The time course of spatial attention: Insights from event-related brain potentials

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1. Introduction

Event-related brain potential (ERP) measures have made important contributions to our understanding of the mechanisms of selective attention. This chapter provides a selective and non-technical review of some of these contributions. It will concentrate mainly on research that has studied spatially selective attentional processing in vision, although research on crossmodal links in spatial attention will also be discussed. The main purpose of this chapter is to illustrate how ERP methods have helped to provide answers to major theoretical questions that have shaped research on selective attention in the past 40 years.

For many years, human perception, cognition, and action, and the role of attentional mechanisms in these domains, have been studied primarily with behavioural measures. The ability to measure neural correlates of these processes is a relatively recent achievement, and ERP research was at the forefront of this development. Although electroencephalographic (EEG) recordings of human brain activity date back to the 1920s, the method of averaging stimulus-locked EEG activity, and using the resulting ERP waveforms to study cognitive processes, has started in a systematic fashion only in the late 1960s. ERPs reflect the synchronised postsynaptic activity of a large number of cortical neurons that is time-locked to specific external or internal events. Typical ERP waveforms consist of a series of successive positive and negative deflections or peaks that are often referred to as ERP components. The ERP technique is attractive to cognitive neuroscientists because of its excellent temporal resolution: ERPs can trace electrical brain activity on a millisecond-by-millisecond basis, and the effects of an experimental manipulation on a distinct ERP component at a specific post-stimulus latency can be helpful to develop models of the temporal organisation of human cognitive abilities. But due to the properties of electrical volume conduction inside the head and across the skull, and because of complex interactions between several simultaneously activity neural generator processes, ERP scalp recordings provide only limited information about the localization of underlying brain processes. Although several methods of reconstructing sources of electrical activity in the brain on the basis of scalp recordings are available, their precision and spatial resolution is not comparable to that of other neuroimaging methods such as fMRI. For this reason, this chapter will focus primarily on research that has used ERP measures to study specific questions about the time course of attentional processing.

The central theoretical issues addressed by attention researchers have changed considerably in the past 40 years, and so have the questions that have been investigated with ERP measures during this period. Traditional models of selective attention have postulated a fundamental distinction between early, capacity-unlimited, and parallel processing stages, and late, capacity-limited, and serial stages. This view, which was most influentially expressed in Donald Broadbent's filter theory of attention (1958), characterizes selective attention as the mechanism that gates the access of perceptual information to late capacity-limited processes. If attention acts as a filter that controls the transition between early parallel and late serial processing stages, it is important to identify where and when in the information processing hierarchy the transition point between early pre-attentive and late attentive mechanisms is located. Because of their excellent temporal resolution, ERP measures have played a prominent role in this quest to specify the locus of attentional selection, and this role will be reviewed in section 2 of this chapter.

In the past twenty years, attention research has moved beyond the traditional debate about early versus late selection. Attempts to develop general models of attentional selectivity have been replaced by investigations of more specific theoretical issues, and this change in emphasis is also reflected by contemporary ERP research on selective attention. As will be described in section 3, it has now become clear that the mechanisms of spatial attention do not operate in a strict modality-specific fashion, but that there are instead strong crossmodal links in spatially selective attentional processing between vision, audition, and touch. In addition, an important distinction has been proposed between control processes in modality-unspecific frontoparietal regions (the "source" of top-down attentional control) and attentional modulations of processing in modality-specific sensory areas (the "sites" where top-down control signals produce their selective effects).

Another major focus of contemporary attention research is the study of competitive interactions between relevant stimuli and distractors in situations where multiple stimuli are simultaneously present. Biased competition accounts of selective attention (e.g., Desimone and Duncan 1995; Beck and Kastner 2009) describe attentional phenomena as the consequence of such competitions for neural and cognitive representation. This competition takes place at different levels of processing, and its outcome is controlled both by top-down selection intentions and bottom-up salience. Visual search paradigms have been particularly useful to study competitive mechanisms in attention, and ERP measures of attentional selectivity have become important tools to investigate the temporal dynamics of competitive interactions in multi-stimulus visual scenes. In section 4 of this chapter, the N2pc component is introduced as an important ERP correlate of the attentional selection of targets among non-targets. Section 5 presents ERP research that has used the N2pc component to address two critical questions about the temporal organisation of stimulus selection in visual search. First, do all stimuli in a multi-stimulus array compete in parallel for attentional selection, or is attention allocated sequentially to specific stimulus locations in the visual field? And second, is the selection of perceptually distinct visual events determined by top-down search intentions, or driven by their bottom-up salience?

2. The locus of attentional selectivity: Early versus late selection

The historically most influential conceptualisation of selective attention in modern times is undoubtedly the filter model proposed by Donald Broadbent (1958). According to this model, basic physical attributes of incoming sensory information are initially analysed in parallel, and the results of this parallel processing stage are stored in an unlimited-capacity short-term buffer. Because subsequent processing stages such as semantic analysis and response selection operate in a serial and capacity-limited fashion, only a fraction of the content stored in the short-term buffer can gain access to these stages. Selective attention acts as a gatekeeper that controls which stimuli are permitted to make the transition from parallel to serial processing. In the filter model, attentional selection is "early", because it operates on the basis of low-level

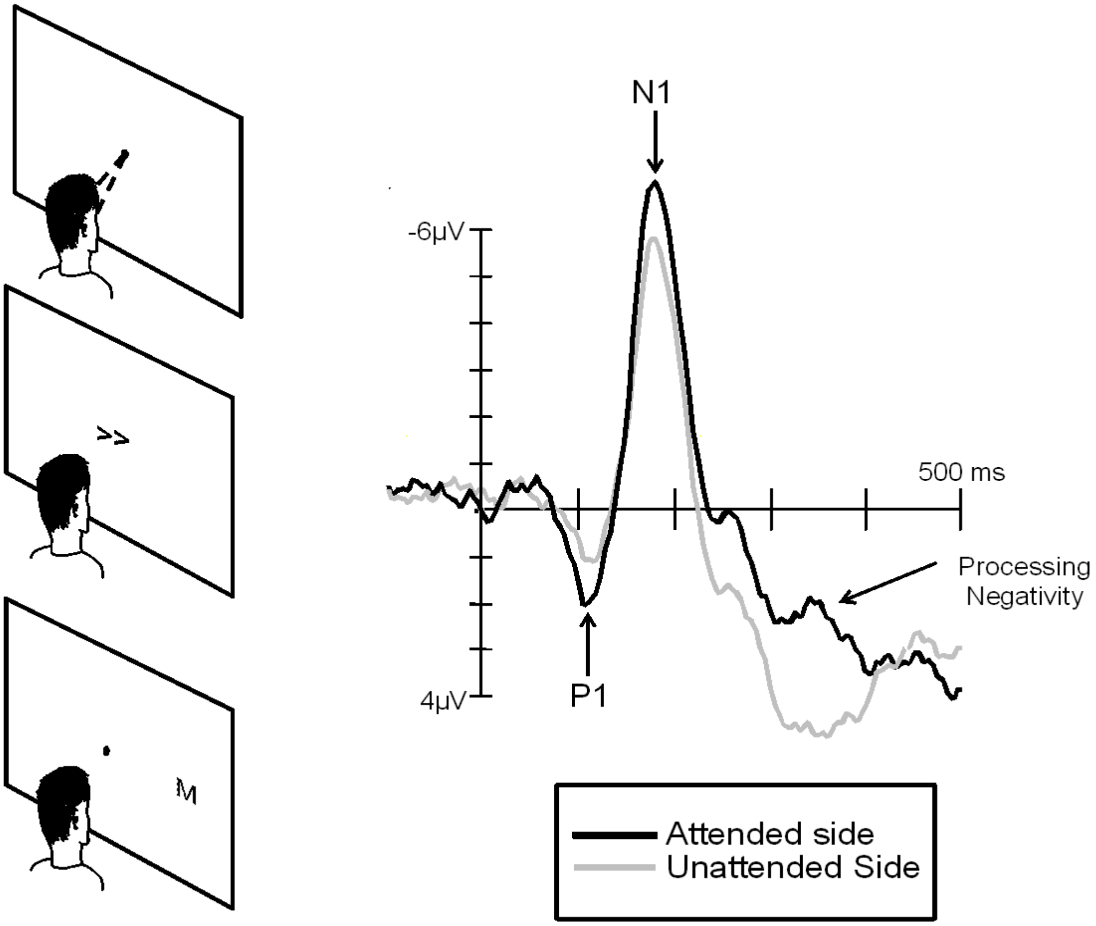

Figure 1. ERPs triggered in response to laterally presented visual stimuli in an experiment where these stimuli were preceded by arrow precues that signalled the to-be-attended location for a visual target/nontarget discrimination on that trial. ERP waveforms were measured at lateral occipital electrodes contralateral to the side where the stimulus was presented, and are shown separately for visual stimuli on the cued/attended side and on the uncued/unattended side. Cued visual-spatial attention produces amplitude enhancements of visual P1 and N1 components and a later sustained processing negativity. Data from Eimer and Schröger (1998).

physical stimulus features that are represented in the short-term buffer, and precedes the semantic analysis of selected stimuli. This early selection hypothesis has not gone unchallenged. Others (e.g., Deutsch and Deutsch 1963) have proposed that selective attention operates at a "late" stage that follows the semantic analysis of attended as well as unattended stimuli.

The debate whether attentional selection is "early" or "late" has dominated mainstream attention research for decades. The critical assumption was that there is a fundamental division in human information processing between early, unlimited-capacity, parallel, and pre-attentive stages, and late, limited-capacity, serial and attentive stages. If this basic dichotomy does in fact exist, it is important to determine exactly where and when the transition from pre-attentive to attentive processing occurs. It has proved to be remarkably difficult to find a decisive answer to this critical question on the basis of behavioural measures, and this is one reason why the early versus late selection controversy has remained an active concern for attention researchers over many years. Because this locus-of-selection debate is essentially a disagreement about the temporal organisation of functionally defined stages of information processing, the ability of ERPs to provide high temporal resolution measures of cognitive processing has come to play an important role in this debate.

In early ERP studies of auditory and visual selective attention (e.g., Hillyard et al. 1973; Van Voorhis and Hillyard 1977), ERPs were recorded to physically identical stimuli in two different conditions where attention was either directed to the location of these stimuli, or was focused at a different location. Results demonstrated that ERP differences between these two conditions emerged remarkably early after stimulus onset: In audition, selective attention resulted in amplitude modulations of the auditory N1 component that started around 80 ms after stimulus onset (Hillyard et al. 1973). In vision, the earliest attentional modulations were observed for the P1 component, which also has a typical post-stimulus onset latency of 80-90 ms (Van Vorhis and Hillyard 1977). In these pioneering ERP investigations of selective spatial attention, participants were usually instructed at the start of each block to direct their attention to one specific location and to keep it focused at this location for an entire experimental block. Later studies have demonstrated that very similar attentional ERP modulations at short post-stimulus latencies are also triggered when the focus of spatial attention is not sustained for an extended period, but is instead manipulated in a trial-by-trial fashion by precues such as left-pointing or right-pointing arrows (e.g., Mangun and Hillyard 1991; Eimer 1994).

