Electrophysiological Correlates of the Focusing of Attention within Complex Visual Scenes: N2pc and Related ERP Components

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Abstract

As discussed in Chapter 11 of this volume, attention plays a role in the perception of simple stimuli, serving as a gain control that enhances the speed or accuracy of feedforward visual processing. However, additional attentional mechanisms are needed to support the iterative, reentrant processes and perception-action loops that are involved in the perception of complex, multiple-element stimulus arrays, and the event-related potential (ERP) correlates of these additional attentional mechanisms will be the focus of the present chapter. The first half of the chapter begins by discussing the computational problems that must be solved by these mechanisms and the sequence of steps involved in processing complex stimulus arrays, which include storing a target template in working memory, detecting relevant features, focusing attention on a peripheral location, shifting overt attention to the attended location, and then expanding or contracting attention around the object at this location. The ERP components corresponding to each of these steps are then described. The second half of the chapter provides a closer look at N2pc and related contralateral components that reflect the focusing of attention onto a peripheral location.

Keywords: event-related potential components, visual attention, P1, N1, N2pc, distractor positivity (PD), sustained posterior contralateral negativity (SPCN)

The General Role of Attention in Visual Perception

The ultimate goal of research on visual perception is to understand how people perceive, remember, and act upon the objects in natural visual environments, such as the scene shown in Figure 12.1. Understanding these high-level aspects of vision requires that we understand the operation of almost the entire brain, because visually guided behavior depends on perceptual systems, memory systems, motor systems, motivational systems, and executive control systems. The perception of complex scenes also involves solving computational problems that are not present in laboratory experiments in which objects are presented one at a time on a blank background (see Feldman, 1985; Luck et al., 1997b). Whereas simple, isolated stimuli may be identified on the basis of a single feedforward sweep of neural activity, the perception of complex, multiple-element arrays involves iterative, reentrant processes and perception-action loops (see Di Lollo et al., 2000; Klyubin et al., 2004). As discussed in Chapter 11 of this volume, attention plays a role in the perception of simple stimuli, serving as a gain control that enhances the speed or accuracy of feedforward visual processing. However, additional attentional mechanisms are needed to support the iterative, reentrant processes and perception-action loops that are involved in the perception of complex, multiple-element stimulus arrays, and the event-related potential (ERP) correlates of these additional attentional mechanisms will be the focus of the present chapter. We will begin by discussing the computational problems that must be solved by these mechanisms and the sequence of steps involved in processing complex stimulus arrays.
A key factor limiting the perception of complex stimulus arrays is that high-resolution information about the visual environment is available to the brain only from the fovea, the central area of the retina (approximately 1 mm in diameter, which represents approximately 2° of visual angle). Receptive fields arising from the fovea are small, giving us the ability to resolve small details of objects presented at the center of gaze, whereas receptive fields from extrafoveal regions are large, making it impossible to resolve small details in objects presented in the periphery. In addition, approximately 50% of neurons in visual cortex are devoted to the tiny foveal region. Because of this limitation, saccadic eye movements are used to orient the direction of gaze so that an object of interest falls into the fovea. These eye movements dramatically improve the perception of the foveated object, and they can be considered a mechanism of attention. Indeed, foveating an object is arguably the visual system’s most important and most potent mechanism of attention. Selecting an object by foveating it is often called overt attention, whereas attending to an object that is not foveated is often called covert attention.

Although foveating an object is a powerful means of focusing attention on it, it is also important to be able to focus processing resources on objects that are not being foveated (for a detailed discussion, see Luck, 2009). Relevant visual information is often defined by nonspatial features (e.g., the color and shape of a pencil when one wishes to write something), and it would be incredibly inefficient to search for a desired object by moving the eyes randomly until an object containing the relevant features appears in the fovea. Consequently, some sort of selective processing of relevant features is often necessary prior to an eye movement. Moreover, even if gaze is directed to the center of an object, some mechanism is necessary to allow perceptual processing mechanisms to expand across the extent of the object, allowing the entire object to be selected without also selecting surrounding objects. For example, after your eyes have been directed to one of the words on this page, some mechanism is necessary to allow the entire word to be processed without interference from other words on the lines above and below the fixated word. Moreover, the size of this attended region must be adjusted to reflect the size of the fixated object and the proximity of surrounding objects. If you bring this text closer to your eyes, for example, the size of the word on your retinas increases and the region of attention must expand. Thus, although shifts of gaze to an object are a powerful mechanism of attention (overt attention), it is also important to be able to allocate processing resources independently of eye position (covert attention).

The operation of overt and covert attention in natural vision typically follows a sequence of steps. First, a goal must be activated to guide the allocation of attention. For example, the shape and color of a pen might be stored as a search template in working memory to guide the process of searching for that pen (see, e.g., Duncan & Humphreys, 1989; Woodman et al., 2007). Second, sensitivity is increased for features specified by the search template so that objects containing those features will have priority for further processing (see, e.g., Hopf et al., 2004; Wolfe, 1994; Wolfe et al., 1989). Third, the presence of an object containing these features triggers a shift of covert spatial attention to the object’s location, facilitating the perception of this object (Carrasco et al., 2000) and causing it to be stored in working memory (Pollinger & Luck, 2007). Fourth if the now-attended peripheral object still appears to match the search template, this may trigger a shift of overt gaze to that location (Peterson et al., 2004). Fifth, once the eyes are centered on the object, attention will expand or contract around the object, depending on its size and the proximity of distracting objects (Hopf et al., 2006; LaBerge et al., 1991).

The remainder of this chapter will discuss the ERP components involved with each of these five steps of visual processing. Most of these components are described in detail in other chapters in this volume and therefore will be discussed only briefly. The N2pc component—which reflects the focusing
of attention on a potential target in a visual search array—is not covered elsewhere in this volume and will therefore be discussed in detail in the second half of this chapter, along with other related components (including the distractor positivity and the sustained posterior contralateral negativity).

