials. (Right) Difference waveforms obtained by subtracting the ERPs recorded in invalid trials from the ERPs recorded in valid trials. Valid trials elicited an enhanced negativity with an initial parietal peak (Nd1) that was followed by a fronto-centrally distributed effect (Nd2).

(Nd2) more than 200 msec post-stimulus. Very similar, although somewhat larger effects were obtained when only validly cued targets required a response. (see Fig. 5).

Can these effects observed at midline electrodes be related to specific attentional mechanisms? Since the Nd2 is elicited more than 200 msec post-stimulus and has a fronto-central scalp distribution, it can be assumed that it reflects an attentional influence at later stages of processing. This effect may be related to a differential processing of attended and unattended information within IT cortex, or to response selection processes that occur after stimulus identification. In contrast, the Nd1 has a latency of about 160 msec and a distinct parietal distribution. It is thus possible that this effect indicates spatially selective activity within the posterior parietal cortex. In the framework of LaBerge and Brown (1989) and LaBerge (1995), the Nd1 may reveal the presence of an attentional gradient that is centred at the cued location. The activity profile generated in posterior parietal cortex by the presentation of targets at cued locations corresponds to the already established location expectation gradient, while the PPC activity elicited by targets at uncued locations does not overlap with the activity related to the attentional gradient. This differential PPC activation, which is assumed to be reflected by the Nd1, may in turn result in an earlier or more effective selective gating of target information from cued locations in the ventral stream (as indicated by the RT advantage observed for valid trials).

Is there additional evidence to support this interpretation of the Nd1 effect? The distinct parietal localization of the Nd1 is in line with the assumption that it is generated within posterior parietal cortex. It has previously been argued that the occipital N1 component (which is presumably generated within the ventral processing stream) has to be distinguished from the parietal N1 component (which may be related to processing within the dorsal pathway). Given its latency and scalp distribution, the Nd1 effect may be considered a selective modulation of the parietal N1. Furthermore, if the Nd1 reflects the spatially selective activity in PPC areas due to the presence of a location expectation gradient that was produced in response to a previously presented precue, it may be elicited with different types of spatial cues. Accordingly, a distinctly parietal Nd1 effect has been observed not only with centrally presented symbolic cues, but also in an experiment (Eimer, 1994a) where precues were presented at a horizontal eccentricity of  $6^\circ$  in the left or right hemifield under conditions where this cue was spatially informative, but also when the cue was not informative with respect to the location of an upcoming target stimulus. Here, the Nd1 effect was present even though no systematic attentional enhancements of occipital P1 and N1 components were observed. This latter finding again suggests that, if the Nd1 reflects the presence of location expectancies within posterior parietal cortex, such expectations do not necessarily result in a spatially selective modulation of processing within the V1-IT pathway. Moreover, the

presence of a Nd1 in response to uninformative peripheral onsets indicates that attentional gradients within PPC may be triggered in a rather reflexive way (Jonides, 1981).

If a parietal location expectation gradient that is generated (either voluntarily or reflexively) in response to spatial precues is reflected by the Nd1, it is conceivable that qualitatively similar effects are elicited for targets of different modalities. Schröger and Eimer (1993) did observe a distinct parietal Nd1 in a study where visual cues and auditory target stimuli were used. Figure 5 compares the ERP results of two experiments where visual (Eimer, 1994b, experiment 2b) or auditory (Schröger, 1994) target stimuli were preceded by informative visual arrow precues and only validly cued targets were relevant for the subjects' response. The ERP waveforms obtained from Pz and from lateral parietal sites (electrodes PL and PR, located halfway between Pz and the ear channels) in response to visual and auditory stimuli are shown together with the resulting valid–invalid difference waveforms. The ERP waveforms elicited by visual and by auditory stimuli were quite different. Auditory stimuli elicited a modality-specific N1 component that peaked around 100 msec post-stimulus (Fig. 5b), whereas the visual N1 peaked about 60 msec later (Fig. 5a). In spite of these differences between modalities, the ERP effects of spatial cueing that can be seen in the difference waveforms, obtained by subtracting the ERPs elicited in invalid trials from the ERPs elicited in valid trials, were strikingly similar (Fig. 5c). A distinct Nd1 of comparable amplitude and latency was elicited for visual as well as for auditory stimuli at all three recording sites. Moreover, the modulations observed in the difference waveforms at longer latencies (Nd2) were also quite similar for the two modalities.

