PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Sensory gain control (amplification) as a mechanism of selective attention: electrophysiological and neuroimaging evidence

Steven A. Hillyard, Edward K. Vogel and Steven J. Luck

Phil. Trans. R. Soc. Lond. B 1998 **353**, 1257-1270
doi: 10.1098/rstb.1998.0281

Sensory gain control (amplification) as a mechanism of selective attention: electrophysiological and neuroimaging evidence

Steven A. Hillyard[1], **Edward K. Vogel**[2] **and Steven J. Luck**[2]

[1]*Department of Neurosciences, University of California, San Diego, La Jolla, CA 92093-0608, USA*
[2]*Department of Psychology, University of Iowa, Iowa City, IA 52242-1407, USA*

Both physiological and behavioral studies have suggested that stimulus-driven neural activity in the sensory pathways can be modulated in amplitude during selective attention. Recordings of event-related brain potentials indicate that such sensory gain control or amplification processes play an important role in visual–spatial attention. Combined event-related brain potential and neuroimaging experiments provide strong evidence that attentional gain control operates at an early stage of visual processing in extrastriate cortical areas. These data support early selection theories of attention and provide a basis for distinguishing between separate mechanisms of attentional suppression (of unattended inputs) and attentional facilitation (of attended inputs).

Keywords: attention; evoked potentials; ERPs; vision; PET; visual cortex

1. INTRODUCTION

In 1990, Corbetta and his colleagues published a groundbreaking study in which they used positron emission tomography (PET) to examine the effects of selective attention on neural activity (Corbetta *et al.* 1990). In this experiment, subjects viewed arrays of moving bars and judged whether successively presented arrays were the same or different. Selective attention was manipulated by instructing the subjects to report size changes in one trial block, colour changes in a second block, velocity changes in a third block, or a change in any of these features in a fourth block. It was found that blood flow was increased in specific cortical regions when a single feature was attended compared with when attention was divided among all three features. Furthermore, different cortical regions were affected for each feature type, such that attending to a given feature appeared to increase blood flow in cortical regions that were specialized for the sensory processing of that feature. For example, attending to stimulus velocity caused an increase in blood flow in the region of the human homologue of areas MT and MST, which studies in both humans and monkeys have shown to be important for motion perception (Zeki *et al.* 1991; Newsome *et al.* 1995; Tootell *et al.* 1995).

Corbetta and associates (Corbetta *et al.* 1990, 1991) suggested that a possible mechanism for these feature-specific changes in regional cerebral bloodflow (rCBF) may involve a 'sensory enhancement', whereby incoming visual information in primed (attended) sensory pathways would trigger stronger and more selective neuronal responses with a higher signal-to-noise ratio than in unprimed pathways. This idea has been expressed more generally in terms of an 'amplification' of neuronal activity within sensory processing areas, such that attended information elicits larger sensory-evoked responses than ignored information (Posner & Driver 1992; Posner & Dehaene 1994). This amplification mechanism is applicable to a wide variety of attentional manipulations. For example, just as attending to motion and ignoring colour is proposed to yield an amplification of activity within motion-processing areas (Corbetta *et al.* 1991), attending to the visual modality and ignoring the auditory modality should lead to a widespread amplification across visual cortex, and attending to the left visual field and ignoring the right visual field should lead to a retinotopically organized amplification of activity corresponding to the left visual field.

The concept of sensory amplification or 'gain control' may be traced to early studies of attentional influences on evoked electrical responses in the sensory pathways in animals (Hernandez-Peon *et al.* 1956; Hernandez-Peon 1966; Oatman & Anderson 1977). In these experiments, the amplitudes of sensory-evoked responses were found to be enlarged when the animal's attention was directed towards a stimulus and reduced when attention was directed elsewhere. These effects were interpreted as reflecting a sensory 'gating' or 'filtering' process whereby unattended inputs were blocked or suppressed (i.e. their gain was reduced) in relation to attended inputs. Contemporaneous theories of attention derived from behavioral studies were based on similar concepts of filtering or attenuation (Broadbent 1958; Treisman 1969).

Subsequent electrophysiological experiments in humans have examined the evoked or event-related potentials (ERPs) that can be recorded non-invasively from the scalp as subjects engage in attention-demanding tasks. The surface recorded ERPs represent the summated electric field arising from populations of nerve cells activated by a stimulus. ERP waveforms consist of a sequence of voltage deflections or components that register the time-course of sensory-evoked activity patterns with a millisecond level of resolution. Early ERP experiments in both auditory and visual modalities showed that stimulus-evoked potentials from cortical sensory areas are strongly modulated by attention, with larger amplitudes for attended stimuli in relation to unattended stimuli (Hillyard *et al.* 1973; Eason 1981; Harter & Aine 1984; Hillyard & Muente 1984). These effects were also interpreted in terms of a sensory gain control mechanism that acts to increase or decrease the magnitude of stimulus-evoked neural activity according to the amount of attention allocated to that input (see, for example, Hillyard & Mangun 1987). If this gain control simply affected the magnitude of the overall stimulus-driven response in a particular brain region without changing the time-course or patterning of the neural activity, this would be reflected in the associated ERP as an amplitude change without any modification of waveform, as shown in figure 1. In this paper we will use the terms 'gain control' and 'amplification' interchangeably to refer to this type of attentional modulation of sensory-evoked activity. Gain control processes have been inferred in a wide range of attention experiments using diverse methodologies including ERPs and neuromagnetic recordings (Hillyard *et al.* 1995), PET (Corbetta *et al.* 1991; Heinze *et al.* 1994; O'Leary *et al.* 1996), single unit neurophysiology (see, for example, Luck *et al.* 1997), and behavioural psychophysics (Hawkins *et al.* 1990; Hikosaka *et al.* 1993; Tsal *et al.* 1994).

Although sensory amplification seems to be involved in a wide range of stimulus selection processes, Desimone and his colleagues (Chelazzi *et al.* 1993; Desimone & Duncan 1995; Luck *et al.* 1997) have identified another general type of attentional mechanism that could also account for attention-related changes in blood flow observed in PET experiments such as those of Corbetta (1990, 1991). Specifically, attending to a feature such as velocity may cause a 'bias signal' to be sent from higher attentional control areas to the sensory areas specialized for motion-processing, and this bias signal might increase tonic neural activity without necessarily modulating sensory-evoked neural responses. This sort of tonic bias would be consistent with cognitive models of attention in which the selection of attended information is achieved by comparing incoming sensory information with an 'attentional template' that specifies the features that are relevant for the current task (Duncan 1981, 1992). The attentional template might be instantiated by an increase in the baseline firing rates of the neurons that normally code stimuli containing the attended feature, and such an increase in baseline firing would be expected to cause an increase in regional cerebral blood flow (rCBF) and thus greater PET activation. In fact, tonic biases might lead to even larger changes in PET activation than amplifications of sensory responses, because the amplification effects would be confined to the relatively brief period of sensory-evoked activity whereas the bias effects would be sustained over longer time intervals.

Several studies of single unit activity in monkeys have demonstrated that attending to a feature or a location may lead to long-lasting, sustained changes in neural activity (Fuster & Jervey 1982; Funahashi *et al.* 1989; Chelazzi *et al.* 1993; Luck *et al.* 1997). In the example shown in figure 2, recordings were obtained from an area V4 neuron while the monkey attended either to a location inside or outside of the neuron's receptive field. For 80% of the neurons, the baseline firing rate was elevated when attention was directed inside versus outside of the receptive field, with an average increase in firing rate of 30% over the entire population. This effect could be seen prior to the sensory response evoked by a stimulus presented inside the neuron's receptive field (figure 2*a*), and it could also be seen in periods without any sensory response, such as when a stimulus was presented outside the neuron's receptive field (figure 2*b*). The transient response elicited by the presentation of a stimulus inside this neuron's receptive field was not influenced by attention (figure 2*a*). This is a clear example of a bias effect in the absence of an amplification effect. Note that, given the size of this bias effect and its widespread occurrence across the population of neurons, this sort of attention

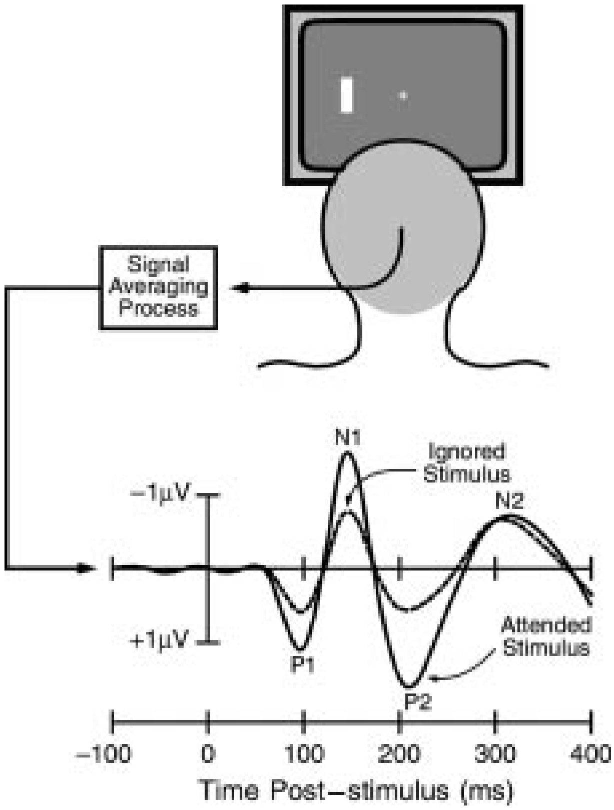

Figure 1. Schematic diagram of a typical ERP attention experiment. The subject fixates the central cross and attends to either the left or right visual field. Bars are flashed to the left and right fields in a rapid, randomized sequence, and the subject responds to occasional targets (e.g. slightly smaller bars) in the attended field. The EEG is recorded during this task, and a signal-averaging process is used to extract the ERPs elicited by the individual stimuli from the ongoing EEG. The ERP elicited by a visual stimulus typically consists of early sensory-evoked components including the P1 and N1 waves, followed by higher-level cognitive components such as the N2 and P3 waves. ERPs shown here are in response to left field stimuli. The early sensory-evoked components are typically found to be larger when a stimulus is presented at an attended location as compared with an unattended location.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