**Step 1: Storing the Target Template in Working Memory (NSW and CDA)**

Chapter 13 of this volume discusses the ERP correlates of working memory storage in detail, so here we will just note that sustained ERP activity is observed while an object is being maintained in working memory. This takes the form of a negative slow wave (NSW) over prefrontal cortex (Ruchkin et al., 2003) and contralateral delay activity (CDA) over temporal-parietal cortex (Vogel & Machizawa, 2004). Analogous single-unit activity has been observed in monkeys when they are preparing to search for a specific target (Chelazzi et al., 1993, 1998). These working memory representations may be used to guide attention to relevant objects when the to-be-attended object varies frequently, but working memory representations do not appear to be used to guide attention in typical visual search experiments in which the target remains the same for several minutes of testing (Woodman et al., 2001, 2007). Under these conditions, attention may be guided by long-term memory representations and by automatic priming from previous trials (Maljkovic & Nakayama, 1993; Meeter & Olivers, 2006). In either case, these representations provide the control signals that guide attention toward relevant features.

**Step 2: Detecting Relevant Features with Feature-Based Attention (Bilateral P2, N2, and P3 Components)**

Once the current goal has been activated in the form of a target template, feature-based attention mechanisms then operate across the visual field to highlight objects containing these features. Several ERP components related to feature-based attention were discussed extensively in Chapter 11. In the experiments described in that chapter, the attended and ignored stimuli were presented at different times, making it easy to isolate ERP activity related to the attended and ignored stimuli. In the natural environment, however, an observer is faced with a simultaneous array of relevant and irrelevant stimuli that are spatially intermixed. Consider, for example, the scene shown in Figure 12.1. If an observer is interested in eating a strawberry, this general goal does not specify the location to be attended. Instead, a search template is activated (i.e., a representation of the color and shape of a strawberry), and this is used to guide attention to locations that contain relevant features and are therefore likely to be the desired object. The visual search paradigm has been used extensively to simulate this sort of situation in the laboratory. In this paradigm, arrays of objects are presented, and the observer presses one of two buttons to indicate whether a predefined target object is present or absent in each array. Alternatively, each array might contain one of several different possible targets, and the observer must indicate which target is present in each array (see the reviews by Treisman, 1986; Wolfe, 1994). This section will discuss ERP components that are observed as subjects search for targets defined by specific features or combinations of features in the visual search paradigm. Some of these components are the same components observed when objects are presented one at a time, but others are found only when relevant and irrelevant objects are presented simultaneously.

When the target in a visual search task is defined by the presence of a simple feature value (e.g., the color red), and the distractor items are homogeneous along that feature dimension (e.g., all are blue), the target will “pop out” from the distractors. That is, subjects will be able to detect the target quickly, irrespective of the number of items in the display. Luck and Hillyard (1994a, 1994b) conducted several ERP experiments with popout stimuli of this nature.

As an example, consider the experiment shown in Figure 12.2A (Experiment 1 from Luck & Hillyard, 1994a). Each stimulus was either a homogeneous array of eight small blue vertical bars or an array of seven of these bars plus one “popout” bar that differed in color (green), orientation (horizontal), or size (large). Homogeneous arrays were presented on 50% of trials, and each of the three types of popout arrays was presented on 16.7% of trials. One of the three popout types was designated the target at the beginning of each trial block, and the subjects pressed one button when the target was present and another button when it was absent (the same nontarget response was made for both nontarget popouts and homogeneous arrays). Thus, different features were task-relevant in different trial blocks. In addition, a given popout type could be either the target or a nontarget, making it possible to assess the automatic allocation of attention to nontarget popout objects. That is, it is possible to ask whether a popout item automatically...
attracts attention whether or not it matches the target template.

Figure 12.2B shows the ERPs recorded at frontal and occipital electrode sites to target popout arrays, nontarget popout arrays, and homogeneous arrays. Several attention-related ERP components can be identified in this experiment: an anterior P2 effect; an anterior N2 effect; a posterior N2 effect (N2pb); a prototypical P3b wave with a centroparietal maximum; and an occipital P3 wave.

THE ANTERIOR P2 COMPONENT
At the frontal sites shown in Figure 12.2B, the P2 wave was larger for target popouts than for either nontarget popouts or homogeneous arrays. This appears to be the same as the P2 effect observed in the one-object-at-a-time feature-based attention studies described in Chapter 11 of this volume. However, the waveforms shown in Figure 12.2B demonstrate that this effect can also be observed when only one object in an array contains the relevant feature and all of the other objects contain irrelevant features; that is, the presence of the relevant feature is the important factor, irrespective of the presence or absence of irrelevant features. Comparisons across experiments indicate that this P2 effect is approximately the same size whether one or all of the items in the array contain the relevant feature.
feature value, suggesting that it reflects the detection of a specific feature rather than the degree of match between the overall stimulus array and the relevant feature value.

Additional experiments demonstrated that this P2 effect is observed only when the target occurs infrequently and that it is also present for non-targets that are highly similar to the target (Luck & Hillyard, 1994a, 1994b). Very little is known about the functional significance of this anterior P2 effect. The fact that it is sensitive to the probability of the target stimulus makes it similar to the P3b component (see Chapter 7, this volume). However, the P2 probability effect is observed only when the target can be distinguished from non-targets on the basis of a fairly simple feature, such as color or letter shape, whereas the P3b probability effect is observed whenever the subject can correctly categorize the stimuli as targets and non-targets.