Analogous results have been found in a number of other trial-by-trial cueing studies that employed auditory target stimuli, suggesting that, in contrast to the attentional modulations of the occipital P1 and N1 components, the Nd1 effect reflects selective processes that are largely independent of stimulus modality. This is in line with the assumption that the Nd1 indicates the existence of a location expectancy gradient within posterior parietal cortex that is generated in response to precues, which in turn operates upon selective thalamic circuits that gate the sensory input to object identification processes. The fact that different brain areas are involved in the initial analysis of visual and auditory stimuli does not rule out the possibility that the control of spatial selectivity within these two modalities is based on partially overlapping mechanisms within the posterior parietal cortex.

What remains to be answered is why behavioural effects of spatial cueing have been observed in the absence of reliable ERP evidence for a selective modulation of processing within the V1–IT pathway. If the Nd1 is a reflection of an attentional gradient within the PPC areas, the absence of attentional effects on occipital P1 and N1 components in the experiment described above cannot be explained by assuming that no specific positional expectancies at all were

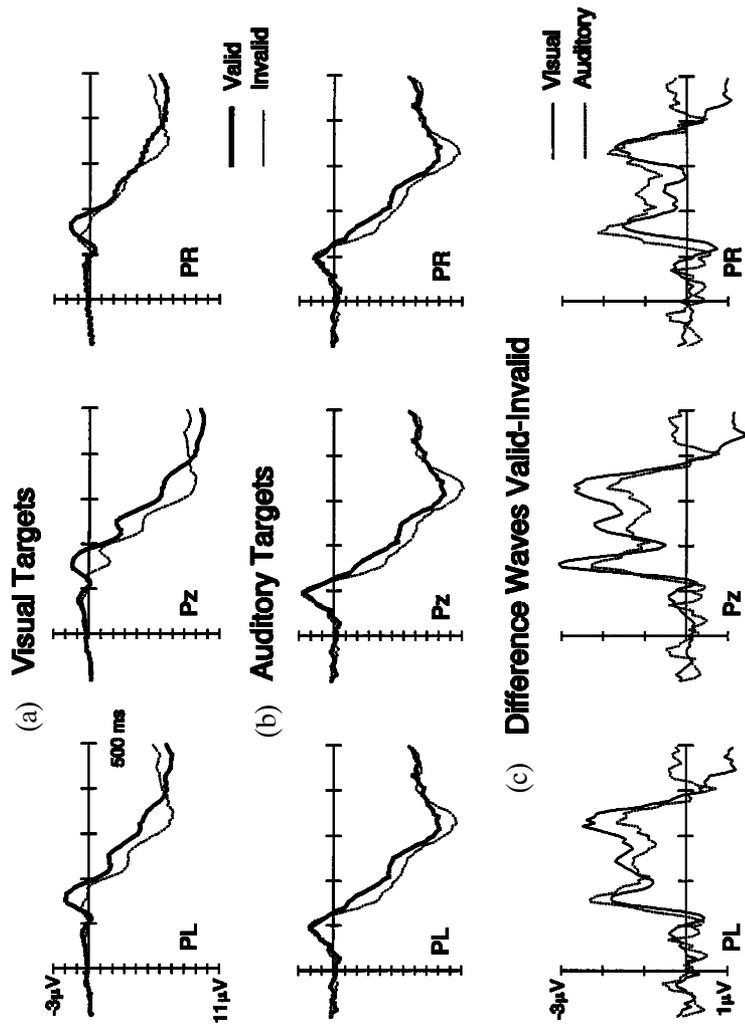


FIG. 5. (a, b) Grand-averaged ERPs elicited at electrodes PL, Pz and PR in trial-by-trial cueing experiments for valid (solid lines) and invalid trials (dotted lines) where visual stimuli (a) or auditory stimuli (b) were preceded by a centrally presented arrow precue. (c) Difference waveforms obtained by subtracting the visual ERPs (solid line) and the auditory ERPs (dotted line) obtained in invalid trials from the visual and auditory ERPs obtained in valid trials.