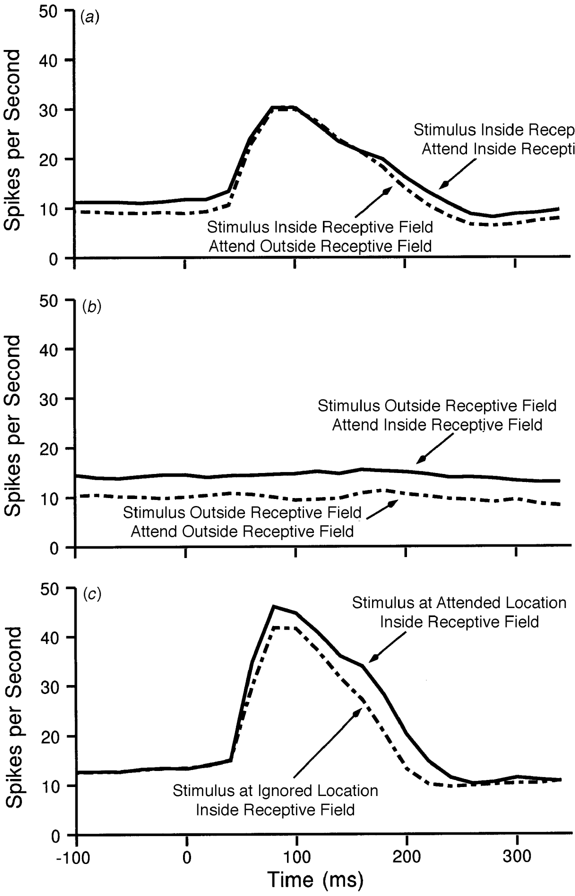

Figure 2. Averaged post-stimulus histograms of neural activity recorded from individual neurons in area V4 of the macaque monkey (Luck *et al.* 1997). Stimulus onset is at time zero. (*a*) Sensory responses elicited by a stimulus presented inside the receptive field when this location was attended compared with when attention was directed to a location outside the receptive field. In this case, attention modulated baseline firing rates but did not influence the stimulus-elicited response. (*b*) Neural activity recorded when a stimulus was presented outside the receptive field. Again, attention can be seen to modulate the spontaneous activity of the neuron. (*c*) Sensory responses elicited by a stimulus presented inside the receptive field when this location was attended compared with when attention was directed to another location inside the receptive field. In this case, attention clearly modulated the stimulus-elicited response. No effects of attention can be observed in the prestimulus period, however, because attention was always directed inside the receptive field in this condition.

effect would presumably lead to a substantial change in blood flow in a PET or functional magnetic resonance imaging (fMRI) experiment.

These same experiments also showed modulations of transient sensory-evoked responses by attention under some conditions, as well as changes in sustained neural activity. For example, when both the attended and ignored locations fell within the receptive field of the neuron being recorded, the neuron's response to a stimulus was larger when the stimulus was presented at the attended location than at the ignored location (figure 2*c*). It should also be noted that there were no sustained shifts in baseline activity under these conditions owing to the fact that the monkey always attended inside the receptive field, thus making it impossible to compare attend-inside with attend-outside conditions.

Several single unit experiments have demonstrated the existence of both amplification effects and sustained bias effects (Chelazzi *et al.* 1993; Miller & Desimone 1994; Luck *et al.* 1997), and it is clear that the two are not mutually exclusive. These mechanisms are conceptually quite distinct, however, and undoubtedly exert very different influences on sensory processing. For example, while a neural firing bias may well correspond to the establishment of a search template, the amplification of sensory-evoked activity may improve the signal–noise ratio of attended inputs and hence increase the discriminability of those signals (Hawkins *et al.* 1990; Luck *et al.* 1994). Another well-known attention effect on neural activity is the re-routing of attended inputs into specialized processing circuits for further analysis; the activation of these separate attention-specific neural populations is associated with 'endogenous' ERP components as opposed to the sensory-evoked components that are subject to amplification effects (Hillyard *et al.* 1995).

In the following sections, we discuss how attention-related amplification has been assessed with electrophysiological techniques, as well as a recent proposal for separating amplification and bias effects through measures of rCBF. We conclude with a discussion of how the general concept of amplification or sensory gain control can be subdivided into more specific mechanisms of attentional suppression and enhancement.

2. VISUAL–SPATIAL ATTENTION: EVIDENCE FOR AN EARLY GAIN CONTROL MECHANISM

It is well established that directing attention to the location of a stimulus can lead to more rapid and accurate discrimination of the information contained in that stimulus (reviewed in LaBerge 1995). A long-running debate still continues, however, concerning the mechanism of these spatial attention effects. Some authors have proposed that stimuli falling within the 'spotlight' of attention are processed more efficiently at early sensory levels (Hawkins *et al.* 1990; Reinitz 1990; Luck *et al.* 1996) and that this early facilitation takes the form of an amplification of perceptual information arising from attended locations (Posner & Dehaene 1994). Alternatively, it has been hypothesized that spatial selection acts at late, post-perceptual levels through the selective biasing of decision or response processes in favour of attended-location stimuli (Sperling & Dosher 1986; Shiu & Pashler 1995).

ERP data recorded during spatial attention tasks have provided useful evidence with respect to this theoretical controversy. Paying attention to the location of a stimulus produces a characteristic pattern of changes in the ERP waveform, which is exemplified in a study by Mangun and colleagues (Mangun *et al.* 1993). As shown in figure 3*a*, this study presented briefly flashed stimuli in random order to four locations in the visual field. Subjects attended to the flashes at one of the locations on each run, ignoring the flashes at the other three locations. Figure 3*b* shows the ERP recorded for the flashes at one location (lower left-field) when they were attended (solid line) and when other locations were attended (dashed

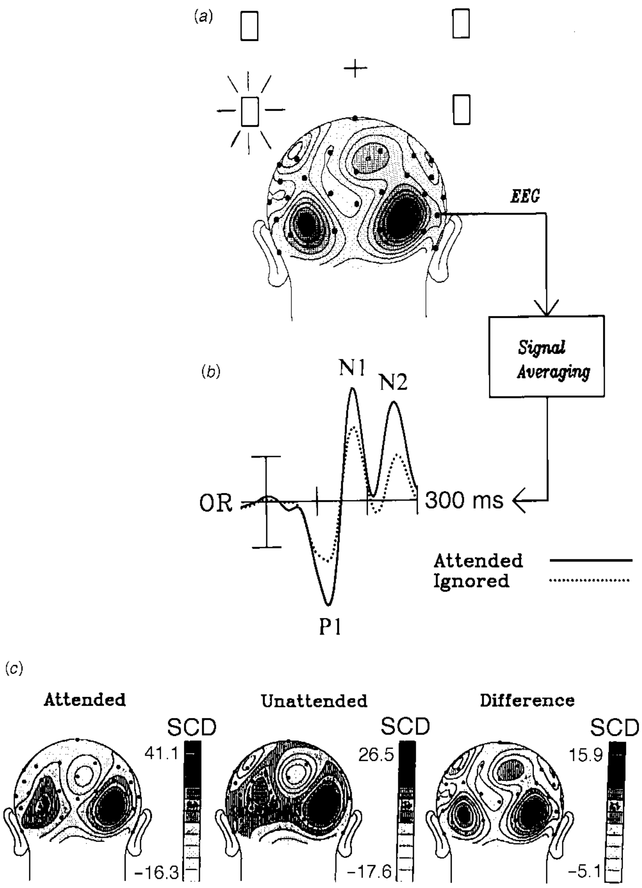

Figure 3. Amplitude modulation of early visual ERP components in the spatial attention experiment of Mangun *et al.* (1993). (*a*) Subjects fixated the centre cross while stimuli (flashed rectangles) were presented one at a time to the four quadrants in random order at intervals of 250–550 ms. Subjects attended to stimuli in only one quadrant during each run. ERPs were recorded from 30 scalp sites, and the map of scalp current density (SCD, the second spatial derivative of voltage) for the P1 component elicited by the lower left stimulus is shown on the schematic head. (*b*) ERP waveforms to lower left flashes when these flashes were attended (solid line) and ignored (dotted line). (*c*) SCD maps for the P1 component in response to lower left stimuli when attended and unattended, and for the attended minus unattended difference wave. Note that the contralateral occipital current source does not change in position with attention. SCD scale values are in microvolts per square metre.

line). Directing attention to the location of these flashes produced amplitude increases in its early evoked ERP components recorded over the posterior visual cortex, including the positive P1 (latency 80–100 ms) and the negative N1 (140–190 ms) waves.

There are several features of this P1–N1 amplitude enhancement suggesting that it reflects an attentional mechanism of early sensory gain control or amplification. The finding that the increment in P1 amplitude with attention has exactly the same scalp topography as the unattended P1 itself (figure 3*c*) supports the hypothesis that attention acts to amplify the neural response that is automatically evoked by that particular stimulus even when it is not attended. In contrast, an attention mechanism that involved activation of a separate neural population that was not activated by unattended stimuli would typically (though not inevitably) produce an altered voltage topography. Furthermore, the finding that the incremented ERP has the same phasic waveform as the unattended ERP strongly favours a gain control process as opposed to either a tonic bias or the activation of a separate neural population.

The idea that spatial attention operates in humans by controlling the gain of sensory-evoked responses was put forward many years ago (Eason 1981; Harter & Aine 1984; Hillyard & Muente 1984) and has received considerable support since then (reviewed in Mangun & Hillyard 1995; Hillyard *et al.* 1996). Important new evidence has come from studies that varied stimulus luminance while recording ERPs in a spatial attention task (Johannes *et al.* 1995; Wijers *et al.* 1997). The rationale for these studies was as follows: if the principal effect of attention is to amplify sensory-evoked activity in the visual pathways, then manipulations of the physical stimulus (such as luminance changes) that affect the latency, waveform or scalp topography of the corresponding ERPs should have a similar influence on the attention-produced enhancements of those ERPs. In particular, the attended and unattended waveforms should remain precisely superimposed in time (as in figure 3*b*), even though their latencies may be affected by changes in stimulus luminance, and the amplified portion of the ERP should maintain a similar scalp distribution to that of the ERP to the same stimulus when unattended (as in figure 3*c*).