It should be noted that, although we are calling this a P2 effect, we cannot be certain that it reflects a change in the amplitude of a unitary P2 component that is simply larger for targets than for non-targets. Instead, this effect may reflect a neural generator source that is present for targets and absent for non-targets, overlapping in time with a different P2 wave that is present equally for targets and non-targets. The term P2 effect is intended to be descriptive, indicating that the effect occurs in approximately the same latency range as the P2 wave and has approximately the same scalp distribution. Indeed, it would be surprising if only one neural generator source were active from 150–250 ms at anterior scalp sites (see Chapters 1 and 3, this volume, for additional discussion of the problem of multiple overlapping components). The terminology used to describe attention-related effects throughout the rest of this chapter is intended to be superficially descriptive in this same manner. It is important, however, to avoid the common mistake of assuming that an effect in the time range of a given component reflects a change in the amplitude of that component.

THE ANTERIOR N2 COMPONENT
In the experiment shown in Figure 12.2, the P2 wave was followed by an N2 wave at anterior scalp sites that was larger for both target and non-target popouts relative to the homogeneous arrays. The presence of this effect for non-targets as well as target popouts might suggest that it reflects an automatic detection of popout stimuli. However, when subjects were asked to discriminate the color of the whole stimulus array rather than the color of a single popout item, orientation popouts no longer generated an enlarged anterior N2 wave (Luck & Hillyard, 1994a, Experiment 3). Thus, the anterior N2 effect is observed only when the subjects are actively searching for an item that differs from the rest of the array (analogous behavioral results can be found in the studies of Bacon & Egeth, 1994; Pashler, 1988).

A similar anterior N2 effect has been observed in the flanker paradigm (Gehring et al., 1992) and in the Stroop paradigm (West & Alain, 1999, 2000; see Folstein & Van Petten, 2008, for an excellent review of these and related N2 effects). In these studies, a larger anterior N2 wave is observed for stimuli that contain conflicting features (e.g., incompatible trials). Conflict is produced in the flanker paradigm by surrounding the target with flanking distractor items that indicate a different response; conflict is produced in the Stroop paradigm by using ink of one color to write the name of a different color. The larger anterior N2 response on these conflict trials has been proposed to reflect the same neural system that generates the error-related negativity (see Chapter 10, this volume, and Yeung et al., 2004). It remains to be seen whether the anterior N2 effect observed for non-target popout features in visual search is actually the same component as the anterior N2 effect observed on conflict trials in the flanker and Stroop paradigms.

THE POSTERIOR N2 COMPONENT
At posterior electrode sites, the N2 wave is enlarged for target popouts compared to non-target popouts and homogeneous arrays. This is the same as the pattern observed for the anterior P2 component, which has a similar onset time at anterior sites. In addition, both of these effects become larger as the probability of the target decreases, and both are larger for color popouts than for orientation or size popouts (Luck & Hillyard, 1994a). It is therefore possible that they reflect the positive and negative sides of a single generator source.

The posterior N2 component can be divided into two subcomponents, one that is larger over the hemisphere contralateral to the side of the target item and one that is equivalent over the contralateral and ipsilateral hemispheres. The contralateral subcomponent is called N2pc (N2-posterior-contralateral) and the bilateral subcomponent is called N2pb (N2-posterior-bilateral). N2pb amplitude varies with target probability and is larger for color popouts, whereas N2pc amplitude is independent of probability and feature dimension (Luck & Hillyard, 1994a). Thus, only
the N2pb component is similar to the anterior P2 component. We will consider the N2pc component in more detail in the second half of this chapter.

The specific neurocognitive process reflected by the anterior P2 and N2pb components is not clear. N2pb may be the same as the component labeled N2 in studies using the oddball paradigm (labeled N2c in the classification scheme proposed by Pritchard et al., 1991). In these studies, task-relevant oddballs will elicit an enlarged N2 wave relative to the standard stimuli, followed by the prototypical P3b component. This pattern is observed for both auditory and visual oddballs, but the scalp distribution is more anterior for auditory stimuli than for visual stimuli (Simson et al., 1977). Renault et al. (1982) proposed that this component reflects the process of categorizing a stimulus, because the duration of the effect depends on the difficulty of the categorization. However, this manipulation also increased the onset time of the P3 wave, and because the N2 wave was cut off by the larger and opposite-polarity P3 wave, it is not clear that the duration of the underlying N2 wave was actually longer for the more difficult categorization task.

THE P3 COMPONENT
In the study shown in Figure 12.2, an enlarged P3 wave was observed for target popouts relative to non-target popouts and homogeneous arrays across the scalp (see Figure 12.2B). However, this P3 effect can be divided into two subcomponents. First, the prototypical P3b component (see Chapter 7, this volume) was present across the scalp with a centro-parietal maximum. This component was probability sensitive and was not present in a follow-up experiment in which target and non-target stimuli were equiprobable (Luck & Hillyard, 1994a, Experiment 2). Second, an occipitally maximal P3 effect was also present for target popouts, but it was present for popout targets even when targets and non-targets were equiprobable. The functional significance of this occipital P3 component is unknown.

THE P1 WAVE AND SENSORY CONFOUNDS
The paradigm shown in Figure 12.2A contains a small but important sensory confound, because the popout arrays are physically different from the homogeneous arrays. This confound has two consequences. First, sensory responses may be different to a popout item than to the surrounding items. Indeed, neurons in area V1 produce a larger response when the receptive field contains a popout item rather than a non-popout item, probably because lateral inhibition is stronger between items that share the same feature value (Knierim & Van Essen, 1992). Second, because most of the items in each array consist of a particular feature value (e.g., small, blue, vertical in the example shown in Figure 12.2A), the visual system will become adapted to these features after several stimulus arrays have been presented, reducing the magnitude of the visual response to these values. Each singleton feature is presented relatively infrequently, especially at a given location in the display, and the visual system will therefore not be as adapted to these feature values, leading to a larger response. For example, blue-selective neurons with receptive fields in the upper-right quadrant of the display will be stimulated on every trial in the task shown in Figure 12.2A, leading to a reduced response when blue is presented in this location. In contrast, green-selective neurons with receptive fields in the upper-right quadrant will be stimulated rarely, leading to a large sensory response when green is presented in this location. Consequently, the overall ERP elicited by a stimulus array should contain a larger sensory response when a popout item is present, and this should be especially evident over the hemisphere containing the neurons that are selective for the popout feature (i.e., the hemisphere contralateral to the popout item).