generated. Alternatively, one may speculate that spatially selective PPC signals influence later stages of visual processing without affecting the V1-IT pathway. Anatomical connections that may subservise this type of influence (e.g. direct link's between areas within PPC and regions in IT cortex) have already been described (Andersen, Asanuma, Essick, & Siegel, 1990).

### TRANSIENT AND SUSTAINED MODES OF SELECTIVE SPATIAL ATTENTION

The Nd1 may reflect location expectation gradients within the posterior parietal cortex that are set up in a transient and possibly reflexive way in response to the presentation of cue stimuli. The reflexive nature of this process is suggested by the finding reported above that distinct Nd1 effects were also observed in response to uninformative peripheral cues (Eimer, 1994a). The transient nature of a position expectation gradient has been stressed by LaBerge and Brown (1989), especially under conditions where to-be-attended locations are eccentric to the fovea. The presence of such a gradient may thus critically depend upon the previous presentation of a precue. If this is the case, one may expect to find differences between experimental situations where the to-be-attended location is cued on each trial (transient attention) and a condition where the relevant location is specified by instruction at the beginning of an experimental block and is kept constant throughout this block (sustained attention). If the Nd1 effect reflects transient activity within PPC areas induced by the previous presentation of a precue, this effect should be attenuated or even absent under sustained attention conditions.

This was investigated in a study by Eimer (1996a, experiment 2), in which the ERP effects of transient and sustained spatial attention were directly compared. In the transient attention condition, a centrally presented arrow precue indicated the location of the next target with 75% validity, and 25% of the trials were invalid. In the sustained attention condition, subjects were informed at the beginning of each experimental block at which location (left or right) targets would appear with 75% probability. Because the precues employed in the transient attention condition may exert an unspecific alerting effect, an uninformative plus sign was presented at the beginning of each trial in the sustained attention condition instead of an arrow precue. In both attention conditions, the subjects' task was to respond to the target letters M and W at attended and at unattended locations with a left-hand or right-hand button press.

Do transient and sustained spatial attention have different effects on overt performance and ERP waveforms? The behavioural data showed no difference at all. Response times for valid and invalid trials were 485 and 509 msec in the transient attention condition, and 487 and 509 msec in the sustained attention condition. This finding, that the behavioural effects of transient and sustained attention on RT are virtually identical, differs from that of Posner et al. (1980,

experiment 1), who found larger effects in a transient attention condition than in a sustained attention condition.<sup>1</sup> Do the ERP waveforms reveal any differences between transient and sustained attention? In both conditions, a small but significant attentional enhancement of the occipital N1 component was elicited, suggesting a moderate selective influence on processing within the V1–IT pathway. Figure 6 shows the ERPs elicited at electrode Pz in valid and invalid trials for the transient and the sustained attention conditions, together with the corresponding difference waveforms. As can be seen, transient and sustained spatial attention had rather different effects on the ERP waveforms. In the transient attention condition, the Nd1–Nd2 pattern discussed in the previous section was again present (Figure 6c). In contrast, the attentional modulations elicited by sustained attention were of much smaller amplitude. Statistical analyses revealed that the Nd1 was virtually absent, and only the Nd2 effect approached significance.

Although the attentional effects on performance were identical, transient and sustained spatial attention resulted in rather different ERP modulations. The absence of the Nd1 effect under sustained attention conditions is in line with the assumptions that the Nd1 reflects transient activity within PPC areas that is critically dependent upon the previous presentation of a cue. If no transient attentional gradient is set up in the sustained attention condition, as suggested by the absence of a Nd1 effect, how can the RT advantage for attended target stimuli observed in this condition be explained? One may speculate that, under sustained attention instructions, a representation of the relevant stimulus location was activated in spatial working memory (possibly within dorso-lateral prefrontal cortex), but that this information does not elicit an attentional gradient within PPC in the same way that such a gradient is set up in response to single precues. With sustained attention, stored spatial expectations may influence object identification processes directly, possibly through links connecting DLPFC with the ventral stream (Felleman & Van Essen, 1991).