Figure 1 illustrates the typical pattern of spatial attention effects on visual ERPs observed in an experiment where the focus of spatial attention was manipulated on a trial-by-trial basis (Eimer and Schröger 1998). On each trial, a single stimulus was presented to the left or right of fixation, and was preceded by an arrow cue. Participants had to direct their attention to the side indicated by the cue, in order to detect and respond to infrequent visual target stimuli on that side, while ignoring all stimuli on the opposite uncued side. The ERPs in Figure 1 were recorded from occipital electrodes over the hemisphere contralateral to the side of a visual stimulus, separately for stimuli that appeared on the attended side, and stimuli that were presented on the uncued/unattended side. The earliest attentional modulation was an increase in the amplitude of the P1 component for attended stimuli. This effect started approximately 80 ms after stimulus onset, and was followed by an attentional enhancement of the N1 component, and then by a sustained "processing negativity" for attended visual stimuli that emerged after more than 200 ms following stimulus onset. The ERP effects shown in Figure 1 have been observed in many ERP studies of visual-spatial attention. Attentional enhancements on P1 amplitudes are often interpreted as the effect of sensory gain control mechanisms that are activated during preparatory shifts of attention towards likely target location. N1 amplitude modulations have been linked to the active engagement of attention at a specific location (e.g., Mangun and Hillyard 1991; Mangun 1995). Attention-induced ERP modulations at post-stimulus latencies of 200 ms and beyond are usually linked to subsequent post-perceptual processing stages (e.g., stimulus identification and/or classification of response-relevant features; e.g., Mangun and Hillyard 1991; Eimer 1996a).

The consistent finding that ERP effects of sustained or transient spatial attention emerge at post-stimulus latencies of 100 ms or even earlier is often interpreted as evidence in support of early selection accounts. At latencies where the visual P1 or auditory N1 components are generated, sensory signals are still processed in modality-specific visual or auditory cortical areas. In the first 100 ms after stimulus onset, sensory processing is assumed to proceed in feedforward fashion, prior to any effects of recurrent modulatory input from higher-level control areas on activity in lower-level cortical regions (Lamme and Roelfsema 2000). Source localisation studies (e.g., Di Russo et al. 2003) have indeed suggested that the neural generators responsible for the visual P1 component are located in relatively early extrastriate cortical regions in middle and ventral occipital cortex, which correspond to visual areas V3 and V4. These observations suggest a direct link between attentional effects on the amplitudes of early sensory-specific ERP components and spatially selective attentional modulations of early stages of sensory-perceptual processing, which is consistent with early selection models of attention. Importantly, there is other ERP evidence which strongly suggests that the initial activation of primary visual cortex (V1) by incoming sensory events is not affected by attention. The arrival of visual input in V1 is reflected by the C1 component, which is triggered approximately 60 ms after stimulus onset, and shows a retinotopic pattern of polarity inversion for stimuli in the upper versus lower visual field (Clark et al. 1995) that strongly points to the calcarine sulcus (which contains area V1) as its origin. In marked contrast to P1 and N1 components, C1 amplitudes remain unaffected by manipulations of spatial attention (e.g., Martinez et al. 1999). The attention-independence of the C1 component and the strong attention-sensitivity of subsequent P1 and N1 components provide temporally precise evidence for the earliest locus of spatial selectivity in the visual processing hierarchy: The initial activation of primary visual cortex that is triggered within 50 or 60 ms after stimulus onset by afferent signals in the geniculostriate pathway can be regarded as genuinely pre-attentive, because it is not modulated by the current focus of spatial attention. In contrast, neural activity in adjacent extrastriate visual cortical areas that is elicited only 20-30 ms after the initial V1 activation is selectively enhanced for visual events that originate from attended locations, and thus marks the transition from pre-attentive to attention-sensitive visual processing.

The observation that spatial attention affects the amplitudes of visual and auditory ERP components which originate in sensory-specific cortical areas and are triggered at post-stimulus latencies of less than 100 ms demonstrates beyond reasonable doubt that brain activity during these early stages of sensory processing is subject to attentional modulations. But documenting early attention-induced effects on activation levels in visual or auditory cortex does not by itself provide conclusive evidence for the veracity of the early selection theories of attention such as Broadbent's filter model. It is problematic to directly link the concept of "attentional selection", as defined in cognitive-psychological debates about the locus of selectivity, and attention-induced amplitude modulations of visual P1 or N1 components. What such ERP effects demonstrate is that the level of neural activation triggered in modality-specific cortical areas is selectively affected by the location of a sensory stimulus within or outside the current focus of spatial attention. But this does not represent selective attentional processing in the sense that is invoked by models which describe the function of attention as allowing specific stimuli access to limited-capacity serial processing stages, and preventing access by other stimuli. Additional arguments are clearly required before attentional effects on the amplitudes of early ERP components (i.e., short-latency modulations of cortical processing) can be interpreted as directly reflecting the transition of sensory information from parallel pre-attentive to serial capacity-limited processing stages.

Another caveat against an uncritical interpretation of spatial attention effects on visual P1 and auditory N1 components as directly demonstrating the early locus of selection comes from the fact that the presence of such effects does by no means preclude the existence of additional attention-induced ERP modulations at later post-stimulus latencies. In fact, many studies have reported effects of selective attention on ERP components that are elicited between 200 ms and 800 ms after stimulus onset and often do not show a sensory-specific scalp topography. These effects are likely to be generated at processing stages that follow the sensory-perceptual analysis of incoming stimuli. Figure 1 shows one example for a late effect of spatial attention - the sustained "processing negativity" that is frequently triggered by potentially task-relevant visual stimuli at attended locations and emerges beyond 200 ms post-stimulus. This enhanced posterior negativity for stimuli at attended versus unattended locations has been linked to stimulus identification and categorization, which often involves their comparison to stored representations of target-defining visual features (e.g., Eimer, 1994; 1996a).

ERP evidence for an even later locus of attentional selectivity has come from experiments that employed the attentional blink (AB) paradigm. In AB experiments, two targets are embedded in a rapidly presented sequential stream of distractors. Detection of the second target (T2) is greatly impaired when it is presented in close temporal proximity to the first target (T1), indicating attentional suppression of T2 processing while T1 is still being analysed (Raymond et al. 1992). To locate the stage at which this suppression takes place, Luck et al. (1996) recorded ERPs in response to T2 stimuli (words) when these were presented during the critical attentional blink interval. Interestingly, there was no attenuation of visual P1 and N1 components, suggesting that perceptual processes were unaffected by attentional suppression. Even more surprisingly, a later ERP component that is associated with semantic processing of words (the N400 component) also remained present during the attentional blink, indicating that in spite of their attentional inhibition, T2 words were still semantically analysed. The one ERP component that was suppressed during the attentional blink interval was the P3, which is often linked to the updating of working memory. These results are clearly inconsistent with the hypothesis that the locus of attentional selectivity is invariably early, because they show that the attentional blink is a post-perceptual effect which is produced at a late stage of information processing which follows semantic identification (e.g., Vogel et al. 1998).

In summary, many ERP studies investigating the locus of attentional selectivity have found evidence for attention-induced modulations of early sensory-perceptual stages of stimulus processing, while others have demonstrated that attention can also affect later stages of processing. These findings suggest that the traditional question whether selective attention is early or late represents a false dichotomy, because attention can operate at different processing stages, and within different cognitive subsystems and cortical areas. This insight is one of the reasons why the search for the locus of selection is no longer regarded as the single most important task for attention researchers. Another reason is that the general theoretical background that motivated this search has now been called into question. This includes the idea that human information processing is organised in a strict serial sequence of processing stages, and that the locus of the attentional bottleneck can be uniquely identified within this sequence (see Allport 1993, for an early incisive critique of these assumptions). The new consensus is that the locus of attentional selectivity can be shifted flexibly and rapidly between stages and subsystems, in accordance with a variety of factors that include stimulus parameters, current task demands, and top-down selection intentions. But ERP measures of attention-induced processing modulations remain valuable, because they allow researchers to track variable loci of attentional selectivity across a wide variety of task contexts.

3. Crossmodal links in spatial attention

Information about external objects and events is often conveyed simultaneously and independently by different sensory systems. However, this information is initially represented within modality-specific coordinate systems (retinotopic in vision, somatotopic in touch, tonotopic in audition), and this makes its integration and the attentional selection of objects that are specified by multisensory signals a non-trivial problem. Spatially selective processing can help to solve this problem, as visual, auditory, or tactile information about the same object originates from the same location in external space. If attentional selectivity is integrated across perceptual modalities, this should be reflected by spatial synergies in the processing of sensory events across vision, audition, and touch. Behavioural studies of crossmodal links in voluntary (endogenous) spatial attention

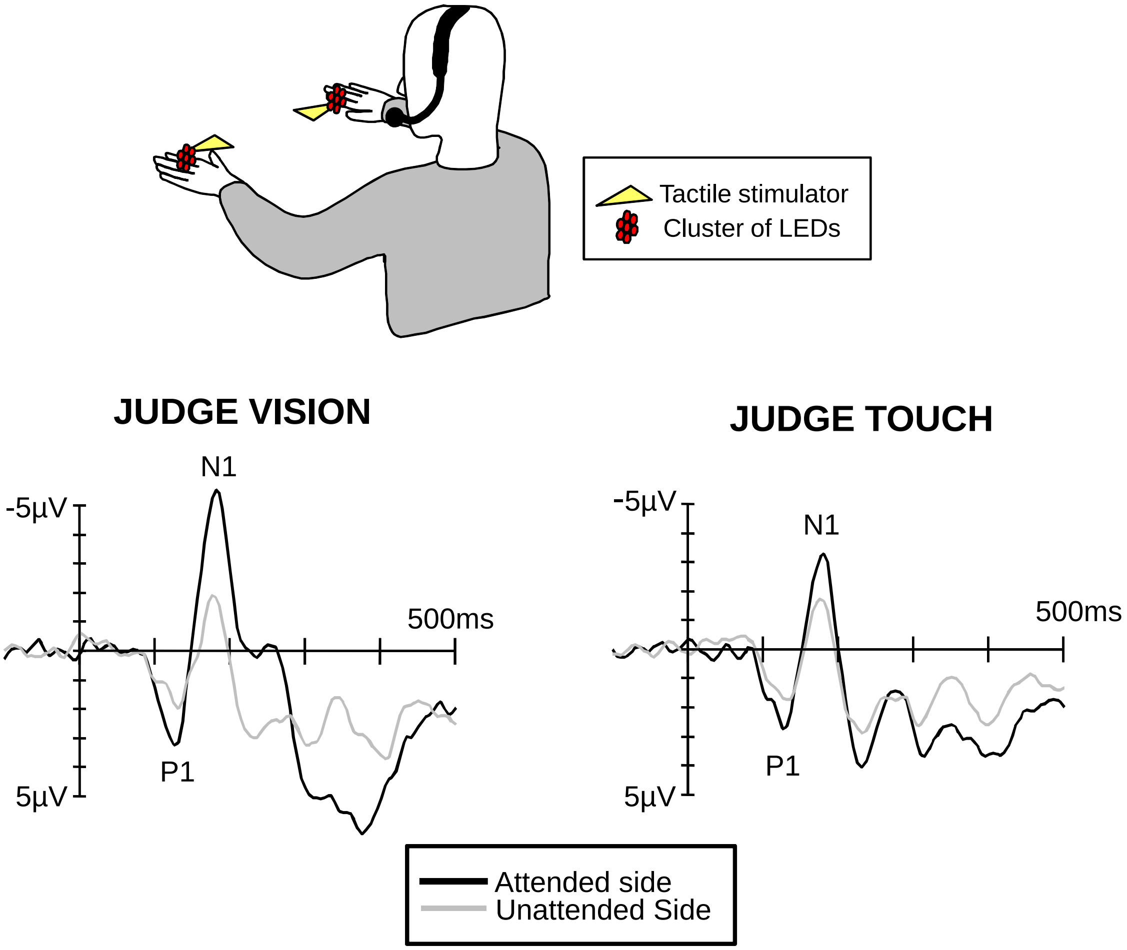

Figure 2. ERPs triggered in an experiment on crossmodal attention where observers directed attention to the left or right side for a visual or tactile task. Visual stimuli were delivered via LEDs, tactile events via punctators. ERPs were recorded in response to laterally presented visual stimuli at contralateral posterior electrodes. In the "Judge Vision" task, visual stimuli on the attended side triggered larger P1 and N1 amplitudes relative to visual stimuli on the opposite unattended side. In the "Judge Touch" task where visual stimuli could be entirely ignored, visual ERP components were generally reduced in amplitude, but attentional modulations of P1 and N1 components were still present. Data from Eimer and Driver (2000).