Because of these factors, any differences between the ERPs elicited by popout arrays and homogeneous arrays could reflect low-level differences in sensory processing rather than higher-level attention effects. Fortunately, all of the ERP effects described so far have been shown to disappear under specific task conditions, demonstrating that they are not simple sensory effects. However, Luck and Hillyard (1994a) also found that the P1 wave was slightly but consistently larger over the hemisphere contralateral to the popout item than over the ipsilateral hemisphere, and this effect was present across all task manipulations, suggesting that it was a sensory effect rather than an attentional effect (note that this effect cannot be seen in Figure 12.2B, which is collapsed across hemispheres). To test whether this P1 effect might reflect adaptation of the neurons coding for the non-popout items, Luck and Hillyard (1994a) conducted an experiment in which the stimulus arrays consisted of either a green popout item among blue distractor items or a blue popout item among green distractor items (randomly intermixed from trial to trial). This manipulation equated the level of adaptation of the blue- and green-selective neurons, and it eliminated the P1 effect, consistent with the hypothesis that the P1
effect was a consequence of sensory adaptation. Moreover, a sequential analysis demonstrated that the P1 was larger over the contralateral hemisphere than over the ipsilateral hemisphere for a given popout color when the preceding array consisted mostly of the other color (e.g., one green item and seven blue items on both trial N and trial N−1), but this effect was absent when the preceding array consisted mostly of the other color (e.g., one green item and seven blue items on trial N and one blue item and seven green items on trial N−1). Thus, this P1 effect does not appear to reflect the automatic allocation of attention to the popout item but instead reflects color-specific sensory adaptation.

This finding demonstrates the importance of using stimuli and experimental designs that control for bottom-up sensory effects (and especially adaptation effects, which can be quite strong). Even though the ERP consequences of the sensory confound in the experiments of Luck and Hillyard (1994a) were limited to the P1 latency range, sensory activity persists for hundreds of milliseconds in many cases, so sensory confounds could produce small effects well into the P2 and N2 latency ranges. It is often possible to design an experiment in a manner that eliminates sensory confounds of this nature (as described in the next section). When this is not possible, it is important to conduct control experiments showing that the effects can be eliminated by changes to the task (see, e.g., Hickey et al., 2009; Sawaki & Luck, submitted).

**Step 3: Focusing Covert Attention on a Peripheral Location (N2pc, SPCN, Pd, and Probe-Elicited Sensory Responses)**

Now that we have discussed how the target template is established and how it can be used to highlight objects containing relevant features, we will consider how attention is shifted to an object containing the relevant features. The ERP component most often used to study this focusing of attention in the context of multiple-object stimulus arrays is the N2pc component. In this section, we will briefly describe N2pc and related components, focusing on how they reflect the process of enhancing target processing and filtering distractors. A more detailed look at these components will be provided in the second half of this chapter.

A typical N2pc paradigm is shown in Figure 12.3 (from the study of Luck et al., 2006). Each stimulus array contains one red square, one green square, and a large number of black distractor squares. The locations of the individual squares vary at random from trial to trial, with the constraint that the two colored items are always on opposite sides of the display. At the beginning of each 5-min block of trials, the observer is instructed to attend either to red or to green. For each array, the observer must press one of two buttons to indicate whether the object drawn in the attended color contains a gap on the top or a gap on the bottom. To avoid spatial compatibility conflicts that arise when a subject must make a left-hand response for a right-side target or vice versa (known as the Simon effect), it is usually preferable to have subjects use two different fingers of the same hand to make the two different responses.

In the example shown in Figure 12.3, the subject would attend to an object in the left visual field (LVF) when red is the attended color and would attend to an object in the right visual field (RVF) when green is the attended color. This design therefore eliminates the sensory confounds described in the previous section.

The N2pc component consists of a greater negativity when the attended item is contralateral to the recording electrode than when the attended item is ipsilateral. It typically occurs during the time range of the N2 wave (200–300 ms) and is observed at posterior scalp sites over visual cortex, with a maximum voltage near the PO7 and PO8 electrodes. In Figure 12.3, the N2pc can be seen as a more negative voltage for RVF targets than for LVF targets over the left hemisphere and as a more negative voltage for LVF targets than for RVF targets over the right hemisphere. To minimize overall differences between LVF and RVF targets and between the left and right hemispheres, it is useful to create a contralateral waveform (average of BVP for the left hemisphere and LVF for the right hemisphere) and an ipsilateral waveform (average of LVP for the left hemisphere and RVF for the right hemisphere). The difference between these contralateral and ipsilateral waveforms is used to isolate the N2pc component from other overlapping ERP components. This is exactly analogous to the derivation of the lateralized readiness potential (LRP; see Chapter 9, this volume). Just as the LRP subtraction procedure guarantees that the brain must have begun to determine which response is associated with the stimulus when the LRP deviates from zero, the N2pc subtraction procedure guarantees that the brain must have begun to determine the location of the target when the N2pc deviates from zero. These two components therefore allow very strong conclusions to be drawn about the timing of neural events (for a detailed discussion, see Luck, 2005, chap. 2).
As will be discussed in detail later in this chapter, the N2pc component appears to reflect the focusing of attention on a potential target item and the filtering of the surrounding distractor items. Thus, one can use the N2pc component to track the time course of the focusing of attention (see, e.g., Kiss et al., 2009; Lorenzo-López et al., 2008; Woodman & Luck, 1999, 2003). For example, if the N2pc onsets at 180 ms, one can conclude that attention has been focused on the target by 180 ms (although note that the onset time in an averaged waveform reflects the trials with the earliest onset times, not the average onset time; see Luck, 2005, pp. 56–57). Of course, attention may have shifted at an earlier time within other brain systems that do not produce an ERP signature on the scalp. The N2pc component appears to be generated at intermediate and late stages of the ventral visual processing pathway, and single-unit studies suggest that shifts of attention in visual search are typically initiated in prefrontal cortex, the frontal eye fields, and posterior parietal cortex, followed at a later time by focusing within the ventral stream (Buschman & Miller, 2007). Indeed, a simultaneous ERP/single-unit study in monkeys found that selective processing occurred in the frontal eye fields prior to N2pc onset (Cohen et al., 2009). Thus, the N2pc component does not reflect the earliest time at which attention becomes focused on a potential target item, although it may reflect the earliest time at which attention becomes focused within the ventral stream.