The results obtained in this experiment generally illustrate how ERP measures can provide information about functional differences between mechanisms of attentional selectivity operating in different experimental circumstances, which are not available on the basis of behavioural data alone. While the RT data were virtually equivalent for the transient and sustained attention conditions, the ERP waveforms revealed marked differences suggesting important functional differences between the underlying selective processes.

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<sup>1</sup>It should be noted that four possible stimulus locations were used in the Posner and co-workers' (1980) experiment, and stimulus eccentricity was much larger (24° and 8°) than in the ERP study reported here.

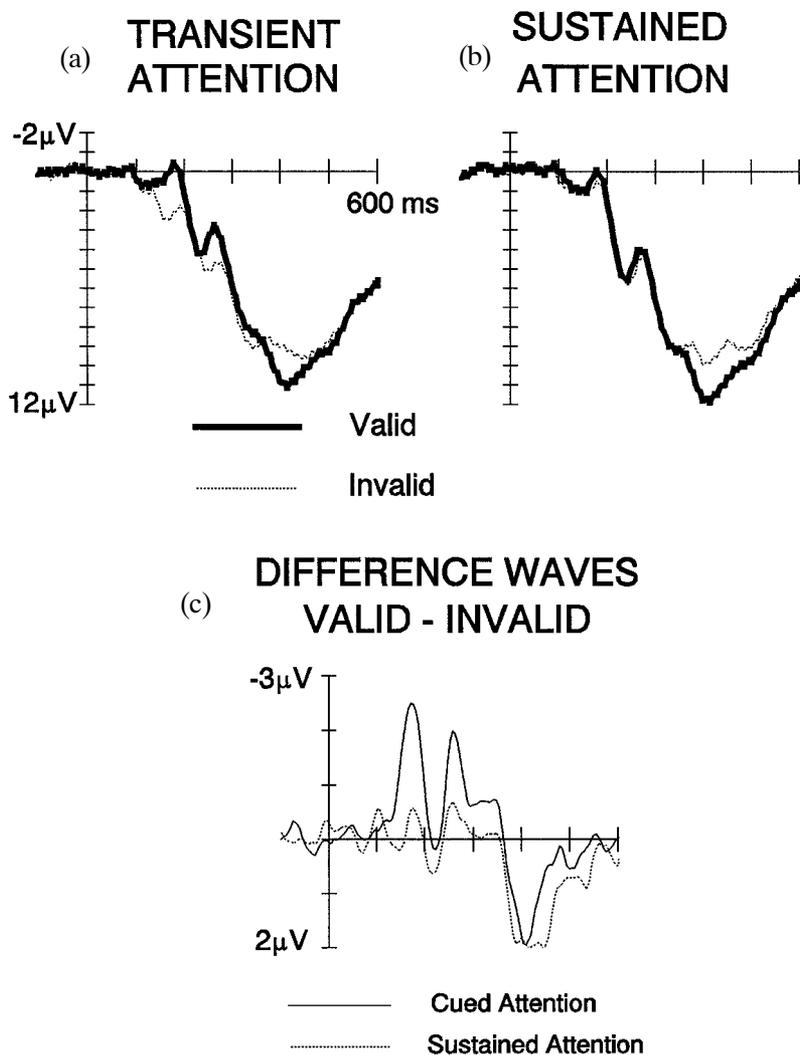


FIG. 6. (a, b) Grand-averaged ERPs elicited at electrode Pz in valid trials (solid lines) and invalid trials (dotted lines) under transient (left) and sustained (middle) attention conditions (see text for details). (c) Difference waveforms obtained by subtracting ERPs obtained in invalid trials from ERPs obtained in valid trials for the transient (solid line) and sustained (dotted line) attention conditions.