between vision and audition (e.g., Spence and Driver 1996) or vision and touch (e.g., Spence et al. 2000) have indeed demonstrated the existence of such synergies (see Chapter 18, this volume, for a detailed discussion). In these experiments, attention was directed to the expected location of target stimuli within one primary modality. Stimuli in the other (secondary) modality were presented only infrequently, and were equally likely (or even more likely) to appear on the side that was unattended in the primary modality. In spite of these contingencies, performance in response to secondary modality targets was superior when they appeared on the side that was attended in the primary modality. These results demonstrate that the locus of endogenous attention within one modality (that is, a spatial expectancy that is specific that modality) affects the processing of information in other modalities. Similarly, rapid shifts of involuntary (exogenous) spatial attention triggered by salient but irrelevant stimuli in one modality modulate performance to subsequently presented stimuli in another modality, demonstrating the existence of crossmodal spatial links in exogenous attention (e.g., McDonald et al. 2000).

While such behavioural observations demonstrate the existence of crossmodal links in spatial attention, they cannot provide direct insight into the locus of such spatial synergies at perceptual and/or post-perceptual processing stages. Because they provide temporally precise markers of attentional effects, ERP measures have been used in many studies to find out when and how crossmodal spatial synergies in endogenous or exogenous attention affects the processing of visual, auditory, and tactile stimuli. In a typical ERP experiment of crossmodal links between vision and touch (Eimer and Driver 2000), visual stimuli were delivered via LEDs, and tactile stimuli by punctators attached to the left and right index finger, close to the location of the LED on the same side (Figure 2, top panel). Participants directed attention to the left or right side, in order to detect and to respond to infrequent targets in one primary modality on the attended side, while ignoring stimuli in the other secondary modality on that side, as well as stimuli in either modality on the unattended side. Attentional modulations of visual and somatosensory ERPs were measured separately for blocks where vision was the attended modality ("Judge Vision"), and for blocks where touch was task-relevant and therefore attended ("Judge Touch").

Figure 2 (bottom panels) shows ERPs measured at occipital electrodes contralateral to the visual field of stimulus presentation in response to visual stimuli on the currently attended side or on the opposite unattended side. As expected, attended visual stimuli triggered enhanced P1 and N1 components in "Judge Vision" blocks where vision was the task-relevant modality, thus confirming that visual-spatial attention modulates activity in early visual areas (see section 2). In "Judge Touch" blocks, P1 and N1 components in response to visual stimuli were generally smaller than in "Judge Vision" blocks, demonstrating that when attention is directed away from vision towards a different task-relevant sensory modality, activation of visual cortical areas is reduced. But even more importantly, early spatially selective modulations of visual ERPs were still reliably present in "Judge Touch" blocks: Visual stimuli presented next to tactually attended locations elicited larger P1 and N1 components than visual stimuli close to the opposite unattended hand, in spite of the fact that participants focussed spatial attention solely on the relevant location of tactile events and visual stimuli could be entirely ignored. The observation that attentional modulations of visual ERPs in "Judge Touch" blocks started within 100 ms after stimulus onset not only provides strong evidence for the existence of crossmodal links in spatial attention, but also demonstrate that links from touch to vision affect early perceptual stages of visual processing. Analogous results were obtained in the same study for ERP components in response to tactile events that were measured over somatosensory cortex: Tactile stimuli at attended locations triggered enhanced sensory-specific N140 components, and this was the case not only in blocks where touch was the task-relevant modality, but also in blocks where vision was primary. Other studies (e.g., Eimer and Schröger 1998; Teder-Sälejärvi et al. 1999) found similar ERP evidence for the existence of symmetrical crossmodal spatial synergies between vision and audition, and have demonstrated that such audiovisual attentional links modulate early perceptual stages of visual and auditory processing.

While these results demonstrate the existence of crossmodal links for endogenous shifts of spatial attention, other ERP studies have studied spatial synergies in involuntary (exogenous) spatial attention. McDonald and Ward (2000) measured ERPs to visual target stimuli that were preceded by spatially uninformative but salient auditory events at the same or at a different location. Responses to visual stimuli were faster on same-location as compared to different location-trials. Critically, this behavioural benefit was accompanied by an enhancement of occipital ERP components for visual stimuli that appeared at the same location as a preceding auditory event, suggesting that crossmodal links in exogenous spatial attention modulate early perceptual stages of visual processing. Along similar lines, salient but irrelevant tactile events improve discrimination performance and trigger enhanced early ERP components in response to subsequent visual stimuli that are presented at the same location (Kennett et al. 2001). Overall, these findings demonstrate that spatial synergies across sensory modalities exist for both endogenous and exogenous attention, and that these synergies modulate the sensory-perceptual processing of visual, auditory, or tactile stimuli at short post-stimulus latencies.

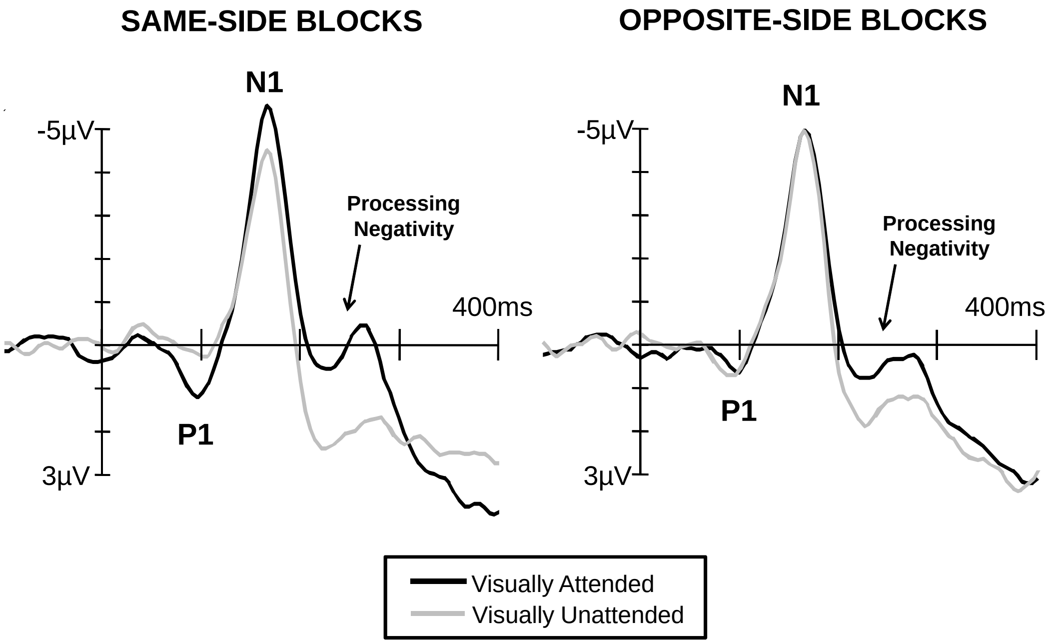

Figure 3. ERPs triggered in response to laterally presented visual stimuli at contralateral posterior electrodes in an audiovisual experiment. In Same-Side blocks, participants directed their visual and auditory attention to the same side in order to detect infrequent visual or auditory targets on that side. Here, larger P1 and N1 amplitudes and a sustained processing negativity were elicited by visual stimuli on the attended side relative to stimuli on the opposite unattended side. In Opposite-Side blocks, where visual and auditory attention were directed to opposite sides, attentional P1 and N1 modulations were completely eliminated and only the late processing negativity remained present. Data from Eimer (1999).

The question remains whether such spatial synergies across sensory modalities, as reflected by ERP effects of crossmodal spatial attention, are due to fixed and possibly hard-wired links between modalities, or instead just reflect a default preference for shifting attention simultaneously to the same locations in different modalities when this does not impair task performance. To answer this question, an experiment was conducted where participants had to detect infrequently presented single visual or auditory targets in the left or right hemifield (Eimer 1999). In Same-Side blocks, attention was directed to the same location in both modalities, because response-relevant visual or auditory targets always appeared at the same location. In Opposite-Side blocks, attention had to be directed to opposite sides in vision and audition, as visual targets had to be detected on the left, and auditory targets on the right, or vice versa. ERP results in Same-Side blocks were as expected (Figure 3, left side): Relative to stimuli on the unattended side, attended visual stimuli elicited enhanced P1 and N1 components and a later sustained processing negativity. A very different pattern of results was observed in Opposite-Side blocks (Figure 3, right side): There were no enhancements of visual P1 and N1 components in response to stimuli on the visually attended side when auditory attention had to be simultaneously directed to the opposite side. Under these conditions, spatially selective ERP effects only emerged at about 200 ms post-stimulus in the form of a sustained processing negativity. Analogous results were observed for auditory ERPs (not shown in Figure 3): In Same-Side blocks, attended auditory stimuli triggered an enhanced negativity that started around 100 ms after stimulus onset and overlapped with the auditory N1 component. In Opposite-Side blocks, this early effect was eliminated. Overall, these findings strongly suggest that spatial synergies between sensory modalities observed in behavioural and ERP studies of crossmodal attention do not just reflect optional attentional allocation strategies, but more permanent, and perhaps event hard-wired links in spatially selective processing across different sensory systems.

While the existence of crossmodal spatial synergies in attentional processing is an important phenomenon in its own right, it may also provide valuable clues about how attentional control mechanisms that initiate and guide shifts of attention are organized. For example, it has been suggested that the control of spatial orienting in different sensory modalities is implemented by a single supramodal system (e.g., Farah et al. 1989). If attentional control was indeed supramodal, strong crossmodal links in spatial attention between vision, audition, and touch would be an obvious consequence. While control processes involved in directing visual-spatial attention have been studied most prominently with fMRI measures (e.g., Corbetta and Shulman 2002; Beck and Kastner 2009; see also Chapters 9, 10, and 11, this issue), important insights into the temporal organisation of these processes have been obtained in ERP studies. In these studies, ERPs were recorded in response to symbolic central cues which directed attention to the left or right side, during the interval prior to the arrival of a subsequent imperative stimulus. Activity unrelated to spatial attention shifts, such as sensory responses to the cue, or ERP correlates of temporal attention, was eliminated by subtracting ERP waveforms obtained during rightward attentional shifts from ERPs during shifts of attention to the left side. It is important to note that this procedure also removes ERP correlates of top-down attentional control that do differ during the orienting of attention to the left versus right side.