Exactly this pattern of results was observed by both Johannes *et al.* (1995) and Wijers *et al.* (1997) for the P1 attention effect, thereby providing strong support for a sensory gain control mechanism at this early level. The effects of attention on the subsequent N1 component were more complicated, however, probably because the N1 consists of summated negative potentials arising from several different cortical sources (see next paragraph), not all of which may be influenced in the same way by attention. Whereas Wijers *et al.* found that the enhancements of N1 amplitude with attention fit the pattern of sensory gain control, Johannes *et al.* observed that the enhanced N1 negativity could be dissociated in time from the unattended N1 waveform, suggesting that attention had initiated activity in a separate neural population.

An amplification of the evoked P1–N1 components has been observed in a number of spatial attention tasks, including situations of sustained attention to randomized stimulus sequences as in figure 3 and in trial-by-trial cueing tasks where each individual stimulus was preceded by a cue that informed the subject of its most probable location. In such cueing tasks stimuli at precued (valid) locations generally evoked enlarged P1 and/or N1 components in association with speeded reaction times and/or improved target detectability relative to when the stimuli occurred at uncued or unexpected locations (Heinze *et al.* 1990; Mangun *et al.* 1993, 1995; Anllo-Vento 1995; Eimer 1997). This correspondence between behavioural improvement and ERP enhancement reinforces the concept of an amplification mechanism that gives inputs from attended locations an improved signal–noise ratio (Hawkins *et al.* 1990) and supports the view that these ERP modulations actually reflect sensory information that is used for perceptual judgements.

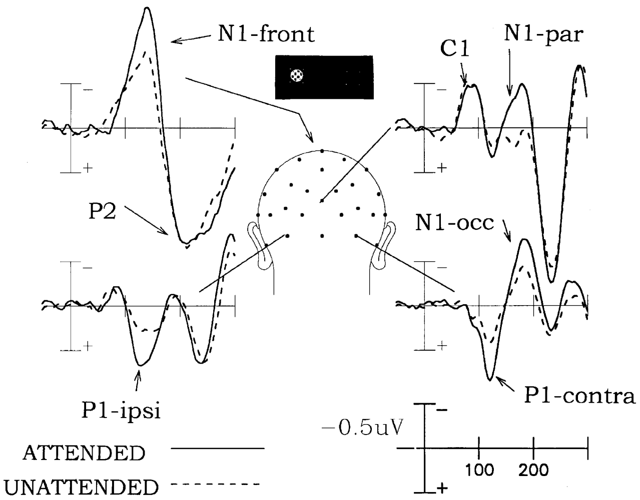

Figure 4. Visual ERPs recorded from four different scalp sites in response to left-field stimuli in a spatial attention task (Clark & Hillyard 1996). Small circular checkerboards were flashed in random order to the left and right visual fields while subjects attended to the stimuli in one visual field at a time. When the left field stimuli were attended (solid lines), the P1 and N1 components were enlarged in relation to when right-field flashes were attended (dashed lines). The earlier C1 component was unaffected by attention.

3. LOCALIZATION OF EARLY ATTENTION EFFECTS

Several recent studies have used ERP source localization techniques to investigate the anatomical level(s) of the visual pathways at which the amplification of attended inputs takes place. These studies have found that the earliest ERP component (termed the 'C1'), which has an onset latency of 50–60 ms, does not show any significant change with spatial attention (Mangun *et al.* 1993; Gomez *et al.* 1994; Johannes *et al.* 1995; Clark & Hillyard 1996; Wijers *et al.* 1997). As shown in figure 4, the C1 component has maximal amplitude over the parieto-occipital scalp near the midline and remained invariant when attention was shifted to and from the location of the evoking stimulus. In contrast, the P1–N1 components over the lateral occipital scalp showed the usual amplitude modulations with attention, as did the N1 waves recorded over parietal, occipital, and frontal scalp sites. Dipole modelling of the C1 voltage topography points to a neural generator in primary visual cortex (figure 5*a*) (Gomez *et al.* 1994; Clark & Hillyard 1996; Johannes *et al.* 1998), and the C1 varies in polarity according to stimulus position in the visual field in a manner consistent with the retinotopic organization of the striate cortex within the calcarine fissure (Mangun *et al.* 1993; Clark *et al.* 1995). These ERP data suggest that visual processing at the level of the striate cortex is not affected by spatial attention. There is some evidence from animal neurophysiological (Motter 1993) and human neuroimaging (Worden & Schneider 1996; Shulman *et al.* 1997) studies, however, which suggests that attention may influence striate cortex activity under certain conditions.

The amplitude modulation of the P1 component starting about 80 ms post-stimulus appears to represent the earliest effect of spatial attention on visual processing. Attempts to localize the neural generators of this P1 modulation by using scalp current density mapping and dipole modelling have indicated a source in ventral–lateral extrastriate cortex (Mangun *et al.* 1993; Gomez *et al.* 1994; Johannes *et al.* 1995; Clark & Hillyard 1996; see figure 5*b*). Given the ambiguities inherent in calculating the intracranial sources of neural activity based on scalp recordings, however, several recent studies have combined ERP recording with PET to take advantage of the anatomical information provided by this blood flow imaging technique. The first experiment of this type (Heinze *et al.* 1994) required subjects to attend to either the right or left side of a bilateral stimulus display, with ERP recordings taken in one session and PET during a second session. Dipole modelling of the P1 enhancement over the hemisphere contralateral to the attended visual field indicated a generator source in the fusiform gyrus of the ventral extrastriate cortex. This calculated source corresponded very closely to the zone of increased regional cerebral blood flow (rCBF) revealed by PET, which strongly suggested that this ventral extrastriate region was the site of the early attentional gain control reflected in the P1 amplitude modulations.

To explore further the anatomical bases of this early P1 attention effect, Mangun *et al.* (1997) compared ERP and PET localizations during the symbol matching task used by Heinze and co-workers (1994) and during a less demanding dot detection task. As seen in figure 6*a*, PET revealed two foci of rCBF increase during the symbol task in the hemisphere contralateral to the attended visual half-field, the first in the posterior fusiform gyrus as was found by Heinze *et al.* and a second, smaller focus in ventral–lateral extrastriate cortex of the middle occipital gyrus. Only the fusiform activation showed an increase for the more difficult symbol task relative to the dot detection task (figure 6*b*), however, and this was paralleled by an increased contralateral P1 amplitude in the symbol task (figure 6*c*). This ERP–rCBF correlation provides further evidence that the P1 attention effect is generated primarily in or near the fusiform gyrus.

A combined ERP–PET study by Woldorff and co-workers (1997) suggested that the amplification of visual evoked activity reflected in the P1 wave takes place in retinotopically organized visual cortex. They found that when stimuli were presented to the lower visual fields, below the horizontal meridian, that spatial attention produced an increase in rCBF in dorsal extrastriate occipital cortex of the contralateral hemisphere; the associated P1 attention effect was also localized by dipole modelling to the same dorsal region. This contrasted with the more ventral PET and ERP localizations obtained by Heinze and co-workers (Heinze *et al.* 1994) and Mangun *et al.* (1997), in whose studies stimuli were presented to the upper visual fields. Such a pattern of results would be expected if spatial attention affected evoked neural activity in retinotopically organized visual areas such as V2, V3–VP, or V4, which have been recently mapped in humans (Sereno *et al.* 1995; DeYoe *et al.* 1996).

No evidence for attentional modulation of short-latency evoked activity in primary visual cortex (V1) was obtained in any of these combined PET–ERP studies nor in a spatial attention study that used a novel optical imaging technique (Gratton 1997). These studies thus offer no support for the hypothesis that visual transmission from

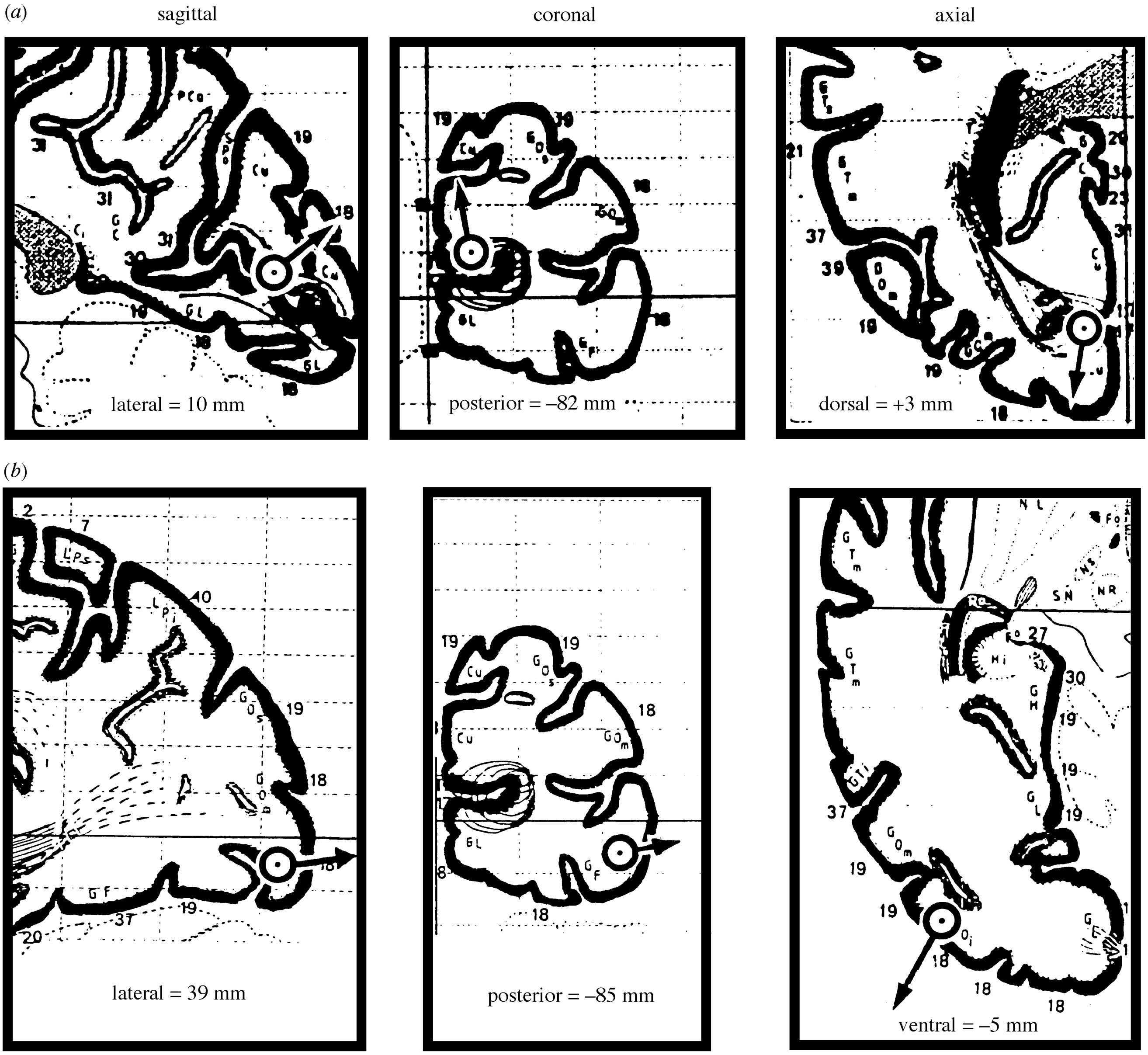

Figure 5. Projections of dipoles representing the estimated sources of the C1 and P1 components onto brain sections of the Talairach & Tournoux (1988) atlas. Best-fit dipole locations were calculated from scalp voltage topographies using the algorithm developed by Scherg (1990). (*a*) The dipole corresponding to C1 was localized to primary visual cortex near the calcarine fissure. (*b*) The dipole corresponding to the P1 attention effect (attended minus unattended P1 voltage distribution) was localized to ventral–lateral extrastriate cortex. Data from Clark & Hillyard (1996).