VISUOSPATIAL ATTENTION IN  
MULTIPLE-STIMULUS ARRAYS

In the studies reported so far, visuospatial attention was investigated where a single target stimulus was presented at attended or unattended locations in front of an otherwise empty background. Although systematic behavioural and electrophysiological effects were obtained under these conditions, it may be argued that this type of circumstance is not ideally suited for the study of attentional mechanisms. Attentional selectivity should be maximal in situations when the visual field contains multiple objects that compete with each other. The role of between-stimulus competition for attentional selectivity has been demonstrated by single-cell studies that have found a modulatory influence of spatial attention on the firing rate of single cells only when both attended and unattended stimuli are located within the receptive field of that cell (Moran & Desimone, 1985).

Attention selectivity should therefore also be studied when several stimuli are displayed simultaneously, and the relevant target position is either specified in advance by precueing (Downing, 1988) or varied randomly from trial to trial as in visual search paradigms (Duncan & Humphreys, 1989). In the ERP experiments reported in this section, a target and one distractor stimulus were presented simultaneously and unpredictably in the left and right visual fields at an eccentricity of about  $3^\circ$ . In a form discrimination task, the letters M and W served as targets (requiring a left-hand and right-hand response, respectively), and an ensemble of two short and two long vertical bars, which was equal in size to the target letters, was presented as a distractor. In a colour discrimination task, blue and green squares were used as targets (again requiring a left or right response), and a yellow square was used as a distractor (Eimer, 1996b, experiment 2).

Which mechanisms of attentional selectivity operate under these conditions? Since the location of the target stimulus (left or right) was unpredictable, no advance positional expectancies can be generated. In the framework described by LaBerge and Brown (1989), instructing subjects to respond to targets characterized by a specific colour (or form) leads to a selective priming of colour or form maps within the V1-IT pathway that may be under the control of feature-specific working memory in ventro-lateral prefrontal areas. This will result in increased activity at the location of stimuli with relevant attributes, which will in turn activate PPC areas and thalamic circuits, finally leading to a selective gating of target information in the ventral stream.

Is there evidence in the ERP waveforms elicited by the target-distractor arrays indicating that this sort of selective processing actually takes place? Figure 7 shows the ERP waveforms recorded at a lateral occipital electrodes ipsilateral and contralateral to the position of the target stimulus in the form and in the colour discrimination task. A systematic influence of target location on