In a pioneering study by Harter et al. (1989), an early negative deflection at posterior electrodes contralateral to the direction of an attentional shift ('Early Directing Attention Negativity'; EDAN) emerged around 200 ms after cue onset, and was followed at about 500 ms post-stimulus by a posterior contralateral positivity ('Late Directing Attention Positivity'; LDAP). Later studies (e.g., Nobre et al. 2000) have also observed an enhanced negativity at frontal electrodes contralateral to the direction of attentional shifts ('Anterior Directing Attention Negativity'; ADAN) with an onset latency of 300-400 ms after cue onset. The earliest of these components (EDAN) may not be a genuine reflection of covert attentional control, but instead a lateralized visual response to non-symmetrical visual cues such as left-pointing and right-pointing arrows (Van Velzen and Eimer 2003). The ADAN is assumed to reflect the activation of dorsolateral frontal control processes that are involved in programming and initiating shifts of attention (Nobre et al. 2000). In line with this hypothesis, source localisation studies have placed the neural generators of the ADAN component in lateral premotor cortex (e.g., Praamstra et al. 2005). The LDAP has been linked to preparatory changes in the excitability of ventral occipitotemporal visual areas in anticipation of an expected visual stimulus at a specific location (Harter

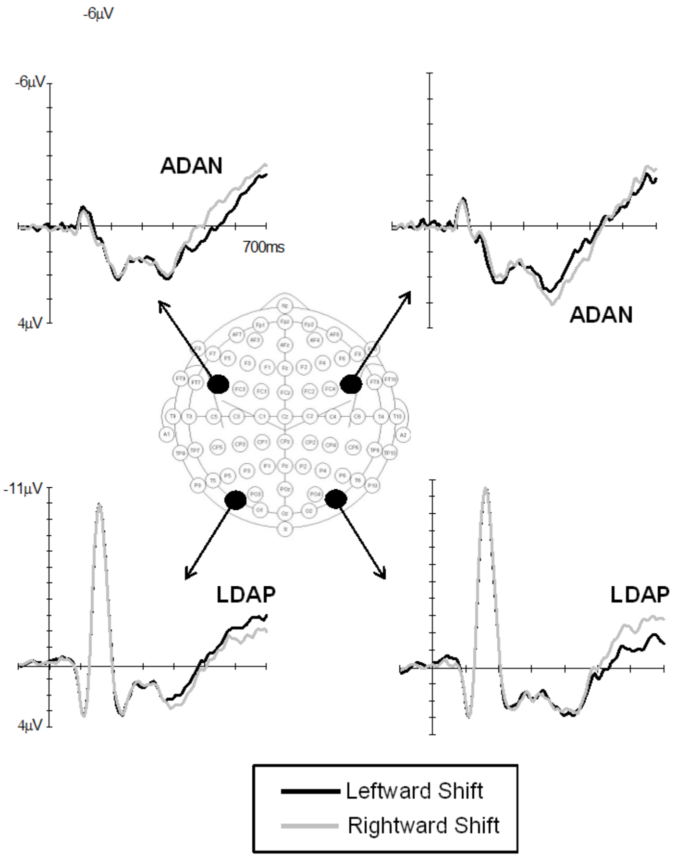

Figure 4. ERPs triggered in response to central arrow precues that directed tactile attention to the left or right side in an experiment where participants had to detect infrequent tactile targets that were delivered to the hand on the cued side. The top panel shows ERPs from the frontocentral electrode pair FC5/6, where the anterior directing attention negativity (ADAN) was elicited at electrodes contralateral to the side of a cued attentional shift. The bottom panel shows ERPs from the posterior electrode pair PO7/8, where the late directing attention positivity (LDAP) emerged contralateral to the side of the attentional shift. Data from Eimer et al. (2002).

et al. 1989).

While most research on ERP correlates of preparatory spatial orienting has investigated shifts of visual attention, other studies have demonstrated that ADAN and LDAP components are also triggered in tasks where attention is directed towards the cued location of auditory or tactile events (e.g., Eimer et al. 2002; Green et al. 2005). This is illustrated in Figure 4, which shows ERPs elicited during rightward and leftward shifts of tactile attention in the 700 ms interval following the onset of a central spatial precue, and prior to the presentation of an imperative stimulus on the left or right side. Observers were instructed by the cue to direct their attention to their left or right hand, in order to discriminate tactile targets and non-targets that were delivered to the index finger of the cued hand. The top panels in Figure 4 show ERPs recorded at a lateral frontocentral electrode pair (FC5 and FC6), the bottom panels show ERPs recorded at a lateral posterior electrode pair (PO7 and PO8). Shifts of tactile attention were accompanied by an enhanced contralateral negativity at anterior frontocentral electrodes (ADAN) that emerged at about 350 ms after cue onset, and a contralateral positivity at posterior electrodes (LDAP) with a post-cue onset latency of approximately 500 ms. Critically, these lateralized components were very similar to ERP effects previously observed during shifts of visual-spatial attention. In addition, virtually identical ADAN and LDAP components were observed in the same study (Eimer et al. 2002) in another task where observers were cued to direct their attention to the location of task-relevant auditory events.

The presence and similarity of ADAN and LDAP components during shifts of visual, tactile, and auditory attention seems to provide strong support for the hypothesis that spatial orienting is controlled by a single multimodal system (Farah et al. 1989). However, alternative interpretations remain possible. It is possible that even when auditory or tactile stimuli are task-relevant, shifts of spatial attention towards these stimuli are always controlled by visual-spatial information, because vision provides superior spatial acuity relative to hearing or touch, and therefore allows a more precise tuning of focal attention. If this was correct, lateralized ERP components that are measured during attentional shifts towards anticipated tactile or auditory events would primarily reflect shifts of attention within visual space. This hypothesis was tested by measuring ERP correlates of attentional orienting in congenitally blind people. Due to the absence of any visual input, the congenitally blind cannot develop a visually defined spatial frame of reference that could guide preparatory shifts of attention towards auditory or tactile events. In a study with congenitally blind participants that measured ERPs during cued attention shifts towards task-relevant tactile stimuli (Van Velzen et al. 2006), the ADAN component was clearly present, indicating that this component reflects attentional control processes that do not rely on visually coded representations of external space. In contrast, the posterior LDAP component was absent in the congenitally blind, which suggests that the preparatory attentional mechanisms associated with this component are strongly dependent upon visually defined spatial reference frames. This dissociation suggests that ADAN and LDAP components may be linked to functionally separable control mechanisms that mediate the control of attentional shifts within vision-independent egocentric/somatotopic and visually mediated allocentric/external frames of reference, respectively.

In summary, the ERP research reviewed in this section has demonstrated the existence of strong spatial synergies in endogenous and exogenous spatial attention between vision, audition, and touch. It has shown that these synergies modulate perceptual processing in modality-specific sensory cortices, that they reflect permanent links rather than optional strategies, and that there are remarkable similarities in ERP correlates of top-down attentional control across modalities. Such observations are in line with two interpretations, which are not necessarily mutually exclusive. Some aspects of attentional control may be genuinely supramodal, while others may be dominated by visually coded spatial representations, irrespective of whether attention is directed in vision, audition, or touch.

4. The N2pc component and attentional target selection in visual search

Most of the ERP studies discussed so far have employed experimental designs where attention is directed in advance to a particular location, and a single stimulus is then presented at this attended location or at a different unattended position in the visual field. This research has demonstrated that spatial attention can modulate sensory activity generated at early stages of perceptual processing, and that shifts of spatial attention and their effects on sensory modulations show remarkable spatial synergies across vision, audition, and touch. However, other important aspects of attentional processing cannot be directly assessed with such experimental designs. In many situations, multiple simultaneous stimuli compete for the control of perception and action, and no advance spatial information is available to guide selective attention towards the location of anticipated task-relevant events. Under such circumstances, a critical function of attention is to resolve the competition between different stimuli in favour of those that are relevant to current task goals, and to filter out others that are not (Desimone and Duncan 1995). To identify mechanisms that operate when there is competition for attentional selection, procedures where single stimuli are presented in an otherwise empty field are insufficient, and multi-stimulus paradigms such as visual search tasks need to be employed.

In visual search experiments, observers are presented with visual arrays that can contain numerous items. Their task is to report the presence or absence of a pre-defined target among distractors. The detection of targets is fast and efficient when they can be distinguished from distractors on the basis of a unique feature, and less efficient when they are defined by a conjunction of features (Treisman and Gelade 1980). An important electrophysiological marker of attentional target selection in visual search is the N2pc component. This component, which was first described by Luck and colleagues (Luck et al. 1993, Luck and Hillyard 1994a, 1994b), represents an enhanced negativity at posterior electrodes contralateral to the target's visual field, and usually emerges around 200 ms after search array onset. This is illustrated in Figure 5, which shows N2pc components measured in response to search arrays that contained a uniquely coloured diamond target (Mazza et al. 2007). In different blocks, observers either had the relatively easy task of localizing these targets in the left versus right hemifield, or the more difficult task of discriminating on which side the target diamond had a cut. Very similar N2pc components were triggered in both tasks (Figure 5, top panels). Difference waveforms obtained by subtracting ipsilateral from contralateral ERP waveforms (Figure 5, bottom left) show that N2pc amplitudes and onset latencies were virtually identical in both tasks, even though the discrimination task was much more difficult. This result suggests that the N2pc component is generated during the initial attentional selection of targets among distractors that precedes the subsequent detailed analysis of specific target features. In contrast, a sustained posterior contralateral negativity (SPCN) that followed the N2pc and emerged around 350 ms after search array onset was much larger during the discrimination task. This SPCN component has also been observed during the retention period of working memory tasks and has been associated with the spatially selective