the lateral geniculate to striate cortex is under the control of spatial attention (Crick 1984). However, the short latency of the extrastriate P1 attention effect (onset at 70–80 ms) and its apparent retinotopic properties indicate that the initial amplification of attended-location inputs takes place in posterior extrastriate cortex in areas where only elementary visual features are represented. This PET–ERP evidence thus provides strong evidence for 'early selection' theories of attention, according to which sensory inputs to attended locations are enhanced at early levels of visual processing prior to full stimulus identification and recognition (reviewed in LaBerge 1995). This early amplification process seems to be applied to all stimuli presented to attended locations, whether they are task relevant or not (Heinze *et al.* 1990; Luck *et al.* 1993) and augments their signal-to-noise ratio so that they may be processed more effectively at higher levels of object and pattern recognition.

4. PET EVIDENCE FOR AMPLIFICATION?

The co-localization of ERP and rCBF modulations during spatial attention to common cortical areas provides evidence that both measures are reflecting the same gain control processes in the same extrastriate cortical regions. It is important to note, however, that these PET data *per se* do not provide unequivocal evidence for a gain control mechanism of attention. The pattern of PET changes observed in the spatial attention tasks reviewed here, like those reported by (Corbetta *et al.* 1991) in tasks involving attention to non-spatial features (colour, shape, movement), consisted of enhanced rCBF

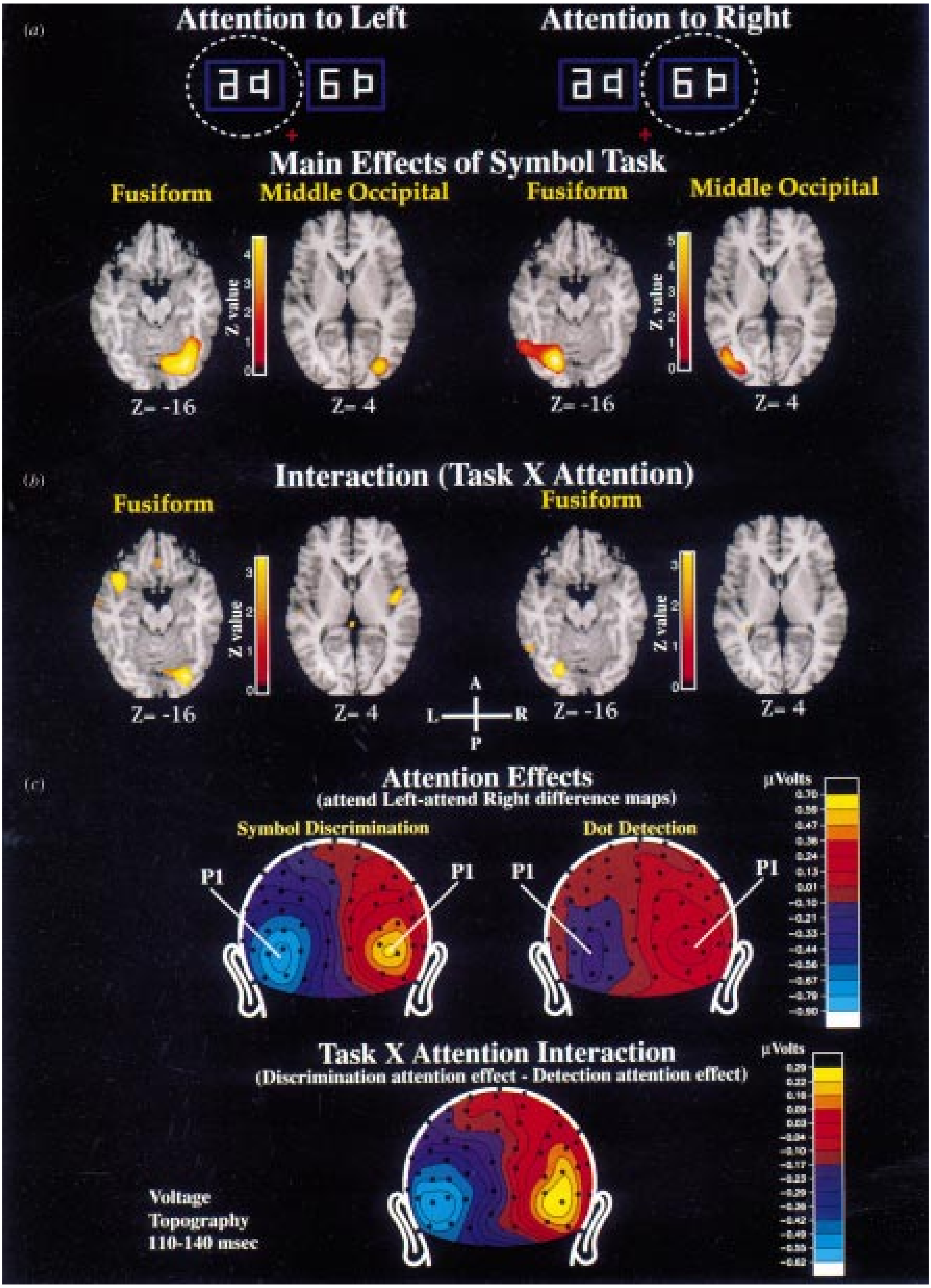

Figure 6. (*a*) Top row shows examples of bilateral symbols used as stimuli in the study by Mangun *et al*. (1997). In different runs subjects attended to the right or left side of the displays, which were presented in rapid, randomized order. Brain sections show that attention to the left-field stimuli produced PET activations in the right fusiform and middle occipital gyri, while attention to the right produced corresponding activations in the left hemisphere. Note that left side of the images corresponds to left side of brain. (*b*) Visual cortex activations were greater for the symbol discrimination task than for a simpler dot detection task only in the contralateral fusiform gyrus. (*c*) Topographical voltage maps of the attention effect on the P1 component (110–140 ms latency) elicited by the bilateral stimuli. Maps represent P1 voltage distributions in attend left minus attend right conditions. Lower head shows that the P1 attention effect was greater for attend-symbol than for attend-dot conditions, as was the fusiform gyrus activation shown in *b*.

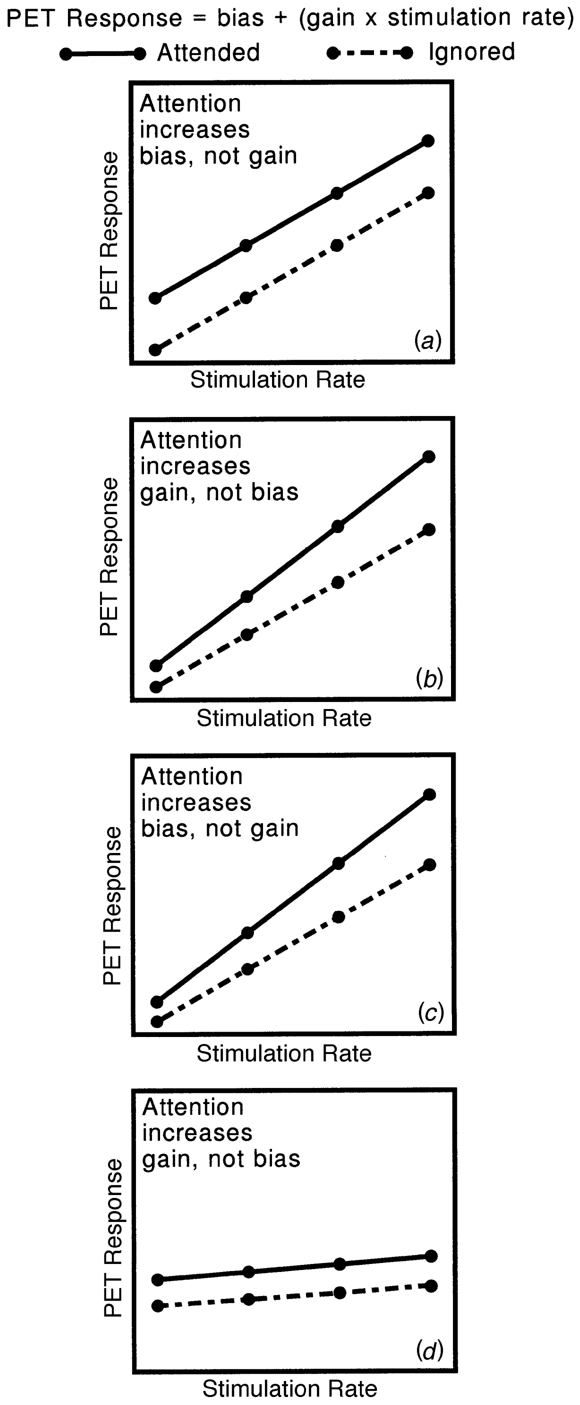

Figure 7. Hypothetical relations between attention, stimulation rate, and PET response (rCBF). (*a*) In this case attention adds a bias signal, and the bias signal and the single-stimulus sensory response are assumed to be unaffected by stimulation rate. Because more stimuli are presented during the data acquisition interval, the PET response will increase as the stimulation rate increases. The effect of adding a constant bias signal will appear as a shift in the intercept of the stimulation rate function. (*b*) In this case, attention increases the sensory gain without any bias signal, and the single stimulus sensory responses are assumed to be unaffected by stimulation rate. Because the response to each individual stimulus is increased by attention, the effect of attention on the PET response will be larger at higher stimulation rates. (*c*) In this case, attention adds a bias signal without influencing gain, as in *a*, but the size of this bias signal is assumed to increase as the stimulation rate increases (owing, for example, to increased attentional requirements at high stimulation rates). The result is a greater slope for the attended stimuli, as in *b*. (*d*) In this case, attention increases the sensory gain without any bias signal, as in *b*, but the single stimulus sensory responses are assumed to decrease as the stimulation rate increases (owing to neural fatigue). This causes the slope of the stimulation rate function to be very shallow, and there is no change in slope for the attended stimuli compared with the ignored stimuli.

in specific sensory areas under conditions of increased attention relative to control conditions. As discussed, such a pattern could be produced by a tonic biasing of baseline neural firing rather than an amplification of sensory-evoked responses.