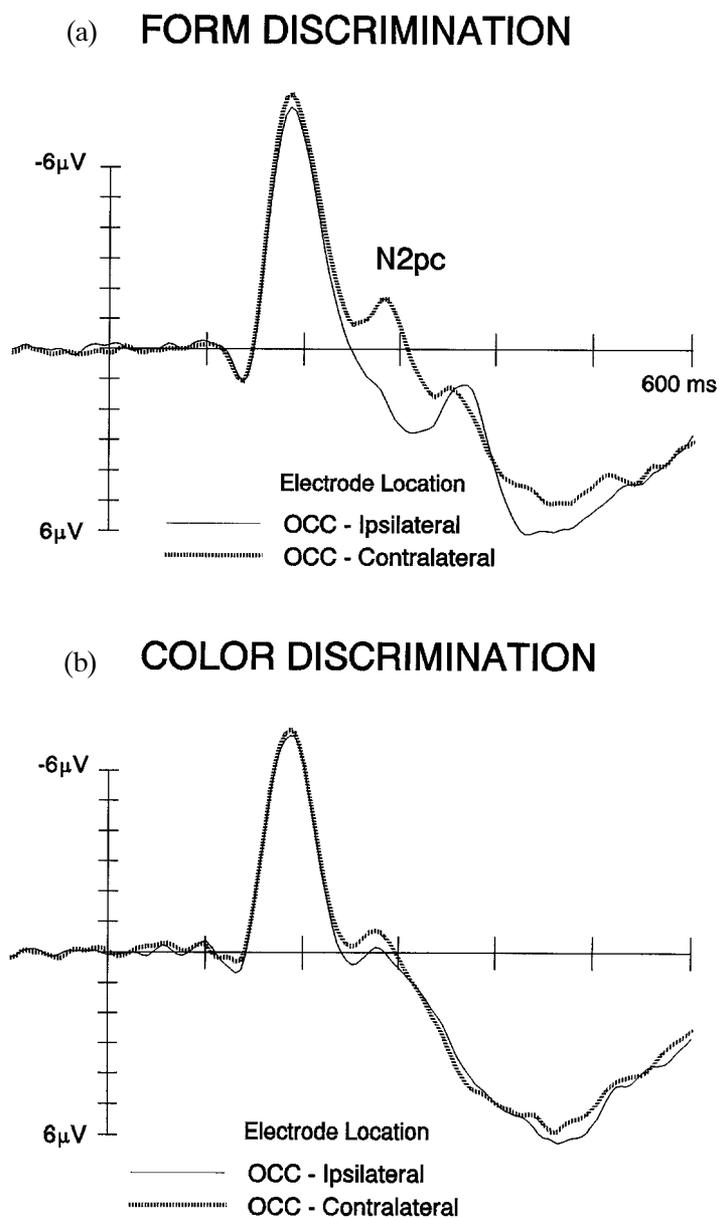


FIG. 7. Grand-averaged ERPs elicited at lateral occipital electrodes ipsilateral (solid lines) and contralateral (dotted lines) to the location of a target stimulus that was presented together with a distractor in the opposite visual hemifield in a form discrimination task (a) and a colour discrimination task (b) (see text for details). An enhanced N2 component was elicited at occipital sites contralateral to the location of the target (N2pc).

the ERPs was present, with enlarged N2 amplitudes elicited at occipital electrodes contralateral to the location of the target. This effect was considerably larger in the form discrimination task (Fig. 7a), but was also present for the colour discrimination task (Fig. 7b). Analogous ERP effects have been reported by Luck and Hillyard (1994) in visual search tasks where one target was presented together with numerous distracting stimuli. The enhanced N2 component at occipital sites contralateral to the position of the target was termed N2pc (N2 posterior-contralateral). Luck and Hillyard (1994) argued that the N2pc may reflect both the selection of relevant stimuli as well as the attentional suppression of irrelevant or conflicting information that may interfere with target identification during visual search. As shown in Fig. 7, the N2pc component is not only elicited in visual search tasks with multiple distractors, but also when a target is presented together with just one distractor in the opposite visual field, and distractor interference should be minimal. It is therefore possible that the N2pc primarily reflects the selective enhancement of target processing that results from a previous localization of task-relevant features.

Given this interpretation, it would be important to localize the generator processes underlying the N2pc component. Luck and Hillyard (1994) estimated the cortical origin of the N2pc with the help of CSD analyses, and found that the focus of this effect was located about the ventro-lateral occipital cortex, close to the estimated locus of the visual P1 component (see above). Although the N2pc is elicited about 150 msec later than the P1 component (see Fig. 7), this result suggests that it is probably also generated in extrastriate occipital areas. The N2pc component may thus be interpreted to reflect a selective gating of information processing in the ventral pathway that is contingent upon the previous detection of task-relevant features. The information about target location obtained through the initial feature analysis is then re-entrantly sent back to extrastriate occipital cortex, possibly mediated by the PPC and the thalamus. Re-entrant signals have been assumed to play an important role in visual integration (Zeki, 1993). The N2pc component might directly reflect the consequences of such re-entrant connections for the selective processing of relevant information.