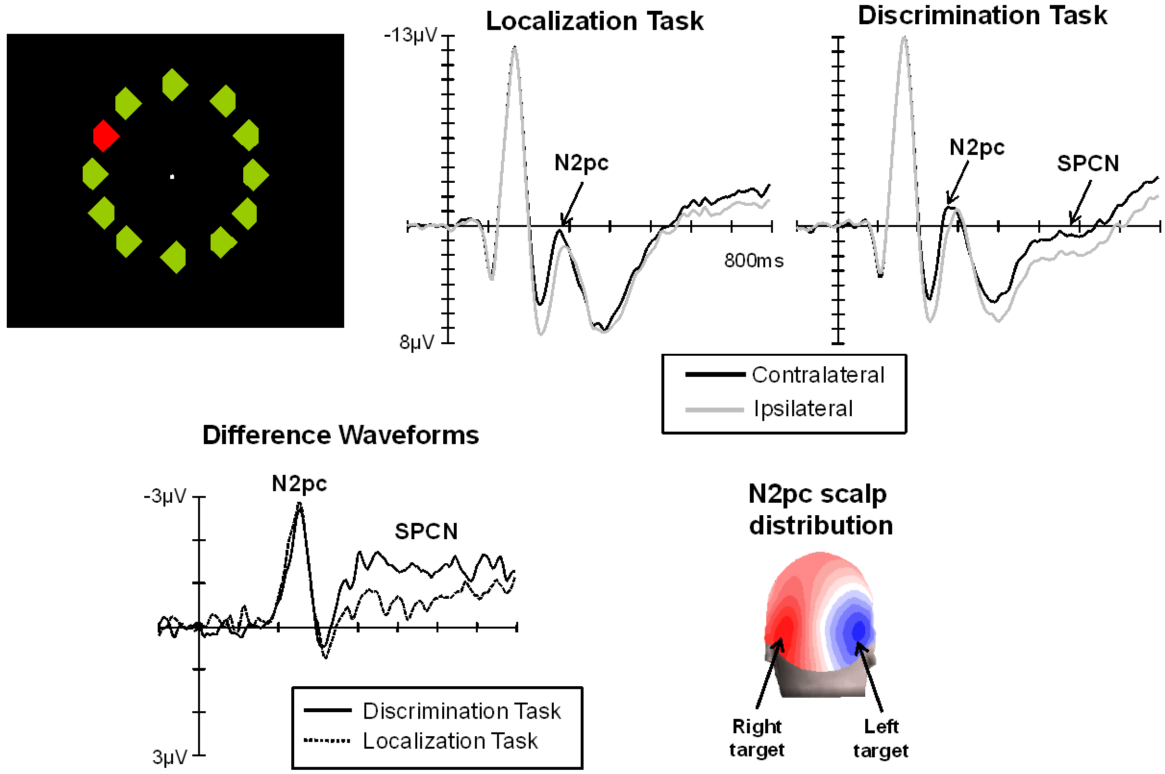

Figure 5. ERPs triggered at posterior electrodes PO7/8 contralateral and ipsilateral to the target side in response to visual search arrays that contained a colour singleton target diamond. Results are shown separately for an easy target localization task and a more difficult target discrimination task. The bottom panels show difference waveforms obtained by subtracting ipsilateral from contralateral ERPs, and a topographic scalp distribution map (back-of-the-head view) of the N2pc component. N2pc components did not differ between the two tasks, but the subsequent sustained posterior contralateral negativity (SPCN) was larger in the discrimination task. Data from Mazza et al. (2007).

activation of visual working memory (e.g., Vogel and Machizawa 2004).

The results shown in Figure 5 demonstrate that N2pc components are triggered by singleton targets that can be discriminated from distractors on the basis of a unique feature (see also Luck and Hillyard 1994a). Other studies have observed an N2pc in response to targets that are defined by a feature conjunction (e.g., Luck et al. 1997). N2pc components are triggered not just by target items, but also by non-targets that possess target-defining features (Luck and Hillyard 1994b). In contrast, even highly salient stimuli such as orientation singletons do not elicit an N2pc when they are task-irrelevant (Luck and Hillyard 1994a). This latter observation underlines that the N2pc component is a genuine marker of spatially selective attentional processing, and not an artefact of asymmetric hemispheric activations that are caused by low-level physical differences between visual fields. Its distinct occipito-temporal focus and its sensitivity to the retinal location of target stimuli (Luck et al. 1997) strongly suggests that the N2pc is generated in retinotopically organised sensory-perceptual regions of visual cortex. Brain source localization analyses based on magnetoencephalographic (MEG) recordings have identified extrastriate occipitotemporal cortex as the main generator region of the N2pc, although activity in posterior parietal areas may also contribute to the early phase of this component (Hopf et al. 2000).

With respect to the functional interpretation of the N2pc, the first thing to note is that this component emerges about 100 ms later than the earliest effects of visual-spatial attention on the P1 component that were discussed in section 2. Attentional P1 modulations are found in experiments where relevant locations are known in advance, and preparatory shifts of spatial attention can take place prior to target onset. The observation that P1 enhancements for visual events at attended locations are elicited for targets as well as for non-target stimuli (e.g., Mangun and Hillyard 1987), demonstrates that the underlying spatially specific modulations of visual processing precede the discrimination between targets and distractors. In contrast, the N2pc component is observed in visual search tasks where target locations are not cued in advance, and is triggered only by candidate target events, but not by events that lack target-defining features. These differences demonstrate attention-induced P1 amplitude enhancements and N2pc components reflect qualitatively distinct attentional effects. The P1 component is triggered during the initial parallel feedforward sweep of visual processing (Lamme and Roelfsema 2000) and its attentional modulation reflects a pre-existing spatial bias that is the result of preparatory shifts of spatial attention prior to stimulus onset. In contrast, the N2pc component is triggered only after evidence for the presence of a task-relevant visual stimulus has been obtained in the course of the initial feedforward analysis of the visual field. If such evidence is present, control signals from higher-level attentional centres in posterior parietal cortex are sent to lower-level extrastriate visual cortex, where they induce spatially selective processing biases, which are reflected by the N2pc (Luck and Hillyard 1994b).

It is important to note that the N2pc indexes the selection of distinct visual objects, and not purely space-based selectivity: N2pc components are triggered when observers select the location of an anticipated target stimulus and this location is marked by a placeholder object, whereas no N2pc is triggered under otherwise identical circumstances in the absence of such placeholders (Woodman et al. 2009). Along similar lines, a study that combined spatial cueing procedures and a visual search paradigm (Kiss et al. 2008) has demonstrated that the N2pc is not associated with shifts of attention in visual space towards the location of anticipated target locations, but instead reflects the subsequent spatial selection of visual target stimuli.

The question whether the N2pc reflects target selection or distractor inhibition has been a matter of considerable debate. Results from early N2pc experiments have suggested that this component might be primarily associated with the inhibition of nontarget stimuli. For example, N2pc components were observed for target stimuli that were surrounded by task-irrelevant distractors, but not when targets were presented in isolation (Luck and Hillyard 1994b). Furthermore, increasing the number of distractors, and thus the need for distractor inhibition, results in larger N2pc amplitudes (Mazza et al. 2009; see also Luck et al. 1997). Such observations have led to the suggestion that the N2pc component is an index for spatially selective distractor inhibition ("spatial filtering") that is activated when distractors and targets compete for attentional selection (Luck and Hillyard 1994b; Luck et al. 1997). Because distractor inhibition should be maximal when target and distractor items are presented in close proximity and thus are strong competitors (Desimone and Duncan 1995), the spatial filtering account implies that the N2pc should be sensitive to the relative spatial locations of targets and distractors. However, this prediction has not been supported by experimental results. An early study (Eimer 1996b) demonstrated that N2pc components are triggered by target stimuli that are presented in isolation in one visual hemifield, and are accompanied by a single distractor stimulus in the opposite hemifield. Under such conditions, target selection should require little if any distractor inhibition. Along similar lines, Mazza et al. (2009) have shown that N2pc amplitudes are unaffected by manipulations of the spatial proximity of targets and distractors, which is inconsistent with the inhibitory spatial filtering account. Such results suggest that the N2pc is primarily associated with the spatially selective attentional enhancement of target processing, rather than the selective inhibition of distractor items.

However, more recent findings suggest that the N2pc may reflect target enhancement as well as distractor suppression. Several ERP studies (Eimer and Kiss 2008; Hickey, Di Lollo, and McDonald 2009; Sawaki and Luck 2010) have reported a lateralized posterior ERP component in response to distractors that is similar to the N2pc in terms of its latency and topography, but shows an inverse polarity (i.e., a contralateral positivity rather than a contralateral negativity). For example, Hickey et al. (2009) found this distractor positivity (Pd) in response to lateral colour distractors in a task where observers had to discriminate the orientation of luminance targets that were located on the vertical meridian, and thus did not elicit any lateralized posterior ERP activity. They interpreted the Pd component as a marker of active distractor inhibition. Interestingly, no Pd was triggered by the same stimuli in a task that required only target detection, suggesting that distractors are only suppressed when the demands on attentional target processing are high. Similar results were reported by Sawaki and Luck (2010), who found a Pd component to salient colour distractors when observers searched for nonsalient target letters. These authors concluded that attentional capture by salient but task-irrelevant stimuli can be prevented by active top-down suppression, and that the Pd reflects this inhibitory process. In line with this interpretation, a Pd component was also observed in a spatial cueing study (Eimer and Kiss 2008; see Figure 7 below) response to salient colour singleton cues in a task where participants searched for size-defined targets, and colour was therefore task-irrelevant. Overall, these recent findings suggest that N2pc components that are triggered in response to search arrays where a target appears among distractor items may be composed of two temporally overlapping sub-components – a negativity contralateral to targets that reflects the attentional enhancement of target processing, and a positivity contralateral to distractors that is associated with their active inhibition. One important task for future ERP investigations into the mechanisms of selective attention in multi-stimulus arrays will be to verify the existence of a distinct Pd component and its relationship to distractor inhibition, and to provide a more detailed account of the relative roles of target enhancement and distractor suppression for the attentional selection of targets among non-targets in visual search.

5. Attentional selectivity in multi-stimulus arrays: Parallel or serial and bottom-up or top-down?

The question about the early versus late locus of selection (see section 2) is not the only important debate among attention researchers that is focused on the time course of attentional selectivity. This final section discusses two other controversies that have arisen about the operation of selective attention in multi-stimulus arrays. Both controversies are based on disagreements about the time course of attentional processes, and both have been addressed with ERP measures of attentional target selection such as the N2pc component. The first debate to be discussed concerns the question whether the allocation of attention to candidate target operates in a serial or parallel fashion. The other debate addresses on the relative roles of top-down intentional control and bottom-up stimulus salience for attentional target selection.

In many visual search tasks, target detection time increases as the number of distractor items (set size) increases. This increase typically occurs when search targets share some features with non-targets, and when non-target items are perceptually heterogeneous (Duncan and Humphreys 1989), and has often been attributed to the necessity of serial visual search. For example, feature integration theory (e.g., Treisman 1988) postulates that in difficult visual search tasks, attention has to be directed on one stimulus at a time and that the focus of attention switches between different objects in a serial fashion. The speed with which attention switches between individual objects has been calculated by measuring the increase in search time when set size is increased, which is typically between 20 and 80 ms per item. Others (e.g., Duncan et al. 1994; Ward et al. 1996) have argued that this procedure seriously underestimates the time demands of focal attentional processing, and that the correct "attentional dwell time" is in the order of several hundreds of milliseconds. This is much longer than would be plausible for any strictly serial model of visual search, and is therefore suggests an alternative parallel search scenario which does not involve a rapid serial focusing and re-allocation of spatial attention to individual stimuli. Instead, all visual objects compete in parallel for attentional processing, with target detection the result of a gradually evolving resolution of this competition (e.g., Desimone and Duncan 1995).