Does the focusing of attention on a potential target item in visual search cause an increase in sensory transmission at the location of the target? This question was addressed in the paradigm shown in Figure 12.4A (from Luck et al., 1993). Subjects performed a visual search task in which each array contained a red T on one side and a green T on the
other side (the sides were randomized from trial to trial). In some trial blocks subjects attended to the red $T$, and in other blocks they attended to the green $T$. The task was to press one of two buttons to indicate whether the attended item was an upright or inverted $T$. When a probe stimulus appeared, it could appear around either the red item or the green item.

As shown in Figure 12.4b, an N2pc component was observed contralateral to the attended $T$ beginning approximately 200 ms after the onset of the array. On a subset of trials, a bright white "probe" square was presented around either the red $T$ or the green $T$, onsetting 250 ms after the onset of the visual search array. The purpose of the probe square was to assess the processing of information at the probed location at the time of the probe. If sensory transmission is enhanced at the location of the attended $T$, then the sensory processing of the probe should be enhanced when it is presented at the location of the attended $T$ compared to when it is presented at the location of the unattended $T$. Indeed, as shown in Figure 12.4c, the P1 and N1 waves elicited by the probe stimulus were larger when the probe was presented at the location of the attended $T$ compared to when the probe was presented at the location of the unattended $T$.

Follow-up experiments showed that these P1 and N1 effects are very much like those observed in spatial cuing studies. When neutral trials are used to provide a baseline in cuing studies, the P1 is found to be suppressed on invalid trials compared to neutral trials, with no enhancement on valid trials, whereas the N1 is found to be enlarged on valid
trials compared to neutral trials, with no suppression on invalid trials (see Luck et al., 1994, and Chapter 11, this volume). A similar pattern is found in visual search tasks when neutral trials are created by presenting arrays that do not contain the attended color (Luck & Hillyard, 1995). That is, the probe-elicited P1 is suppressed when the probe is presented at a location on the opposite side of the display from the attended item compared to when the attended item is absent, with no enhancement at the location of the attended item, whereas the N1 is enhanced when the probe is presented at the location of the attended item but is not suppressed (relative to the neutral trials) when the probe is presented on the opposite side of the display from the attended item. Moreover, the probe P1 effect is eliminated when the task simply involves detecting the attended color rather than discriminating the form of the object presented in this color. Thus, focusing attention on the location of an object in a visual search array leads to the same pattern of changes in sensory processing that occurs when attention is explicitly cued to a location in space.

Step 4: Shifting Overt Attention to the Attended Peripheral Object (Presaccadic Positivity and Spike Potential)

In natural vision, an individual will almost always fixate an important object that is being discriminated because this brings the object into the high-resolution foveal region of the retina. Thus, shifts of covert attention to the periphery do not usually serve the purpose of directly discriminating the identity of the attended object, but instead facilitate shifts of gaze (overt attention) to the object (for a detailed discussion, see Luck, 2009). For example, shifts of covert attention can be used to determine whether a peripheral object is likely to be a target and therefore worth fixating, and they may allow the location of the object to be determined more precisely so that a more accurate eye movement to this object can be programmed. Indeed, the N2pc component is larger when an object must be localized or fixated than when it must merely be detected (Hyn et al., 2009a; Luck et al., 1997b).

Only a few studies have examined the ERPs associated with saccadic eye movements, and these studies have identified several consistent components. First, there is a slow frontal negativity far in advance of the eye movement, which appears to be analogous to the contingent negative variation (see Chapter 8, this volume) and reflects preparation for the saccade-eliciting stimulus. This is followed by a parietally maximal component called the presaccadic positivity that onsets approximately 150 ms prior to the eye movement. Richards (2003) proposed that this component reflects the planning of the saccade. A sharp spike potential is then observed beginning approximately 20 ms prior to the saccade and peaking at saccade onset; this potential is negative at the frontal pole and positive at posterior scalp sites, and it is thought to reflect the motor activity associated with executing the saccade. Although behavioral studies suggest that shifts of gaze are necessarily preceded by shifts of covert attention (Deubel & Schneider, 1996; Hoffman & Subramaniam, 1995), no ERP component has been identified that reflects this specific shift of covert attention. This may reflect the fact that the eye movement studies have generally used tasks involving a single highly salient target stimulus, with no competition from simultaneous distractors. As described below, the N2pc component appears to depend on the presence of this kind of competition.

Step 5: Expanding or Contracting Attention Around the Fixated Object

Once the eyes have been directed to the desired object, attention presumably plays an important role in contracting or expanding around this object to minimize distraction from other surrounding objects. In the image shown in Figure 12.1, for example, an observer may wish to see the details of the sliced orange near the right edge of the image. Once the eyes have fixated this orange, attention may need to filter out the surrounding fruits and nuts to prevent the features of those other objects from interfering with the perception of the orange. The retinal size of an object will depend on both the object’s actual size and its distance, and so the size of the attentional window surrounding the object will typically be adjusted on the basis of the incoming sensory information rather than being set in advance.