Another experiment (Eimer, 1996b, experiment 3) was conducted to investigate if these hypothesized mechanisms are also sensitive to more abstract target-defining features. Instead of letters or coloured squares, word strings were used as targets and distractors. The target words differed from the distractors with respect to their meaning, as location words (the German words for "left" and "right") were used as targets, and colour words (the German words for "white" or "brown") as distractors. Subjects were instructed to respond to the target words, either by pressing the button indicated by their meaning (left vs right), or by pressing the button spatially corresponding to the target location. Figure 8 shows the ERP waveforms elicited by target words in

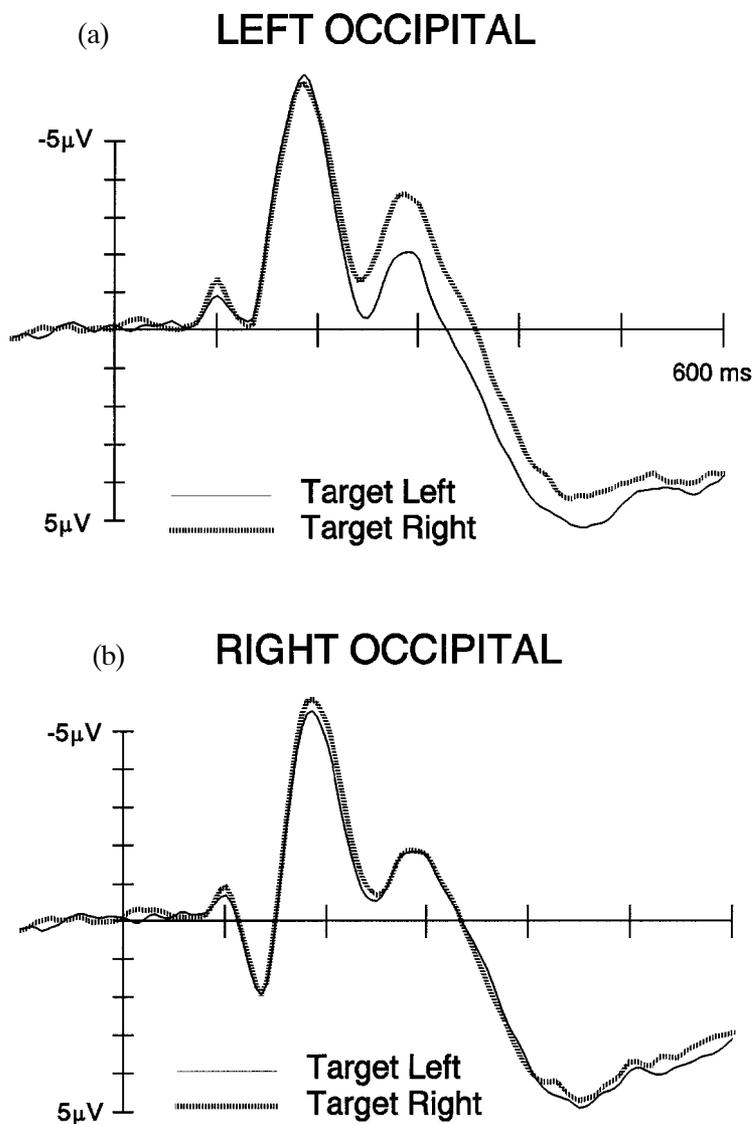


FIG. 8. Grand-averaged ERPs elicited at left occipital (a) and right occipital (b) electrodes by stimulus arrays that contained a target word in the left (solid lines) or right (dotted lines) visual field. An N2pc was elicited at left occipital electrodes (a) but not over the right hemisphere (b).

the left and right visual fields at left and right occipital electrodes. Over the left hemisphere, a larger N2 component was elicited for target words presented at the contralateral (right) side (Fig. 8a). While this is in line with the results obtained before, no N2pc was elicited at all over the right occipital hemisphere (Fig. 8b).

The fact that an N2pc was observed over left occipital cortex when targets and distractors were words that had to be distinguished on the basis of their meaning, suggests that the attentional gating of processing within the ventral stream is controlled by selective mechanisms that are sensitive not only to physical stimulus properties, but also to more abstract semantic features. However, in contrast to the experiment reported above, this N2pc effect was confined to the left hemisphere. A possible explanation for this asymmetry is that it reflects the activity of the language-dominant left hemisphere when between-word discriminations are required. However, additional empirical evidence is clearly needed with respect to the hemispheric asymmetry of the N2pc effect when linguistic material is used.