In a series of ERP studies, Woodman and Luck (1999, 2003) have used the N2pc component as a temporal marker of attentional target selection in perceptually demanding visual search tasks in order to discriminate between serial and parallel models. Observers had to perform a difficult gap localization task in response to infrequent targets, which were squares with a gap at a particular location (Figure 6, left panel). In one experiment (Woodman and Luck 1999), search arrays contained four differently coloured objects among black background items, and one of these objects was likely to be the target. To control the order in which candidate target objects were selected, participants were informed that targets would have one colour (e.g., red) on 75% of all target trials, and another colour (e.g., blue) on 25% of these trials. If visual search was serial, this manipulation should ensure that red objects would be selected first, followed by blue objects. Figure 6 (right) shows ERPs from target-absent trials where the objects in the two possible target colours were presented in opposite visual fields. An N2pc component initially emerged over the hemisphere contralateral to the object in the more likely target colour (C_{75}), and then shifted to the hemisphere contralateral to the object in the other less likely colour (C_{25}). This pattern of results supports serial models of visual search, because it suggests that attention was shifted within about 100 ms between the two candidate target objects. Parallel models of visual search should predict a sustained N2pc contralateral to the more likely target colour, indicative of a top-down task set for this colour that biases attentional competition in a spatially specific fashion. In a second experiment, Woodman and Luck (1999) determined search order was determined by presenting one candidate target object near fixation and another at a greater eccentricity, as observers tend to examine near objects prior to far objects. Here, the N2pc emerged initially contralateral to the near object, and shifted after about 100 ms to the far object, which again supports serial models of visual search.

There is however an important methodological problem for the interpretation of these N2pc polarity reversals in terms of serial search. Because the N2pc component is quantified as the difference between occipital ERP amplitudes at contralateral versus ipsilateral electrodes, it is not an absolute measure of attentional allocation to one specific object in a multi-stimulus search array, but instead reflects the difference in the degree to which attention is focused on a stimulus in the left versus right visual field. Because of this fact, the N2pc results observed by Woodman and Luck (1999) may still be consistent with models that assume that

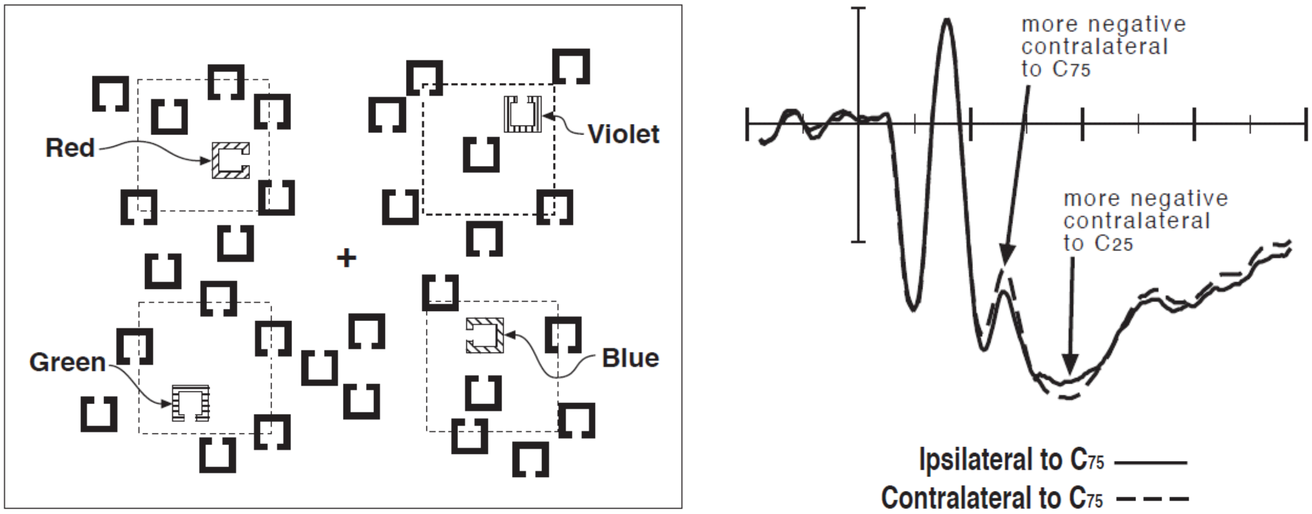

Figure 6. The left panel shows the visual search task employed by Woodman and Luck (1999). Search arrays contained four different colour singletons among black background items. Observers had to detect a target square defined by a specific gap location. 75% of all targets had one specific colour (C_{75}), and 25% had another colour (C_{25}). ERPs shown in the right panel are from nontarget trials where the C_{75} and C_{25} items appeared on opposite sides, and were obtained at posterior electrodes contralateral and ipsilateral to the C_{75} item. The N2pc was triggered first contralateral to the C_{75} item, and then contralateral to the C_{25} stimulus. Reproduced with permission from Woodman and Luck (2003).

attention was allocated in parallel to both candidate target objects, and that only the relative bias in favour of one versus the other objects changed slightly across time. To meet this challenge, Woodman and Luck (2003) employed search arrays where one candidate target object was located on the vertical meridian and the other on the horizontal meridian. The contralateral nature of this component implies that visual stimuli on the vertical midline will elicit no N2pc, and that an N2pc measured on such trials can be exclusively interpreted as reflecting the attentional selection of the other candidate target object on the left or right side. Search order was again manipulated via stimulus eccentricity. Results were straightforward: The N2pc emerged about 150 ms earlier in search arrays with near horizontal targets than in arrays with far horizontal targets, and there was very little temporal overlap between the N2pc components elicited by these two search array types. These findings suggest that attention was not allocated in parallel to both possible targets, but was first shifted to near targets, and then re-oriented to far targets. Overall, the N2pc results reported by Woodman and Luck (1999, 2003) provide novel insights into the time course of attentional allocation in visual search, and demonstrate the power of ERP measures as temporal markers of selective attention. Their findings provide strong evidence for the sequential nature of attentional processing in demanding visual search tasks, and thus support serial models of visual search such as Feature Integration Theory (Treisman 1988) or Guided Search (Wolfe 1994), but are more difficult to reconcile with parallel models of visual search (e.g., Ward et al. 1996).

It is important to underline that the detection of target items in visual search does not always require the serial allocation of spatial attention. When there is one stimulus with a distinct feature in a context of perceptually uniform stimuli (e.g., one red apple on a plate of green apples), it will usually ‘pop out’ and rapidly capture attention. In contrast to targets that are defined by feature conjunctions, the speed of detecting such feature singleton targets is unaffected by the number of distractor items in a visual search array (Treisman and Gelade 1980). It is natural to assume that such feature singletons capture attention in an automatic bottom-up fashion that is determined exclusively by their perceptual salience, and is independent of current top-down search goals (see also Chapter 8, this volume). In fact, the relative roles of bottom-up and top-down factors in the control of attentional capture by feature singletons remain controversial, and ERP measures such as the N2pc component have recently played an important role in this debate.

In several models of attentional selectivity, stimulus salience is represented in a topographical map that combines local contrast signals from different dimension- and feature-specific maps (e.g., Koch and Ullman 1985; Itti and Koch 2000). Attention will normally be directed towards the location with the highest combined salience value, but the controversial question is whether and to what degree this salience-driven attentional capture can be modulated or even prevented by top-down control processes (e.g., Fecteau and Munoz 2006). Behavioural studies that have investigated the relative roles of top-down task sets and bottom-up salience for attentional capture by feature singleton stimuli in visual search tasks have yielded apparently inconsistent results. When observers search for a shape singleton (e.g., a unique diamond target presented among distractor circles) the presence of an additional salient but task-irrelevant stimulus (e.g., a colour singleton; Theeuwes 1991) slows down reaction times relative to trials where no irrelevant singleton is present. This observation appears to suggest that salient singleton stimuli capture attention in a bottom-up fashion that is unaffected by current selection goals (Theeuwes 2010). In contrast, experiments by Folk and colleagues (Folk et al., 1992, 1994; Folk and Remington 1998) have demonstrated that attentional capture by salient but irrelevant visual singletons is determined by top-down task sets. In their experiments, spatially non-predictive singleton cues were presented prior to the onset of a target search display. Responses were faster for targets at cued as compared to uncued locations, indicating that the cues captured attention. Critically, these spatial cueing effects were only present when cue features matched the current task set. For example, when observers searched for a colour-defined target, cueing effects were found for colour singleton cues that matched the current target colour, but not for cues in a different colour, or for singletons defined in a different dimension (e.g., abrupt onset items). These findings strongly suggest that attentional capture by visual singletons is not a bottom-up phenomenon driven by salience, but is instead determined by whether or not these objects match task-relevant attributes as defined by an active task set.

The controversy whether attentional capture by salient visual feature singletons is determined by current top-down task set or is triggered in a purely bottom-up fashion has continued for two decades. On both sides of this debate, specific assumptions about the time course of attentional capture have been invoked, and these have proved to be difficult to confirm or reject on the basis of behavioural performance data. The observation that target detection is delayed when visual search arrays contain an additional task-irrelevant salient singleton item has been attributed to the increased visual complexity of such search arrays, which extends pre-attentive processing and thus delays attention shits towards targets (Folk and Remington 1998). On the other side, the observation that spatial cueing effects are eliminated for salient singleton cues that do not match current target-defining features has been explained by assuming that such cues do initially capture attention in a bottom-up fashion, but that attention is then rapidly disengaged, thereby preventing the emergence of spatial cueing effects in response to subsequently presented target stimuli (e.g., Theeuwes et al. 2000).

Again, ERP markers of attentional target selection such as the N2pc component allow more precise insights into the time course of the attentional selection processes that are elicited by visual arrays that contain salient feature singletons, and thus offer the possibility to decide between competing top-down and bottom-up accounts of attentional capture. Hickey et al. (2006) measured the N2pc during visual search for shape singleton targets that were accompanied by salient but task-irrelevant colour singleton distractors on some trials. Critically, an N2pc component was triggered by laterally presented colour singleton distractors on trials where shape targets were located on the vertical meridian, and thus did not elicit any N2pc activity. This observation appears to provide strong evidence for the bottom-up capture of attention by salient distractors. Further support for this bottom-up account comes from the finding that in trials where a shape target and a colour distractor appeared in opposite hemifields, a small N2pc to distractors preceded the N2pc to targets, suggesting that attention was initially drawn to the distractor before it was re-allocated to the target.