Although substantial behavioral research has examined variations in the size of the attended region in the periphery (e.g., Eriksen & St. James, 1986; Eriksen & Yeh, 1985), relatively little behavioral research—and almost no ERP research—has examined the expansion and contraction of attention around the fixated object. This is a ripe area for future research.

A Closer Look at N2pc and Related Components

Now that we have considered the ERP components associated with various processes involved with the
perception of multiple-element scenes, we will take a closer look at the N2pc component and other lateralized components that reflect the focusing of attention on individual objects.

**Discovery of the N2pc Component**

The N2pc component was first observed in the two tasks shown in Figure 12.5 (Luck & Hillyard, 1990). In the *parallel search task*, the target was an arrow and the distractors were triangles. In this task, the horizontal line that forms the shaft of the arrow pops out from the display, and observers can detect the target rapidly and effortlessly without scanning through the array. In the *serial search task*, the triangle was the target and the arrows were distractors. In this task, the target does not contain a distinctive feature that is absent from the distractors, and observers must perform a slow and effortful search through the array to find the target (for an extensive discussion of this pattern of results, see Treisman & Gormican, 1988; Treisman & Souther, 1985).

In both of these conditions, the N2pc component can be seen as a more negative voltage when the target is contralateral to the electrode site relative to when it is ipsilateral. When the target popped out, this component was present from approximately 200–300 ms. When the target required a serial search, however, the N2pc was visible from 200 ms through the end of the recording epoch. This broad N2pc likely reflects the fact that the amount of time required to find the target is highly variable under serial search conditions, and the onset time of the N2pc component presumably varied widely from trial to trial in this condition, yielding a broad component when the data were averaged across trials (for similar results, see Wolber & Wascher, 2003). That is, even if the N2pc has a short duration on each individual trial, it will appear to have a long duration when trials with different N2pc onset times are averaged together. For this reason, most N2pc studies use targets that can be found in a short and consistent amount of time, as in the experiments shown in Figures 12.2 and 12.3.

**Defining the N2pc Component as a Contralateral-Minus-Ipsilateral Difference**

As discussed earlier in this chapter, the N2pc component is defined as the difference in amplitude between the contralateral and ipsilateral waveforms. Indeed, researchers sometimes construct contralateral-minus-ipsilateral difference waves to visualize the N2pc without distortions from overlapping components. This is shown in the right panel of Figure 12.3. Contralateral-minus-ipsilateral difference waves are particularly useful when one wishes to compare the time course of the N2pc

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**Fig. 12.5.** Stimuli and grand average ERP waveforms from the study in which the N2pc component was first observed (Luck & Hillyard, 1990). In the parallel search condition, the arrow was the target and the triangles were the distractors; in the serial search condition, the triangle was the target and the arrows were the distractors. Subjects pressed one of two buttons for each array to indicate whether the target was present \((p = .5)\) or absent \((p = .5)\). The ERPs shown here were recorded from posterior temporal electrode sites (T5 and T6) and were averaged across arrays containing 4, 8, or 12 items. An N2pc component can be observed in both conditions as a difference between the contralateral and ipsilateral waveforms beginning at approximately 225 ms poststimulus, but the N2pc lasted much longer in the serial search condition than in the parallel search condition.
across different conditions. For example, Figure 12.6 shows the data from the experiment shown in Figure 12.3, but separated as a function of whether subjects attended to the red popout or the green popout. The red popouts were more salient than the green popouts in this experiment, which led to an earlier N2pc onset latency when the red item was attended than when the green item was attended. Although it is possible to see this when the contralateral and ipsilateral waveforms are overlaid (Figures 12.6A and 12.6B), it is much easier to see this latency difference when the contralateral-minus-ipsilateral difference waves for the red and green targets are overlaid (Figure 12.6C). Moreover, it would be very difficult to accurately measure the onset latency of the N2pc component without first constructing contralateral-minus-ipsilateral difference waves. That is, to measure the time at which the contralateral and ipsilateral waveforms diverged from each other, one cannot legitimately measure the onset latencies in the contralateral and ipsilateral waveforms separately. Note, however, that mean amplitude over a given time range does not need to be measured from the difference waves; because mean amplitude is a linear measure, the same results will be obtained whether you first make a difference wave and then measure mean amplitude or whether you first measure the mean amplitude from the contralateral and ipsilateral waveforms and then compute the difference between these measures (for a detailed discussion of linear versus nonlinear ERP measures, see Luck, 2005, pp. 232–235).

Because the N2pc component is defined as the difference between the contralateral and ipsilateral

Fig. 12.6. Grand average ERP waveforms from a study using the stimuli shown in Figure 12.3 (Luck et al., 2006), showing the contralateral and ipsilateral waveforms for red targets (A) and green targets (B), along with the contralateral-minus-ipsilateral difference waveforms for the red and green targets (C). This study examined the N2pc component in schizophrenic patients and healthy control subjects, and the data from the control subjects are shown here. Note that the red color was more salient than the green color, leading to faster reaction times and earlier N2pc onset and peak latencies.
waveforms, overlapping activity from other components does not distort the N2pc component. For example, an experimental manipulation that increases the amplitude of the P3 wave in one condition relative to another condition will influence the amplitude measured in the P2 and N2 waveforms, but it will not influence the difference in amplitude between the contralateral and ipsilateral electrode sites (assuming that the P3 wave is not lateralized with respect to the position of the attended item, which it is not). This is enormously important, because overlap among different components often makes ERP experiments difficult to interpret (for more discussion, see Chapter 1, this volume). As discussed earlier in this chapter, the LRP is also isolated by means of a contralateral-minus-ipsilateral difference wave, and both N2pc and LRP are therefore easier to isolate than most other ERP components.