Recently, it has been suggested that PET data could be used to distinguish between attentional mechanisms of gain control over sensory input versus tonic biasing of neural activity by studying how rCBF changes vary as a function of stimulus repetition rate (Rees *et al.* 1997). The reasoning is illustrated in figure 7. As repetition rate increases, more stimulus-evoked responses will occur during the PET imaging period, leading to a greater PET (rCBF) response. If attention simply adds a bias signal but does not influence the actual sensory responses, then the increase in rCBF will be independent of the stimulation rate, as shown in figure 7*a*. However, if attention amplifies the sensory response to each stimulus, then the number of amplified responses will increase as more stimuli are presented during the PET imaging period, and the effect of attention will, therefore, be greater at higher stimulation rates. This is illustrated in figure 7*b*. In other words, changes in gain will influence the slope of the stimulation-rate function, whereas changes in bias will only influence the intercept. When Rees and colleagues applied this reasoning to a visual search experiment, they concluded that attention acted to modulate the gain of responses in the precuneus, the left cerebellum, and the premotor cortex, whereas attention added a bias signal to activity in the left inferior temporal gyrus and the right cerebellum.

The validity of this approach for distinguishing the two types of modulatory effects of attention would appear to depend on several assumptions that are open to question. In particular, this approach assumes that the effects of attention on bias and gain are constant across stimulation rates and that the neural responses elicited by individual stimuli also remain constant with changes in stimulation rate. There are many ways in which these assumptions might be expected to be violated, however, and we will consider two particularly likely and problematic scenarios. First, it is likely that different attentional strategies will be employed when the stimulation rate increases, owing both to the need for increased perceptual selectivity under conditions of high load (Lavie 1995) and to the increased ease of maintaining an attentional template when the relevant stimuli occur more frequently. These factors could lead to progressive increases in an attentional bias signal at higher stimulation rates and, therefore, a steeper slope in the stimulation-rate function, even if attention did not influence the gain of the sensory response (figure 7*c*). Second, it is well-known that sensory-evoked responses to repeated stimuli often exhibit decreased amplitudes at higher stimulation rates owing to refractory or fatigue effects (Naatanen 1992). As shown in figure 7*d*, this could lead to a shallow slope in the function relating blood flow to stimulation rate, because the increase in the number of stimuli presented during the PET imaging period would be partly offset by the decreased size of the neural response to each stimulus (this function could also be nonlinear, flat, or even declining). If attention then increased the gain of sensory responses by a constant factor but did not affect their refractory properties, this amplification effect could lead to a change in intercept rather than a change in slope. Additional nonlinearities might arise if there were ceiling effects on total neuronal activity that would prevent the divergence of the two curves in figure 7*b* or if the function relating increased neural activity to increased blood flow were nonlinear. Even more complex interactions could be envisaged if the bias signals from attentional control areas acted not only to change tonic firing rates in the target brain areas but also affected the sensory gain factor, which seems like a reasonable possibility. A final type of complication could ensue if the attentional process led to a reorganization of cellular firing patterns within a brain region rather than simple additive or multiplicative effects. In this latter case different neuronal subpopulations may be affected in opposing ways, making the net influence on rCBF difficult to predict.

Because of this multiplicity of confounding factors that may perturb the relation between neuronal responses (manifested in rCBF changes) and stimulation rate as a function of attention, it is difficult to accept the proposal that diverging curves (such as in figure 7*b*) are uniquely associated with a gain control mechanism and parallel curves (figure 7*a*) with a bias mechanism. Indeed, the example given by Rees and colleagues (Rees *et al.* 1997) of diverging response slopes that was interpreted as indicating a sensory gain change (their figure 1*d*) does not seem to be straightforward, as the slope of the function in one of the attention conditions appears to be close to zero. In such a case, increasing the gain *per se* would not seem capable of producing a line of steeper slope. Given these complexities in interpreting the PET data, it appears that gain control and bias mechanisms can be distinguished (at least for the present) more clearly by means of ERP, neuromagnetic, or single unit recordings where time-course and waveform information are also available.

5. ATTENTIONAL COSTS AND BENEFITS

Although the concept of sensory gain control or amplification appears to be a useful first approximation for describing the effects of attention on perceptual processes, it is clearly not the whole story. In particular, electrophysiological studies have provided evidence that the suppression of inputs at unattended locations and the facilitation of signals at attended locations may be done by separate mechanisms, associated with attentional costs and benefits, respectively. In addition, the facilitative mechanism seems to be preferentially engaged in situations where task-relevant stimuli must be discriminated rather than simply detected.

As was shown in figures 1 and 3, the P1 and N1 waves are typically larger in amplitude for attended-location stimuli than for unattended-location stimuli. A simple explanation for this pattern of results is that the sensory gain is increased for the attended location at an early stage and that this effect propagates forward to increase the amplitudes of the subsequent ERP components. However, several studies have now shown that the P1 and N1 attention effects are dissociable and reflect qualitatively different aspects of attention. An example of this is shown in figure 8*a*, which illustrates the results of a spatial cueing experiment (Luck *et al.* 1994). In this experiment, each trial consisted of a spatial cue followed by a brief luminance-increment target and a pattern mask. The subject's task was to report the presence or absence of the luminance-increment target at the masked location. In most of the trials, a single location was cued and the target–mask complex appeared at the cued location; these were called 'valid' trials. In a small percentage of trials, a single location was cued but the target–mask complex appeared at an uncued location; these were called 'invalid' trials. In yet a third type of trial, cues were pointed toward all possible target locations and the target–mask complex was equally likely to appear at any of these locations; these were called 'neutral' trials. In neutral trials attention was presumably unfocused or broadly focused, which provided a baseline condition that made it possible to distinguish between suppressive and facilitatory attention effects. Specifically, larger ERP amplitudes on valid trials than on neutral trials would indicate a relative facilitation of processing at the attended location, whereas smaller amplitudes on invalid trials than on neutral trials would indicate a relative suppression of processing at the ignored locations.

Several patterns of data were possible in this experiment. For example, attention may operate simply to increase the sensory gain at the attended location, which would result in larger P1 and N1 waves on valid trials than on neutral trials, with no suppression in invalid trials relative to neutral trials. Alternatively, attention may decrease the gain at the ignored locations, resulting in decreased P1 and N1 amplitudes in invalid trials relative to neutral trials. As shown in the bar graphs of figure 8*a*, however, neither of these patterns was observed. Instead, the P1 and N1 waves (both recorded over the occipital scalp) showed completely different attention effects: the P1 wave was reduced in invalid trials relative to neutral trials with no additional enhancement in valid trials, whereas the N1 wave was enhanced in valid trials relative to neutral trials with no additional reduction in invalid trials. In other words, the P1 wave exhibited only suppression at the ignored locations (associated with behavioural 'costs' i.e. reduced target detectability), whereas the N1 wave exhibited only facilitation at the attended location (associated with behavioural 'benefits' i.e. improved target detectability). This pattern of results is not compatible with the hypothesis of an early, single stage modulation of sensory gain but rather indicates that attention may have qualitatively different effects at different stages of processing.

To assess the generality of this dissociation between the P1 and N1 waves during spatial attention, we did an analogous manipulation of attention using a very different