While the N2pc results reported by Hickey et al. (2006) appear to provide clear ERP evidence for the bottom-up nature of attentional capture, findings from other N2pc studies that used spatial cueing procedures strongly support the view that capture is always contingent on top-down task set. Figure 7 (left) shows the setup of an experiment where spatially uninformative colour singleton cues preceded target search arrays (Eimer and Kiss 2008). In different blocks, observers either searched for red targets among grey distractors (Colour Task), or for a small target bar among larger distractor bars (Size Task). In the Colour Task, colour singleton cues elicited a large N2pc indicative of attentional capture (Figure 7, right side). In contrast, no N2pc was triggered by physically identical colour singleton cues in the Size Task where colour was task-irrelevant. In fact, Figure 7 shows that under these task instructions, these cues triggered an enhanced contralateral positivity. As mentioned earlier, this Pd component is thought to reflect active top-down inhibition (e.g., Hickey et al., 2009). The observation that an N2pc was elicited by perceptually salient colour

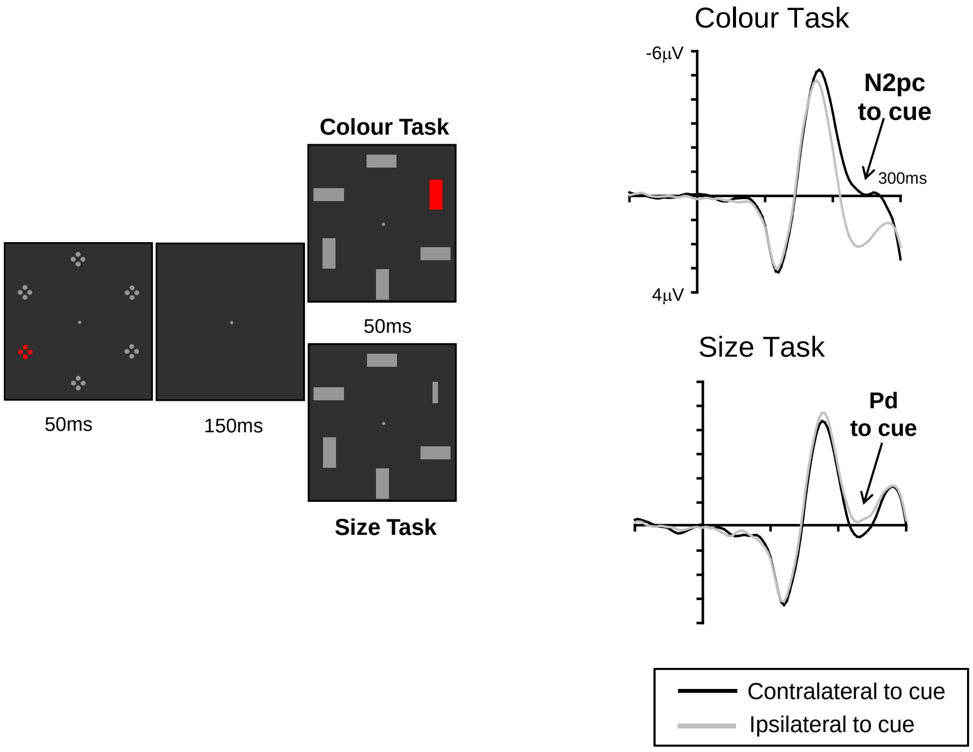

Figure 7. ERPs triggered in response to spatially uninformative cue arrays that contained a red colour singleton, measured in a task where participants searched for red target singletons, and a task where they searched for size singletons. An N2pc was triggered by colour singleton cues in the colour task, whereas a contralateral positivity (Pd) was elicited by the same cues in the Size task. Data from Eimer and Kiss (2008).

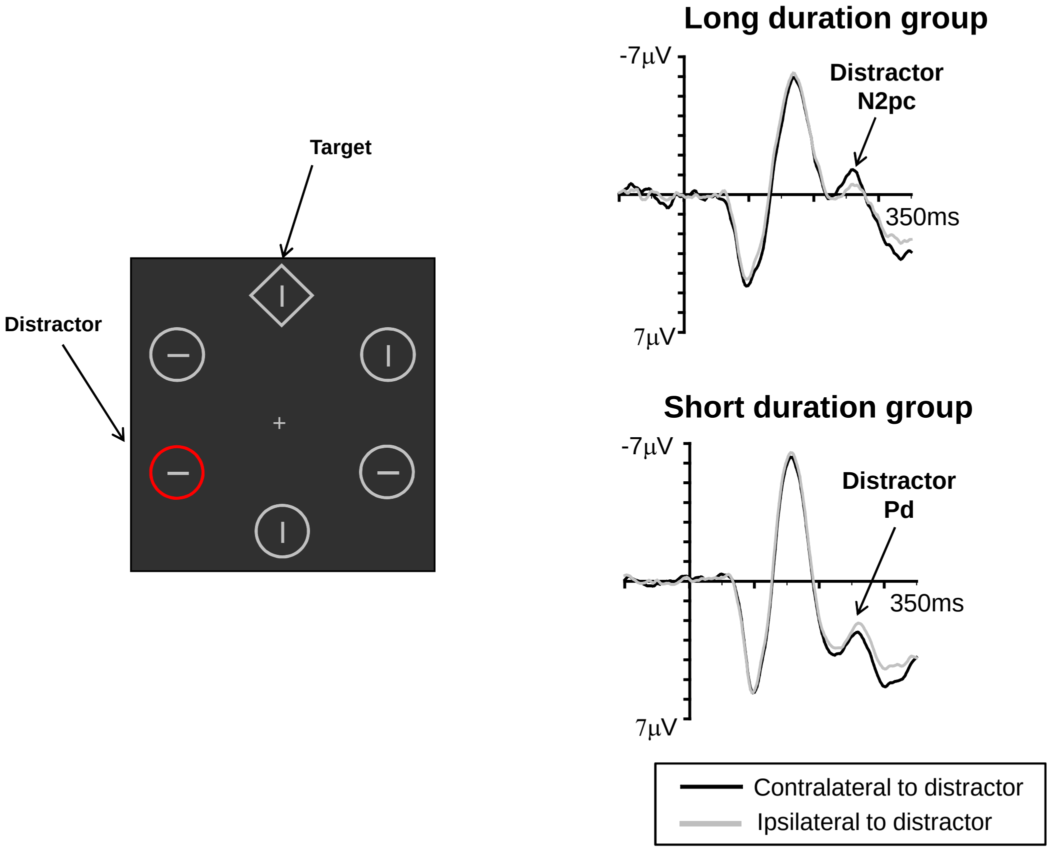

Figure 8. ERPs triggered in response to visual search arrays that contained a shape target on the vertical meridian and a lateral task-irrelevant colour singleton. For participants in the long duration group, arrays remained visible until response execution. In the short duration group, they disappeared after 200 ms. In the long duration group, colour distractors triggered an N2pc indicative of attentional capture. In the short duration group, the same distractors elicited a Pd component, indicating that they were subject to active inhibition. Data from Kiss et al. (2011).

singleton cues only when colour was task-relevant strongly suggests that attentional capture depends on top-down task sets, and is not driven in a bottom-up fashion by stimulus salience (see also Lien et al. 2008; Eimer et al. 2009, for additional N2pc evidence for top-down control of capture). The absence of any early-onset N2pc component to colour singleton cues that did not match the current top-down task set also casts doubt on the hypothesis that these cues trigger rapid salience-driven attentional capture which is later followed by rapid disengagement (see also Ansorge et al. 2011, for more direct N2pc evidence against this rapid disengagement account).

There is an obvious conflict between N2pc studies which employed the additional singleton paradigm and found evidence for the bottom-up salience-driven nature of attentional capture (e.g., Hickey et al. 2006), and N2pc results from spatial cueing experiments which seem to demonstrate that capture is fully controlled by top-down task sets (e.g., Eimer and Kiss 2008). However, this apparent discrepancy might be linked to the time demands that are imposed on attentional selectivity in these two different paradigms. In additional singleton experiments, search displays usually remain visible until a response is executed, and observers therefore have sufficient time to select and identify targets even if attention is initially drawn to a more salient distractor. In spatial cueing experiments, search array durations are typically much shorter, which imposes stricter temporal demands on target selection, as attentional capture by distractors will likely result in targets being missed. To investigate the impact of temporal task demands on the top-down versus bottom-up control of attentional capture by feature singletons, a recent ERP study (Kiss et al. 2011) measured lateralized posterior ERP components in response to search arrays that contained a shape singleton target and a colour singleton distractor. The critical factor was display duration, as search arrays remained visible until response execution for one group of participants, but were presented for only 200 ms for another group. Figure 8 shows lateralized ERP component measured for both groups at posterior electrodes. In the long duration group, salient colour distractors triggered an N2pc, confirming earlier observations by Hickey et al. (2006), and demonstrating these distractors did capture attention even though they were known to be task-irrelevant. But in the short duration group, the same colour distractors elicited no N2pc, but instead a contralateral positivity (Pd). Because this Pd component has believed to mark the top-down inhibition of salient distracters, its presence under conditions of high temporal task demands suggests that attentional capture by salient distractors can be prevented by active inhibition when it would otherwise disrupt task performance. These ERP findings point towards a resolution of the dispute between bottom-up and top-down accounts of attentional capture. Salience-driven capture may represent a default mode attentional selectivity, such that salient distracters will capture attention when the time demands on target selection are relatively relaxed. However, salience-driven capture is not strongly automatic, because it can be prevented by top-down inhibitory control when this is necessitated by the demands of a specific task context.

In summary, the results discussed in this section have illustrated the special role that ERP measures can play in investigations of attentional processes that govern the selection of targets in multi-stimulus arrays. As temporally precise markers of attentional processes, ERP components such as the N2pc have been particularly useful to shed new light on controversial issues about the functional and temporal organisation of the mechanisms that are responsible for spatially selective stimulus processing.

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References

Allport, A. (1993). Attention and control: Have we been asking the wrong questions? A critical review of twenty-five years. In D.E. Meyer and S. Kornblum (Eds.), *Attention and Performance XIV.* Cambridge, MA: MIT Press, pp.183-218.

Ansorge,U., Kiss, M., Worschech, F., and Eimer, M. (2011). The initial stage of visual selection is controlled by top-down task set: New ERP evidence. *Attention, Perception, & Psychophysics*, 73, 113–122.

Beck, D.M., and Kastner, S. (2009). Top-down and bottom-up mechanisms in biasing competition in the human brain. *Vision Research,* 49, 1154-1165.

Broadbent, D.E. (1958). *Perception and Communication.* New York: Elsevier.

Clark, V.P., Fan, S., and Hillyard, S.A. (1995). Identification of early visually evoked potential generators by retinotopic and topographic analysis. *Human Brain Mapping,* 2, 170–187.

Corbetta, M., and Shulman, G.L. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nature Reviews Neuroscience*, 3, 215-229.

Desimone, R., and Duncan, J. (1995). Neural mechanisms of selective visual attention. *Annual Review of Neuroscience*, 18, 193–222.

Deutsch, J.A., and Deutsch, D. (1963). Attention: Some theoretical considerations. *Psychological Review,* 70, 80-90.

Di Russo, F., Martinez, A., and Hillyard, S.A. (2003). Source analysis of event-related cortical activity during visuo-spatial attention. *Cerebral Cortex*, 13, 486-499.

Duncan, J., and Humphreys, G.W. (1989). Visual search and stimulus similarity. *Psychological Review,* 96, 433-458.

Duncan, J., Ward, R., and Shapiro, K. (1994). Direct measurement of attentional dwell time in human vision. *Nature,* 369, 313-315.

Eimer, M. (1994). 'Sensory gating' as a mechanism for visuo-spatial orienting: Electrophysiological evidence from trial-by-trial cueing experiments. *Perception & Psychophysics*, 55, 667-675.

Eimer, M. (1996a). ERP modulations indicate the selective processing of visual stimuli as a result of transient and sustained spatial attention. *Psychophysiology*, 33, 13-21.

Eimer, M. (1996b). The N2pc component as an indicator of attentional selectivity. *Electroencephalography and Clinical Neurophysiology*, 99, 225–234.

Eimer, M. (1999). Can attention be directed to opposite locations in different modalities? An ERP study. *Clinical Neurophysiology*, 110, 1252-1259.

Eimer, M., and Driver, J. (2000). An event-related brain potential study of cross-modal links in spatial attention between vision and touch. *Psychophysiology*, 37, 697-705.