However, it is worth considering in more detail the logic behind using this sort of difference to define and measure an ERP component. If a component is generated exclusively in the contralateral hemisphere, then the amplitude of the contralateral-minus-ipsilateral difference will be linearly proportional to the magnitude of the underlying generator source. This is true even if some voltage is conducted to the ipsilateral hemisphere. Imagine, for example, that \( X \) is the magnitude of the underlying generator source, 10\% of \( X \) is the voltage measured over the contralateral hemisphere, and 3\% of \( X \) is the voltage measured over the ipsilateral hemisphere. In this case, the amplitude of the contralateral-minus-ipsilateral difference wave will be 7\% of \( X \) (because 10\% - 3\% = 7\%). If we manipulate some factor that causes the magnitude of the generator to double (making it now \( 2X \)), these percentages will still be true (because voltages propagate linearly through a conductor), and the new amplitude of the difference wave will be 7\% of \( 2X \). That is, the voltage measured from the difference wave will double if the magnitude of the underlying generator source doubles.

What if the component is generated by sources in both hemispheres but is simply stronger in the contralateral hemisphere than in the ipsilateral hemisphere? If a given experimental effect produces a proportional change in the magnitudes of the contralateral and ipsilateral generator sources, then the amplitude measured from the contralateral-minus-ipsilateral difference wave will also be proportional to the change in the magnitudes of the internal generator sources. (The algebra is analogous to that described in the preceding paragraph.) Thus, measuring the amplitude of the difference between the contralateral and ipsilateral sites is a very reasonable way to assess the magnitude of the underlying generator sources.

However, there are at least three limitations on this approach. First, the difference between contralateral and ipsilateral activity will necessarily approach zero for electrode sites near the midline. Thus, one must be careful when using contralateral-minus-ipsilateral differences to assess the scalp distribution of the N2pc or LRP. Second, although this difference-based approach eliminates the contributions of most overlapping components, it will not eliminate overlap from other components that are lateralized with respect to the target (for the N2pc) or to the response (for the LRP). As discussed later in this chapter, several distinct components have now been identified that are lateralized with respect to the target, and these may distort measurements of N2pc amplitude or latency. Finally, any factor that changes the proportional difference between generators in the contralateral and ipsilateral hemispheres will be difficult to assess by measuring the difference between the contralateral and ipsilateral hemispheres. For example, a manipulation that caused an increase in the amplitude of the N2pc in the ipsilateral hemisphere but not in the contralateral hemisphere would lead to a decrease in the contralateral-minus-ipsilateral difference. Similarly, a manipulation that caused an increase in the activation of the incorrect response hand in an LRP study would lead to a decrease in the apparent LRP amplitude. Thus, although measuring N2pc and LRP amplitude as the difference in amplitude between the contralateral and ipsilateral waveforms has many advantages, one must think carefully when using this approach.

The N2pc component is typically superimposed on a large positive voltage produced by the P2 wave, and the waveform for both contralateral and ipsilateral targets is therefore on the positive side of the baseline in the N2pc latency range (see Figures 12.3–12.5). How, then, do we know that the N2pc is actually a negative-going component over the contralateral hemisphere rather than a positive-going component over the ipsilateral hemisphere? Defining N2pc amplitude as contralateral-minus-ipsilateral implicitly assumes that the N2pc is larger over the contralateral hemisphere, because it subtracts out the (supposedly) lesser amplitude recorded over the ipsilateral hemisphere. As we shall see later in this chapter, the N2pc may actually consist of the combination of a contralateral negativity and an ipsilateral positivity. However, the contralateral
negativity appears to be the dominant subcomponent under most conditions.

In addition, if an experiment includes trials on which no target is present, the N2pc appears to consist primarily of an increased negativity over the contralateral hemisphere in the target waveforms compared to the no-target waveforms. For example, Figure 12.7A shows that the target-elicited N2pc consists mostly of an increased negativity for contralateral popouts rather than an increased positivity for ipsilateral popouts relative to arrays in which no popout was present (homogeneous arrays). Moreover, when the waveforms elicited by nontarget popouts are subtracted from the waveforms elicited by target popouts, the overlapping P2 component is largely subtracted away. In these difference waves, the N2pc clearly consists of a negativity contralateral to the target, with little or no voltage observed over the contralateral hemisphere (see Figures 12.14A and 12.15A, which will be discussed in detail later in this chapter). Together, these findings suggest that the N2pc component consists primarily of a negative potential over the hemisphere contralateral to the target.

When the waveforms from the left and right hemispheres are collapsed into contralateral and ipsilateral waveforms, we lose the ability to see any differences between the left and right hemispheres. It is possible, instead, to overlay the waveforms from the left and right hemispheres for targets on a particular side and see the differences between the two hemispheres. However, any overlapping components that differ in overall amplitude across the two hemispheres, irrespective of target location, will influence the difference in voltage between the left and right hemispheres, making this comparison difficult to interpret. For example, in the waveforms shown in Figure 12.3, the voltage at 300 ms is more positive over the right hemisphere than over the left hemisphere, irrespective of the position of the target. This difference between hemispheres probably reflects other components that overlap with N2pc.

A better approach is to overlay the waveforms elicited by LVF and RVF targets for a given hemisphere and ask whether the difference between these waveforms is bigger for the left hemisphere or the right hemisphere. In Figure 12.3, for example, the difference between LVF and RVF targets is somewhat larger over the left hemisphere than over the right hemisphere. This might suggest that attention operated more strongly in the left hemisphere than in the right hemisphere in that experiment. However, any differences in neural activity between LVF and RVF targets that are present in both hemispheres will distort this comparison (see Figure 9.1 in Chapter 9, this volume, for a discussion of the same set of issues in the context of the LRP). For example, if LVF targets elicited a larger P2 wave than RVF targets over both hemispheres in the experiment shown in Figure 12.3, this would increase the contralateral-minus-ipsilateral difference over the left hemisphere and decrease this difference over the right hemisphere. Thus, differences across the left and right hemispheres in the degree of lateralization cannot be unambiguously interpreted as differences in N2pc amplitude between the hemispheres.