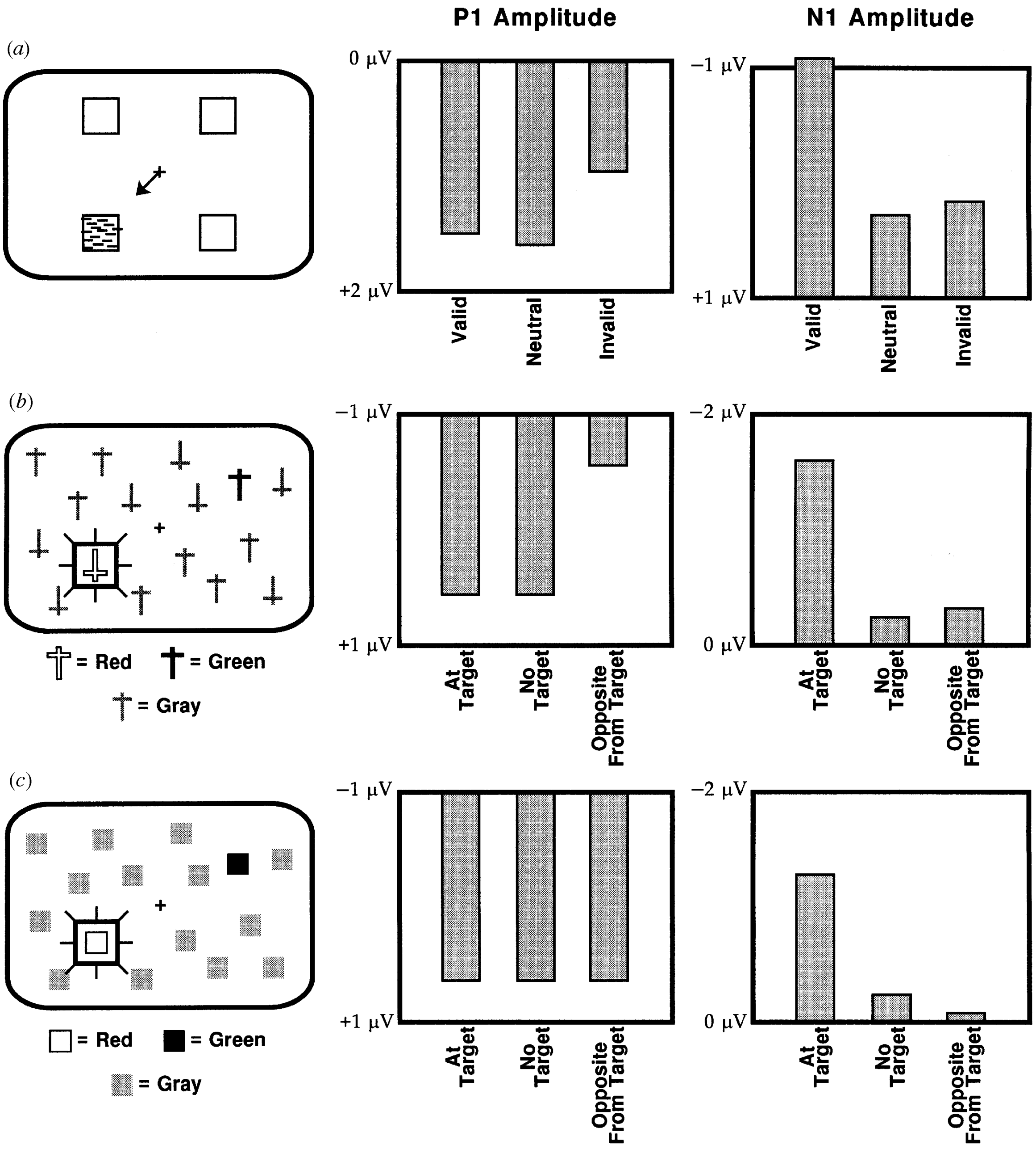

Figure 8. Dissociations between the P1 and N1 attention effects in a spatial cueing experiment and two visual search experiments. (*a*) Stimuli and ERP results from spatial cueing experiment of Luck *et al.* (1994). Each trial began with an arrow cue, followed 200–500 ms later by a luminance target and pattern mask. P1 and N1 components were elicited at occipital sites by target-mask complex under three modality conditions. (*b*) Stimuli and ERP amplitudes in conjunction search experiment of Luck & Hillyard (1995). Subjects reported orientation of 'T' in designated target colour. P1 and N1 components were elicited by irrelevant probe square that either surrounded the target, surrounded a 'T' opposite to the target, or occurred in the absence of a target. (*c*) Same as *b*, but subjects only had to report the presence or absence of the target colour.

task, namely visual search (Luck & Hillyard 1995). As illustrated in figure 8*b*, the stimuli in this experiment were arrays of 16 upright and inverted Ts, 14 of which were grey and two of which were different colours (selected at random from red, green, blue, or violet). At the beginning of each trial block, subjects were instructed to attend to one of the colours and to press one of two buttons for each stimulus array to indicate whether the T drawn in the attended colour was upright or inverted, if it was present at all (they were instructed to press neither button if the attended colour was absent). Because the ERP elicited by the visual search arrays reflected the processing of all of the items in the array, it was not possible to use these ERPs to assess the processing of stimuli at attended and ignored locations. Instead, a task-irrelevant 'probe' square was presented around one of the coloured Ts in each array, and the ERP elicited by this probe stimulus was used as a measure of sensory processing at the probed location. In some trials, the probe was presented at the location of the attended-colour T (the target); because we assume that attention was directed to the location of the target, this trial type is analogous to a valid trial in a cueing paradigm. In other trials, the probe was presented at the location of a coloured T on the opposite side of the array from the attended target (analogous to an invalid trial). In a third type of trial, the attended colour was absent and one of the two irrelevant-colour Ts was probed; because attention was presumably unfocused or diffusely focused on these trials, these were analogous to neutral trials. The probe was presented 250 ms after the onset of the search array to provide time for attention to be allocated to the location of the target.

As shown in the bar graphs of figure 8*b*, the same pattern of P1 and N1 attention effects was obtained in this visual search experiment as in the cueing experiment illustrated in figure 8*a*. The N1 component was enhanced for probes presented at the location of the target compared with probes presented on target-absent trials, but there was no suppression of the N1 when the probe was presented at a location in the opposite hemifield from the target. In contrast, the P1 component was suppressed when the probe was presented at a location in the opposite hemifield from the target compared with probes presented on target-absent trials, but there was no enhancement of P1 amplitude when the probe was presented at the location of the target compared with probes presented on target-absent trials. This provides additional evidence that the P1 reflects a suppression of processing at ignored locations whereas the N1 reflects a facilitation of processing at attended locations.

It could be argued that it does not matter whether the gain is increased at attended locations or decreased at ignored locations; in either case, the result is a larger signal for attended locations relative to ignored locations. Indeed, this would be true if attention merely controlled the gain of sensory processing (and if neural responses were not bounded by maximum and minimum firing rates). However, there is increasing evidence that the N1 enhancement observed at attended locations may reflect more than a simple increase in sensory gain. This derives from two additional dissociations that have been observed between the P1 and N1 attention effects. First, when the visual search paradigm shown in figure 8*b* was changed so that subjects had only to indicate the presence or absence of the attended colour, the P1 attention effect was eliminated while the N1 effect remained (Luck & Hillyard 1995). This is shown in figure 8*c*. Second, in a series of cueing experiments, Mangun & Hillyard (1991) found that the N1 attention effect was eliminated when subjects performed a simple-RT task in which they pressed a single button as fast as possible when they detected the target, regardless of its identity. The N1 effect returned, however, when the subjects performed a choice-RT task in which they were required to quickly press one of two buttons to indicate whether the target was a tall bar or a short bar. The P1 attention effect was present in both the simple- and choice-RT tasks. On the basis of these results, it was proposed that the P1 attention effect does reflect a reduction in sensory gain that attenuates potentially interfering information from ignored locations, whereas the N1 attention effect reflects the application of a limited-capacity discriminative process to stimuli at the attended location (Luck 1995).

This hypothesis for P1 is based on observations suggesting that the P1 attention effect occurs primarily under conditions that might lead to interference. For example, when a subject performs a difficult luminance detection task, noise from other locations might impair performance. Similarly, when a subject must respond as quickly as possible to the appearance of a stimulus, a low motor-response threshold will be established, and it is necessary to suppress noise that might otherwise trigger a spurious motor response. Suppression of irrelevant inputs will also be useful in a conjunction discrimination task such as that shown in figure 8*b*, because it is necessary to avoid combining the form of a distractor item with the colour of the target item. These are all conditions under which the P1 wave is modulated by attention. In contrast, no P1 suppression was observed in a simple feature detection task (figure 8*c*) (Luck & Hillyard 1995), presumably because simple, suprathreshold features can be identified with very little interference from concurrently presented distractor items (Treisman 1988 & 1996). Thus, several lines of evidence suggest that the P1 attention effect reflects a suppression of processing (i.e. a gain reduction) at unattended locations that serves to mitigate interference between attended and unattended information.

The proposal that the N1 attention effect reflects the application of a limited-capacity discriminative process to the attended location was initially based on the finding that this effect was present when subjects performed discriminations, but not when they performed simple-reaction time (RT) tasks (Mangun & Hillyard 1991). More recent evidence for this hypothesis is considered in § 6.

6. A LIMITED-CAPACITY DISCRIMINATIVE PROCESS

The ERP correlates of discriminative processing were examined some years ago by Ritter and colleagues with foveally presented stimuli (Ritter *et al.* 1983, 1988). The logic behind these experiments was straightforward; if the same stimulus was presented during a simple-RT task and during a choice-RT task, then the use of discriminative mechanisms in the choice-RT task would lead to additional ERP activity that could be visualized by comparing the ERPs elicited during the simple- and choice-RT conditions. When Ritter and co-workers (1983, 1988) made this comparison, they found a greater negativity during the choice-RT task that included several distinct phases, the earliest of which coincided in time and scalp distribution with the occipito-temporal N1 wave. Ritter and colleagues termed this entire negative component the 'NA' wave and proposed that it was an index of a pattern discrimination and recognition process.

In a recent series of experiments, we examined more closely the early phase of the NA—which coincides with the N1 wave and is here termed the N1 discrimination effect—to evaluate the hypothesis that it truly reflects a perceptual discrimination process and to determine its relation to the attention-related modulations of the N1 wave described here. Before describing these experiments, however, it is necessary to distinguish between two different varieties of N1 attention effects. The N1 wave can be observed at both anterior and posterior scalp sites, but it peaks 30–60 ms earlier at anterior sites. Both the anterior and posterior N1 waves are larger for attended-location stimuli than for unattended-location stimuli,

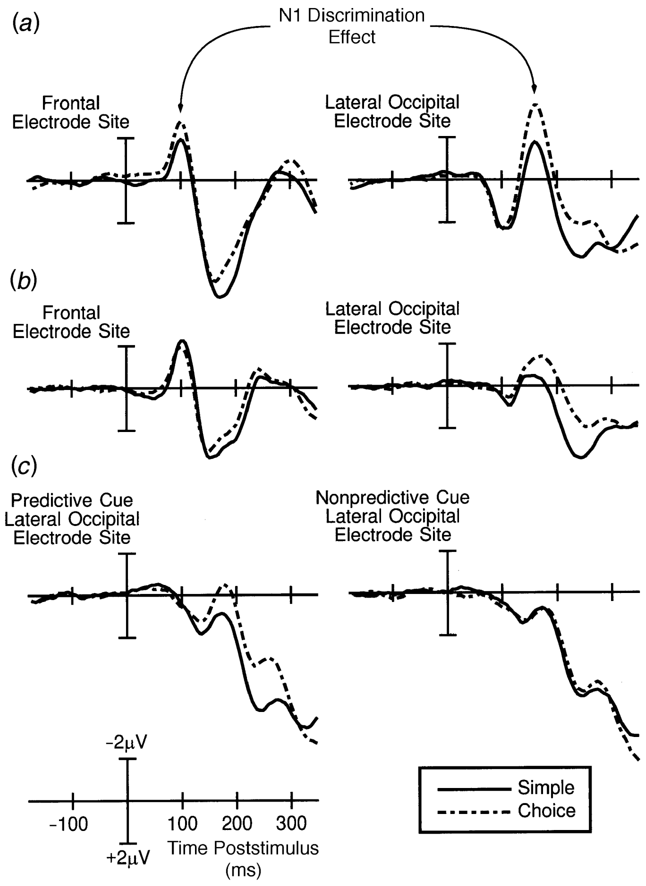

Figure 9. N1 discrimination effect in three experiments (Vogel & Luck 1997). (*a*) ERPs elicited at anterior and posterior electrode sites by non-target stimuli in a simple-RT task and a choice-RT task. An N1 discrimination effect can be seen at both the anterior and posterior electrode sites. (*b*) ERPs elicited at anterior and posterior electrode sites by non-target stimuli in a simple-count task and a choice-count task. An N1 discrimination effect can be seen only at the posterior electrode site. (*c*) ERPs elicited at posterior electrode sites by non-target stimuli when preceded by a predictive cue (left) or a nonpredictive cue (right). An N1 discrimination effect can be seen only when the cue was predictive.

but these effects are differentially influenced by several experimental manipulations (Luck *et al.* 1990). It is the posterior N1 attention effect that we propose reflects the application of a discriminative process to attended-location stimuli (Luck 1995).