Eimer, M., and Kiss, M. (2008). Involuntary attentional capture is determined by task set: Evidence from event-related brain potentials. *Journal of Cognitive Neuroscience*, 20, 1423–1433.

Eimer, M., Kiss, M., Press, C., and Sauter, D. (2009). The roles of feature-specific task set and bottom-up salience in attentional capture: An ERP study. *Journal of Experimental Psychology: Human Perception and Performance*, 35, 1316–1328.

Eimer, M., and Schröger, E. (1998). ERP effects of intermodal attention and cross-modal links in spatial attention. *Psychophysiology*, 35, 313-327.

Eimer, M., Van Velzen, J., and Driver, J. (2002). Crossmodal interactions between audition, touch and vision in endogenous spatial attention: ERP evidence on preparatory states and sensory modulations. *Journal of Cognitive Neuroscience*, 14 254-271.

Farah, M.J., Wong, A.B., Monheit, M.A., and Morrow, L.A. (1989). Parietal lobe mechanisms of spatial attention: Modality-specific or supramodal? *Neuropsychologia*, 27, 461–470.

Fecteau, J.H., and Munoz, D.P. (2006). *Salience, relevance, and firing: a priority map for target selection. Trends in Cognitive Sciences*, 10, 382–390.

Folk, C.L., and Remington, R.W. (1998). Selectivity in distraction by irrelevant featural singletons: Evidence for two forms of attentional capture. *Journal of Experimental Psychology: Human Perception and Performance,* 24, 847-858.

Folk, C.L., Remington, R.W., and Johnston, J.C. (1992). Involuntary covert orienting is contingent on attentional control settings. *Journal of Experimental Psychology: Human Perception and Performance,* 18, 1030-1044.

Folk, C.L., Remington, R.W., and Wright, J.H. (1994). The structure of attentional control: Contingent attentional capture by apparent motion, abrupt onset, and colour. *Journal of Experimental Psychology: Human Perception and Performance,* 20, 317-329.

Green, J.J., Teder-Sälerjärvi, W.A., and McDonald, J.J. (2005). Control mechanisms mediating shifts of attention in auditory and visual space: a spatio-temporal ERP analysis. *Experimental Brain Research*, 166, 358-369.

Harter, M.R., Miller, S.L., Price, N.J., LaLonde, M.E., and Keyes, A.L. (1989). Neural processes involved in directing attention. *Journal of Cognitive Neuroscience*, 1, 223-237.

Hickey, C., Di Lollo, V., and McDonald, J.J. (2009). Electrophysiological indices of target and distractor processing in visual search. *Journal of Cognitive Neuroscience*, 21, 760–775.

Hickey, C., McDonald, J.J., and Theeuwes, J. (2006). Electrophysiological evidence of the capture of visual attention. *Journal of Cognitive Neuroscience*, 18, 604-613.

Hillyard, S.A., Hink, R.F., Schwent, V.L., and Picton, T.W. (1973). Electrical signs of selective attention in the human brain. *Science,* 182, 177-180.

Hopf, J.-M., Luck, S.J., Girelli, M., Hagner, T., Mangun, G.R., Scheich, H., and Heinze, H.J. (2000). Neural sources of focused attention in visual search. *Cerebral Cortex*, 10, 1233–1241.

Itti, L., and Koch, C. (2000). A saliency-based search mechanism for overt and covert shifts of visual attention. *Vision Research*, 40, 1489–1506.

Kennett, S., Eimer, M., Spence, C., and Driver, J. (2001). Tactile-visual links in exogenous spatial attention under different postures: Convergent evidence from Psychophysics and ERPs. *Journal of Cognitive Neuroscience*, 13, 462-478.

Kiss, M., Grubert, A., Petersen, A., and Eimer, M. (2011). Attentional capture by salient distractors during visual search is determined by temporal task demands. *Journal of Cognitive Neuroscience*, doi:10.1162/jocn_a_00127

Kiss, M., Van Velzen, J., and Eimer, M. (2008). The N2pc component and its links to attention shifts and spatially selective visual processing. *Psychophysiology*, 45, 240-249.

Koch, C., and Ullman, S. (1985). Shifts in selective visual attention: towards the underlying neural circuitry. *Human Neurobiology*, 4, 219–227.

Lamme, V.A.F., and Roelfsema, P.R. (2000). The distinct modes of vision offered by feedforward and recurrent processing. *Trends in Neuroscience*, 23, 571-579.

Lien, M-C., Ruthruff, E., Goodin, Z., and Remington, R.W. (2008). Contingent attentional capture by top-down control settings: Converging evidence from event-related potentials. *Journal of Experimental Psychology: Human Perception and Performance*, 34, 509–530.

Luck, S.J., Fan, S. and Hillyard, S.A. (1993). Attention-related modulation of sensory-evoked brain activity in a visual search task. *Journal of Cognitive Neuroscience*, 5, 188-195.

Luck, S.J., Girelli, M., McDermott, M.T., and Ford, M.A. (1997). Bridging the gap between monkey neurophysiology and human perception: An ambiguity resolution theory of visual selective attention. *Cognitive Psychology*, 33, 64-87.

Luck, S.J., and Hillyard, S.A. (1994a). Electrophysiological correlates of feature analysis during visual search. *Psychophysiology,* 31, 291–308.

Luck, S.J. and Hillyard, S.A. (1994b). Spatial filtering during visual search: evidence from human electrophysiology. *Journal of Experimental Psychology*: *Human Perception and Performance*, 20, 1000-1014.

Luck, S. J., Vogel, E. K., and Shapiro, K. L. (1996). Word meanings are accessed but cannot be reported during the attentional blink. *Nature*, 383, 616-618.

Mangun, G.R. (1995). Neural mechanisms of visual selective attention. *Psychophysiology,* 32, 4-18.

Mangun, G.R., and Hillyard, S.A. (1987). The spatial allocation of visual attention as indexed by event-related brain potentials. *Human Factors*, 29, 195–211.

Mangun G.R., and Hillyard S.A. (1991). Modulation of sensory-evoked brain potentials provide evidence for changes in perceptual processing during visual-spatial priming. *Journal of Experimental Psychology: Human Perception and Performance,* 17, 1057–1074.

Martínez, A. Anllo-Vento, L., Sereno, M.I., Frank, L.R., Buxton, R.B., Dubowitz, D.J., Wong, E.C., Hinrichs, H., Heinze, H.J., and Hillyard, S.A. (1999). Involvement of striate and extrastriate visual cortical areas in spatial attention. *Nature Neuroscience*, 2, 364-369.

Mazza, V., Turatto, M., and Caramazza, A. (2009). Attention selection, distractor suppression, and N2pc. *Cortex*, 45, 879-890.

Mazza, V., Turatto, M., Umiltà, C., Eimer, M. (2007). Attentional selection and identification of visual objects are reflected by distinct electrophysiological responses. *Experimental Brain Research,* 181, 531-536*.*

McDonald, J.J., Teder-Sälejärvi, W.A., and Hillyard, S.A. (2000). Involuntary orienting to sound improves visual perception. *Nature*, 407, 906-908.

McDonald, J.J., and Ward, L.M. (2000). Involuntary listening aids seeing: Evidence from human electrophysiology. *Psychological Science*, 11, 167-171.

Nobre A.C., Sebestyen, G.N., and Miniussi, C. (2000). The dynamics of shifting visuospatial attention revealed by event-related brain potentials. *Neuropsychologia,* 38, 964-974.

Praamstra, P., Boutsen, L, and Humphreys, G.W. (2005). Frontoparietal control of spatial attention and motor intention in human EEG. *Journal of Neurophysiology*, 94, 764–774.

Raymond, J.E., Shapiro, K.L., and Arnell, K.M. (1992). Temporary suppression of visual processing in an RSVP task: An attentional blink? *Journal of Experimental Psychology: Human Perception and Performance,* 18, 849-860.

Sawaki, R., and Luck, S. (2010). Capture versus suppression of attention by salient singletons: Electrophysiological evidence for an automatic attend-to-me signal. *Attention, Perception & Psychophysics*, 72, 1455–1470.

Spence, C., and Driver, J. (1996). Audiovisual links in endogenous covert spatial attention. *Journal of Experimental Psychology: Human Perception and Performance,* 22, 1005-1030.

Spence, C., Pavani, F., and Driver, J. (2000). Crossmodal links between vision and touch in covert endogenous spatial attention. *Journal of Experimental Psychology: Human Perception and Performance,* 26, 1298-1319.

Teder-Sälejärvi, W.A., Münte, T.F., Sperlich, F.J., and Hillyard, S.A. (1999). Intra-modal and cross-modal spatial attention to auditory and visual stimuli: An event-related brain potential (ERP) study. *Cognitive Brain Research*, 8, 327-343.

Theeuwes, J. (1991). Cross-dimensional perceptual selectivity. *Perception & Psychophysics,* 50, 184-193.

Theeuwes, J. (2010). Top-down and bottom-up control of visual selection. *Acta Psychologica*, 135, 77–99.

Theeuwes, J., Atchley, P., and Kramer, A.F. (2000). On the time course of top-down and bottom-up control of visual attention. In S. Monsell and J. Driver (Eds.) *Attention and Performance XVIII.* Cambridge, MA: MIT Press, pp.105-124.

Treisman, A., (1988). Features and objects: The Fourteenth Bartlett Memorial Lecture. *Quarterly Journal of Experimental Psychology*, 40A, 201-237.

Treisman, A., and Gelade, G. (1980). A feature integration theory of attention. *Cognitive Psychology*, 12, 97-136.

Van Velzen, J., Eardley, A., Forster, B., and Eimer M. (2006). Shifts of attention in the early blind: An ERP study of attentional control processes in the absence of visual spatial information. *Neuropsychologia*, 44, 2533-2546.

Van Velzen, J., and Eimer, M. (2003). Early posterior ERP components do not reflect the control of attentional shifts towards expected peripheral events. *Psychophysiology*, 40, 827-831.

Van Voorhis S., and Hillyard S. (1977). Visual evoked potentials and selective attention to points in space. *Perception & Psychophysics,* 22, 54–62.

Vogel, E.K., Luck, S.J., and Shapiro, K.L. (1998). Electrophysiological evidence for a postperceptual locus of suppression during the attentional blink. *Journal of Experimental Psychology: Human Perception and Performance*, 24, 1656-1674.

Vogel, E.K., and Machizawa, M.G. (2004). Neural activity predicts individual differences in visual working memory capacity. *Nature*, 428, 748-751.

Ward, R., Duncan, J., and Shapiro, K.L. (1996). The Slow Time-Course of Visual Attention. *Cognitive Psychology,* 30, 79-109.

Wolfe, J.M. (1994). Guided Search 2.0: A Revised Model of Visual Search. *Psychonomic Bulletin & Review*, 1, 202-238.

Woodman, G.F. Arita, J.T., and Luck, S.J. (2009). A cuing study of the N2pc component: An index of attentional deployment to objects rather than spatial locations. *Brain Research, 1297,* 110-121.

Woodman, G.F., and Luck, S.J. (1999). Electrophysiological measurement of rapid shifts of attention during visual search. *Nature,* 400, 867-869.

Woodman, G. F., and Luck, S. J. (2003). Serial deployment of attention during visual search. *Journal of Experimental Psychology: Human Perception and Performance*, 29, 121-138.