In summary, the N2pc component observed in experiments where target stimuli are presented at unpredictable locations simultaneously with at least one distractor could serve as an important tool in further investigations of attentional selectivity, because it may reflect the gating of information from potentially relevant locations within the ventral stream in search-like situations, thus possibly indicating a modulatory influence of parietal signals that are not due to positional expectancies, but are generated on the basis of an initial pre-attentive feature analysis.

## CONCLUSIONS

Attentional processes serve various functions and may affect different stages of information processing. In this paper, a review of recent findings regarding effects of visuospatial attention on ERP waveforms was presented, suggesting that there are different cortical loci of spatial selectivity. Spatial attention may influence processing in the ventral stream within the pathways linking V1 with IT cortex. This was indicated by the attentional modulation of the occipital P1 and N1 components observed in precueing experiments, as well as by the existence of the N2pc component that is elicited in response to targets presented simultaneously with distracting stimuli. However, these two effects are likely to be under the control of rather different attentional mechanisms. While the attentional effects on exogenous components in precueing contexts are likely to result from positional expectancies within parietal areas that gate the flow of information within the V1–IT pathway, either directly or through the thalamus, the N2pc is assumed to be contingent upon a previous detection of task-relevant features within the ventral stream.

Additional evidence was collected with respect to the spatially selective attentional gradient postulated by LaBerge and Brown (1989), which is assumed to be located within posterior parietal areas. A distinct ERP effect (Nd1) that was maximal over parietal cortex was interpreted to reflect the presence of such a location expectation gradient. It was assumed to indicate the differential activation of PPC areas in response to targets at cued and uncued location, which may in turn influence processing in the ventral stream. The fact that similar Nd1 effects were elicited in response to centrally presented symbolic precues and peripheral precues (even when these are uninformative with respect to the location of the target) suggests that spatially selective parietal activation patterns might be relevant for voluntary as well as for reflective spatial attention. Very similar Nd1 effects have also been observed in studies where either visual or auditory targets were preceded by visual cues. This is interpreted as evidence for the assumption that spatially selective parietal processes underlying the Nd1 effect are not entirely modality-specific. Moreover, the Nd1 was found to be virtually absent in a sustained attention condition. This may indicate that location expectation gradients within PPC areas, as evidenced by the Nd1, are transient in nature and thus critically depend upon the previous presentation of cue stimuli.

Some preliminary evidence has also been obtained with respect to the relation between spatially selective processes within posterior parietal cortex (indexed by the Nd1) and location-specific modulations of processing in the V1-IT pathway (indexed by the attentional effects on occipital P1 and N1 amplitude). The selective modulation of processing within the ventral stream seems to be optional rather than obligatory, as it was found to be markedly reduced when uncued locations were potentially relevant. However, a distinct Nd1 was elicited in this condition, indicating the presence of an attentional gradient within PPC. These location expectancies may have selectively influenced later stages in the ventral stream (like stimulus identification) even in the absence of modulatory effects within the V1-IT pathway, possibly via direct or indirect links from PPC to IT cortex. Attentional modulations of exogenous components may even be found in the absence of corresponding parietal Nd1 effects, as in the sustained attention experiment described above. In the present framework, this would suggest a spatially selective gating of information within the V1-IT pathway without corresponding transient positional expectancies generated in PPC areas. Such an influence could possibly be mediated by direct links from the dorso-lateral prefrontal cortex (one potential site for spatial short-term memory) to the ventral stream.

In conclusion, it has to be stressed that the above interpretations of specific ERP modulations, observed in experiments on selective spatial attention that were guided by the model of attentional selectivity depended by LaBerge and Brown (1989) and LaBerge (1995), are highly speculative at the present time, and further research is required to confirm them. Measuring attentional effects

on event-related brain potentials is just one way of investigating the nature of selective processes, and ERP waveforms reflect only a fraction of the activities within the brain that may be modulated by attention. The aim of the present paper was to illustrate that ERP studies may provide one valuable source of information about the nature of the mechanisms underlying selective attention. Uncovering these mechanisms requires the joint activity of researchers that employ different, but complementary, techniques.

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