Figure 9*a* illustrates the basic N1 discrimination effect. When subjects performed either a colour discrimination task or a letter discrimination task, there was a greater negativity in the N1 latency range than when the subjects performed a simple-RT task with the same stimuli. This effect was present at both anterior and posterior scalp sites. However, it is possible to explain this effect in terms of differences in motor preparation rather than the application of a discriminative process. Because the subjects knew what response was to be made even before stimulus onset in the simple-RT task but not in the choice-RT task, they may have begun preparing the response before stimulus onset in the simple-RT task. This early preparation would probably be associated with negative 'motor potentials' arising from the motor cortex that began earlier in the simple-RT condition and added extra negativity to the measured N1 wave.

Several experiments were aimed at distinguishing motor–preparatory from sensory–discriminative influences on the N1 wave (Vogel & Luck 1997). In one experiment, differences in anticipatory activity were minimized by using a highly variable interstimulus interval, making it difficult for the subjects to anticipate the onset time of the stimuli. In addition, differences in motor activity were eliminated by requiring subjects to silently count the stimuli rather than making overt motor responses to them. In the 'simple-count' condition, subjects silently counted the number of stimuli that were presented in a trial block and reported this number at the end of the block. In the 'choice-count' condition, subjects counted the number of stimuli containing the colour red rather than counting all of the stimuli. The primary difference between the tasks was the requirement of colour discrimination in the choice-count condition. As shown in figure 9*b*, there was a greater negativity in the N1 latency range for the choice-count condition than for the simple-count condition, and this effect was restricted to posterior, occipitotemporal scalp sites. On the basis of these results and other similar findings, we concluded that the anteriorly distributed N1 discrimination effect is probably attributable to differential motor preparation but that the posteriorly distributed N1 difference does indeed reflect the engagement of a visual discrimination process.

Once motor preparatory activity had been eliminated, the scalp distribution of the N1 discrimination effect was found to be similar to the scalp distribution of the posterior N1 attention effect, with a maximum at occipitotemporal electrode sites. To provide further evidence that these effects reflect the same underlying neurocognitive process, we examined the N1 discrimination effect in a spatial cueing experiment. If this effect reflects a limited-capacity process that can be allocated to a single location in the visual fields, then it should be present only when the target location is known in advance. This hypothesis was tested in an experiment with four conditions: simple-predictive, simple-nonpredictive, choice-predictive, and choice-nonpredictive. In the predictive conditions, a cue at the beginning of each trial indicated (with 100% reliability) the location at which the subsequent target would be presented; in the nonpredictive conditions, a cue was presented but was not correlated with the location of the subsequent target. Figure 9*c* compares the simple-RT and choice-RT tasks for the predictive and nonpredictive conditions. A significant N1 discrimination effect was observed for the predictive condition, but not for the nonpredictive condition. Thus, both the N1 discrimination effect and the N1 attention effect are present only when the subject knows the location of the to-be-discriminated stimulus. We, therefore, tentatively conclude that these effects reflect the same underlying neural and cognitive mechanisms and that spatial attention operates, in part, by controlling the allocation of a limited-capacity discriminative process to attended-location signals. This may well involve both gain control–amplification of the evoked N1 generators plus the engagement of specialized discriminative neural activity that extends beyond the N1 latency range.

7. CONCLUSION

As we have outlined here, recent studies using the methods of cognitive neuroscience have refined and extended the decades-old notion of attentional gain control in several ways. First, these methods have allowed amplification mechanisms to be differentiated from bias mechanisms, even when both mechanisms operate in the same brain regions and in the same tasks. Second, they have identified the neural loci at which amplification occurs, demonstrating that sensory gain control mechanisms operate in extrastriate areas of visual cortex, but not in striate cortex. These data strongly support 'early selection' models of visual attention. Third, these studies have distinguished between different subcategories of gain-control mechanisms, indicating the existence of separable mechanisms for suppressing unattended sources of information and for enhancing the processing of attended sources. Further work is needed to decipher the specific neural codes that represent perceptual information and to delineate the neural circuitry that exerts attentional control over perceptual experience.

We thank our many colleagues who have contributed to the studies reviewed here, including L. Anllo-Vento, L. Chelazzi, V. Clark, R. Desimone, S. Fan, C. Gomez, S. Hackley, J. Hansen, H. Heinze, H. Hinrichs, R. Mangun, T. Muente, T. Picton and M. Woldorff. Supported by Grants from NIMH (MH25594 and MH56877), NIH (NS17778), ONR (N00014-93-I-0942), and the McDonnell-Pew Program in Cognitive Neuroscience (95-38).

REFERENCES

Anllo-Vento, L. 1995 Shifting attention in visual space: the effects of peripheral cueing on brain cortical potentials. *Int. J. Neurosci.* **80**, 353–370.

Broadbent, D. E. 1958 *Perception and communication*. New York: Pergamon.

Chelazzi, L., Miller, E. K., Duncan, J. & Desimone, R. 1993 A neural basis for visual search in inferior temporal cortex. *Nature* **363**, 345–347.

Clark, V. P. & Hillyard, S. A. 1996 Spatial selective attention affects early extrastriate but not striate components of the visual evoked potential. *J. Cogn. Neurosci.* **8**, 387–402.

Clark, V. P., Fan, S. & Hillyard, S. A. 1995 Identification of early visually evoked potential generators by retinotopic and topographic analyses. *Hum. Brain Mapp.* **2**, 170–187.

Corbetta, M., Miezin, F. M., Dobmeyer, S., Shulman, G. L. & Petersen, S. E. 1990 Attentional modulation of neural processing of shape, color, and velocity in humans. *Science* **248**, 1556–1559.

Corbetta, M., Miezin, F. M., Dobmeyer, S., Shulman, G. L. & Petersen, S. E. 1991 Selective and divided attention during visual discriminations of shape, color, and speed: functional anatomy by positron emission tomography. *J. Neurosci.* **11**, 2383–2402.

Crick, F. 1984 Function of the thalamic reticular complex: the searchlight hypothesis. *Proc. Natn. Acad. Sci. USA* **81**, 4586–4590.

Desimone, R. & Duncan, J. 1995 Neural mechanisms of selective visual attention. *A. Rev. Neurosci.* **18**, 193–222.

DeYoe, E. A., Carman, G. J., Bandettini, P., Glickman, S., Wieser, J., Cox, R., Miller, D. & Neitz, J. 1996 Mapping striate and extrastriate visual areas in human cerebral cortex. *Proc. Natn. Acad. Sci. USA* **93**, 2382–2386.

Duncan, J. 1981 Directing attention in the visual field. *Percept. Psychophys.* **30**, 90–93.

Duncan, J. & Humphreys, G. W. 1992 Beyond the search surface: visual search and attentional engagement. *J. Exp. Psychol. Hum. Percept. Perf.* **18**, 578–588.

Eason, R. G. 1981 Visual evoked potential correlates of early neural filtering during selective attention. *Bull. Psychon. Soc.* **18**, 203–206.

Eimer, M. 1997 Attentional selection and attentional gradients: an alternative method for studying transient visual-spatial attention. *Psychophysiology* **34**, 365–376.

Funahashi, S., Bruce, C. J. & Goldman-Rakic, P. S. 1989 Mnemonic coding of visual space in the monkey's dorsolateral prefrontal cortex. *J. Neurophysiol.* **61**, 331–349.

Fuster, J. M. & Jervey, J. P. 1982 Neuronal firing in the inferotemporal cortex of the monkey in a visual memory task. *J. Neurosci.* **2**, 361–375.

Gomez, C. M., Clark, V. P., Luck, S. J., Fan, S. & Hillyard, S. A. 1994 Sources of attention-sensitive visual event-related potentials. *Brain Topogr.* **7**, 41–51.

Gratton, G. 1997 Attention and probability effects in the human occipital cortex: an optical imaging study. *NeuroReport* **8**, 1749–1753.

Harter, M. R. & Aine, C. J. 1984 Brain mechanisms of visual selective attention. In *Varieties of attention* (ed. R. Parasuraman & D. R. Davies), pp. 293–321. London: Academic Press.

Hawkins, H. L., Hillyard, S. A., Luck, S. J., Mouloua, M., Downing, C. J. & Woodward, D. P. 1990 Visual attention modulates signal detectability. *J. Exp. Psychol. Hum. Percept. Perf.* **16**, 802–811.

Heinze, H. J., Luck, S. J., Mangun, G. R. & Hillyard, S. A. 1990 Visual event-related potentials index focused attention within bilateral stimulus arrays. I. Evidence for early selection. *Electroencephalogr. Clin. Neurophysiol.* **75**, 511–527.

Heinze, H. J. (and 11 others) 1994 Combined spatial and temporal imaging of brain activity during visual selective attention in humans. *Nature* **372**, 543–546.

Hernandez-Peon, R. 1966 Physiological mechanisms in attention. In *Frontiers in physiological psychology* (ed. R. W. Russell), pp. 121–147. New York: Academic Press.

Hernandez-Peon, R., Scherrer, H. & Jouvet, M. 1956 Modification of electrical activity in the cochlear nucleus during attention in unanesthetized cats. *Science* **123**, 331–332.

Hikosaka, O., Miyauchi, S. & Shimojo, S. 1993 Focal visual attention produces illusory temporal order and motion sensation. *Vis. Res.* **33**, 1219–1240.

Hillyard, S. A. & Muente, T. F. 1984 Selective attention to color and locational cues: an analysis with event-related brain potentials. *Percept. Psychophys.* **36**, 185–198.

Hillyard, S. A., Hink, R. F., Schwent, V. L. & Picton, T. W. 1973 Electrical signs of selective attention in the human brain. *Science* **182**, 177–179.

Hillyard, S. A., Mangun, G. R., Woldorff, M. G. & Luck, S. J. 1995 Neural systems mediating selective attention. In *The cognitive neurosciences* (ed. M. S. Gazzaniga), pp. 665–681. Cambridge, MA: MIT Press.

Hillyard, S. A., Anllo-Vento, L., Clark, V. P., Heinze, H. J., Luck, S. J. & Mangun, G. R. 1996 Neuroimaging approaches to the study of visual attention: a tutorial. In *Converging operations in the study of visual selective attention* (ed. A. K. M. Coles & G. Logan), pp. 107–138. Washington, DC: American Psychological Association.

Johannes, S., Muente, T. F., Heinze, H. J. & Mangun, G. R. 1995 Luminance and spatial attention effects on early visual processing. *Cogn. Brain Res.* **2**, 189–205.

Johannes, S., Knalmann, U., Mangun, G. R., Heinze, H. J. & Munte, T. F. 1998 The visual Cl component: scalp topography, dipole sources, and effects of luminance and spatial attention. In *Mapping cognition in time and space* (ed. H. J. Heinze, T. F. Muente, G. R. Mangun & H. H. Scheich). Boston, MA: Birhauser. (In the press.)

LaBerge, D. 1995 Computational and anatomical models of selective attention in object identification. In *The cognitive neurosciences* (ed. M. S. Gazzaniga), pp. 649–661. Cambridge, MA: MIT Press.

Lavie, N. 1995 Perceptual load as a necessary condition for selective attention. *J. Exp. Psychol. Hum. Percept. Perf.* **21**, 451–468.

Luck, S. J. 1995 Multiple mechanisms of visual-spatial attention: recent evidence from human electrophysiology. *Behav. Brain Res.* **71**, 113–123.

Luck, S. J. & Hillyard, S. A. 1995 The role of attention in feature detection and conjunction discrimination: an electrophysiological analysis. *Int. J. Neurosci.* **80**, 281–297.

Luck, S. J., Heinze, H. J., Mangun, G. R. & Hillyard, S. A. 1990 Visual event-related potentials index focused attention within bilateral stimulus arrays. II. Functional dissociation of Pl and Nl components. *Electroencephalogr. Clin. Neurophysiol.* **75**, 528–542.

Luck, S. J., Fan, S. & Hillyard, S. A. 1993 Attention-related modulation of sensory-evoked brain activity in a visual search task. *J. Cogn. Neurosci.* **5**, 188–195.

Luck, S. J., Hillyard, S. A., Mouloua, M., Woldorff, M. G., Clark, V. P. & Hawkins, H. L. 1994 Effects of spatial cuing on luminance detectability: psychophysical and electrophysiological evidence for early selection. *J. Exp. Psychol. Hum. Percept. Perf.* **20**, 887–904.

Luck, S. J., Hillyard, S. A., Mouloua, M. & Hawkins, H. L. 1996 Mechanisms of visual-spatial attention: resource allocation or uncertainty reduction. *J. Exp. Psychol. Hum. Percept. Perf.* **22**, 725–737.

Luck, S. J., Chelazzi, L., Hillyard, S. A. & Desimone, R. 1997 Neural mechanisms of spatial selective attention to areas V1, V2, and V4 of macaque visual cortex. *J. Neurophysiol.* **77**, 24–42.

Mangun, G. R. & Hillyard, S. A. 1991 Modulations of sensory-evoked brain potentials indicate changes in perceptual processing during visual-spatial priming. *J. Exp. Psychol. Hum. Percept. Perf.* **17**, 1057–1074.

Mangun, G. R. & Hillyard, S. A. 1995 Attention: mechanisms and models. In *Electrophysiology of mind–event-related potentials and cognition* (ed. M. D. Rugg & M. G. H. Coles), pp. 40–85. Oxford University Press.

Mangun, G. R., Hillyard, S. A. & Luck, S. J. 1993 Electrocortical substrates of visual selective attention. In *Attention and performance XIV* (ed. D. Meyer & S. Kornblum), pp. 219–243. Cambridge, MA: MIT Press.

Mangun, G. R., Hopfinger, J., Kussmaul, C. L., Fletcher, E. & Heinze, H. J. 1997 Covariations in ERP and PET measures of spatial selective attention in human extrastriate visual cortex. *Hum. Brain Mapp.* **5**, 1–7.

Miller, E. K. & Desimone, R. 1994 Parallel neuronal mechanisms for short-term memory. *Science* **263**, 520–522.

Motter, B. C. 1993 Focal attention produces spatially selective processing in visual cortical areas V1, V2 and V4 in the presence of competing stimuli. *J. Neurophysiol.* **70**, 909–919.

Naatanen, R. 1992 *Attention and brain function.* Hillsdale, NJ: Lawrence Erlbaum.

Newsome, W. T., Shadlen, M. N., Zohary, E., Britten, K. H. & Movshon, J. A. 1995 Visual motion: linking neuronal activity to psychophysical performance. In *The cognitive neurosciences* (ed. M. S. Gazzaniga), pp. 401–414. Cambridge, MA: MIT Press.

Oatman, L. C. & Anderson, B. W. 1977 Effects of visual attention on tone burst evoked auditory potentials. *Exp. Neurol.* **57**, 200–211.

O'Leary, D. S., Andreason, N. C., Hurtig, R. R., Hichwa, R. D., Watkins, G. L., Boles Ponto, L. L., Rogers, M. & Kirchner, P. T. 1996 A positron emission tomography study of binaurally and dichotically presented stimuli: effects of level of language and directed attention. *Brain Lang.* **53**, 20–39.

Posner, M. I. & Dehaene, S. 1994 Attentional networks. *Trends Neurosci.* **17**, 75–79.

Posner, M. I. & Driver, J. 1992 The neurobiology of selective attention. *Curr. Opin. Neurobiol.* **2**, 165–169.

Rees, G., Frackowiak, R. & Frith, C. 1997 Two modulatory effects of attention that mediate object categorization in human cortex. *Science* **275**, 835–838.

Reinitz, M. T. 1990 Effects of spatially directed attention on visual encoding. *Percept. Psychophys.* **47**, 497–505.

Ritter, W., Simson, R. & Vaughan, H. G. 1983 Event-related potential correlates of two stages of information processing in physical and semantic discrimination tasks. *Psychophysiology* **20**, 168–179.

Ritter, W., Simson, R. & Vaughan, H. G. 1988 Effects of the amount of stimulus information processed on negative event-related potentials. *Electroencephalogr. Clin. Neurophysiol.* **69**, 244–258.

Scherg, M. 1990 Fundamentals of dipole source potential analysis. In *Auditory evoked magnetic fields and potentials. Advanced audiology*, vol. 6 (ed. F. Grandori, M. Hoke & G. L. Romani), pp. 40–69. Basel: Karger.

Sereno, M. I., Dale, A. M., Reppas, J. B., Kwong, K. K., Belliveau, J. W., Brady, T. J., Rosen, B. R. & Tootell, R. B. H. 1995 Borders of multiple visual areas in humans revealed by functional magnetic resonance imaging. *Science* **268**, 889–893.

Shiu, L. P. & Pashler, H. 1995 Spatial attention and vernier acuity. *Vis. Res.* **35**, 337–343.

Shulman, G. L., Corbetta, M., Buckner, R. L., Raichle, M. E., Fiez, J. A., Miezin, F. M. & Petersen, S. E. 1997 Top-down modulation of early sensory cortex. *Cerebr. Cortex* **7**, 193–206.

Sperling, G. & Dosher, B. A. 1986 Strategy and optimization in human information processing. In *Handbook of perception and human performance*, vol. 1 (ed. L. K. K. R. Boff & J. P. Thomas), pp. 2–65. New York: Wiley.

Talairach, J. & Tournoux, P. (eds) 1988 *Co-planar stereotaxic atlas of the human brain: 3-dimensional proportional system: an approach to cerebral imaging.* New York: Thieme Medical Publishing Inc.

Tootell, R. B. H., Reppas, J. B., Kwong, K. K., Malach, R., Born, R. T., Brady, T. J., Rosen, B. R. & Belliveau, J. W. 1995 Functional analysis of human MT and related visual cortical areas using magnetic resonance imaging. *J. Neurosci.* **15**, 3215–3230.

Treisman, A. 1969 Strategies and models of selective attention. *Psychol. Rev.* **76**, 282–299.

Treisman, A. 1988 Features and objects: the Fourteenth Bartlett Memorial Lecture. *Q. J. Exp. Psychol.* **40**, 201–237.

Treisman, A. 1996 The binding problem. *Curr. Opin. Neurobiol.* **6**, 171–178.

Tsal, Y., Shalev, L., Zakay, D. & Lubow, R. E. 1994 Attention reduces perceived brightness contrast. *Q. J. Exp. Psychol.* A **47**, 865–893.

Vogel, E. K. & Luck, S. J. 1997 ERP evidence for a general-purpose visual discrimination mechanism. *Soc. Neurosci. Abstr.* **23**, 158.

Wijers, A. A., Lange, J. J., Mulder, G. & Mulder, L. J. M. 1997 An ERP study of visual spatial attention and letter target detection for isoluminant and nonisoluminant stimuli. *Psychophysiology* **34**, 553–565.

Woldorff, M. G. (and 10 others) 1997 Retinotopic organization of the early visual-spatial attention effects as revealed by PET and ERPs. *Hum. Brain Mapp.* **5**, 280–286.

Worden, M. & Schneider, W. 1996 Visuospatial attentional selection examined with functional magnetic resonance imaging. *Soc. Neurosci. Abstr.* **22**, 1856.

Zeki, S., Watson, J. D. G., Lueck, C. J., Friston, K. J., Kennard, C. & Frackowiak, R. S. J. 1991 A direct demonstration of functional specialization in human visual cortex. *J. Neurosci.* **11**, 641–649.