As a result, most researchers collapse the two hemispheres into contralateral and ipsilateral waveforms to isolate the N2pc, and separate waveforms for the left and right hemispheres are not usually shown in publications. An interesting exception is that Eimer (1996) reported that the N2pc was present over both hemispheres for color and form targets but was present only over the left hemisphere for word targets (see also Dell’Acqua et al., 2007). This may reflect an important difference between the hemispheres in the role of attention for
linguistic stimuli. However, it is possible that the apparent hemispheric asymmetry in the N2pc for words reflects an overall difference in some other component between word targets presented in the left and right hemispheres rather than a true asymmetry in the N2pc component. Other methods (e.g., current source density transformations) would be necessary to distinguish between these alternatives.

**Sensitivity of N2pc to Basic Parameters**

The N2pc component is typically observed for target stimuli but is absent or considerably smaller for nontarget stimuli. For example, Figure 12.7 shows the contralateral and ipsilateral waveforms for target and nontarget popouts in the experiment shown in Figure 12.2A. A substantial difference was observed between the contralateral and ipsilateral waveforms for the target popout stimuli, but this difference was much smaller for the nontarget popout stimuli. In fact, the orientation and size popouts produced no difference at all between contralateral and ipsilateral electrodes when they were nontargets. The small difference shown in Figure 12.7 was entirely due to the color popouts, which were highly salient. However, as we shall see in the next section, nontarget stimuli will elicit an N2pc if they are so similar to the target that focused attention is needed to determine whether the stimulus is a target or nontarget.

Unlike the anterior P2, posterior bilateral N2, and P3b components shown in Figure 12.2, the N2pc component is largely insensitive to the probability of the eliciting stimulus. An example is shown in Figure 12.8, which used the same stimuli shown in Figure 12.2 but varied the probability of the target popout stimulus (17% in one condition and 50% in another). The P3b component was substantially larger when the target was 17% probable than when it was 50% probable, whereas the N2pc component was equally large in these two conditions (see especially the contralateral-minus-ipsilateral difference waves).

The N2pc can be elicited by many types of lateralized visual targets. It has been observed in response to targets defined by color, orientation, size, motion, various types of shape, letter identity, word identity, Kanizsa figures, biological motion, facial expression, and direction of eye gaze (see, e.g., Conci et al., 2006; Doi et al., 2009; Eimer, 1996; Fenker et al., 2009; Girelli & Luck, 1997; Hirai & Hiraki, 2006; Holmes et al., 2009; Kiss et al., 2008; Luck & Hillyard, 1990, 1994a; Woodman & Luck, 1999). It has even been observed when subjects search stimuli stored in visual working memory rather than visible stimuli (Busch et al., 2009; Dell’Acqua et al., 2010), and it has also been observed when the target is defined by a difference between a stimulus array and a visual working memory representation of a previously presented array (Eimer & Mazza, 2005; Hyun et al., 2009b; Schankin & Wascher, 2008). No obvious differences in scalp distribution have been observed for these different target types, although it is possible that subtle differences exist.

Given that the N2pc component—defined as the contralateral-minus-ipsilateral difference—cannot begin until the brain has determined the location of the target stimulus, N2pc onset would be expected to depend on the salience of the target. Evidence for this has been observed in several experiments in which different types of popout stimuli were compared and both N2pc onset latency and reaction
time were earlier for some popout stimuli than others (e.g., Girelli & Luck, 1997; Luck & Hillyard, 1994a; Luck et al., 2006). An example of this was described earlier in the context of Figure 12.6, which shows that the N2pc was earlier for the more salient red targets than for the less salient green targets. Both target discrimination reaction time and N2pc onset latency were 40–50 ms faster when the red item was the target than when the green item was the target.

**Sequence of Lateralized Components**

Figure 12.8 shows a commonly observed pattern in which the contralateral waveform is more negative than the ipsilateral waveform initially (from approximately 175 to 300 ms), then becomes more positive for approximately 100 ms, and then becomes more negative again for an extended period of time (this is more evident for the infrequent condition than for the frequent condition). The middle phase does not always cross over to become positive; instead, the initial contralateral negativity may fade to a near-zero value during this period and then become large again in the late period (see, e.g., Figure 12.4B, the parallel search waveforms in Figure 12.5, and Figure 12.7A). However, sometimes the waveform remains negative from the onset of the N2pc until the end of the averaging epoch (see, e.g., Figure 12.6). This middle positive phase has not been extensively studied. One study found that the middle phase was more laterally distributed than the initial phase and was enlarged when the distance between the target and a salient distractor was decreased (Hilimire et al., 2009), suggesting that it reflects competition must be resolved. In a somewhat different paradigm, Luck et al. (1997b) found that the initial negative phase rather than the middle positive phase was increased when a distractor was placed next to the target. However, it is possible that the initial phase continued into the time range of the middle phase and the increased amplitude of the negative first phase canceled out the increased positivity of the second phase. This sort of overlap problem may make it difficult to determine the psychological correlates of the second phase.

Jolicoeur and his colleagues have called the late negative phase the *sustained posterior contralateral negativity* (SPCN), and they have proposed that it reflects continued processing of the attended item. For example, SPCN amplitude is increased when the difficulty of the discrimination is increased (Mazza et al., 2007; Prime & Jolicoeur, 2009). Jolicoeur and his colleagues have further proposed that it may be the same as the contralateral delay activity (CDA) observed during the delay period of visual working memory experiments (see Chapter 13, this volume). Perron et al. (2009) found that the N2pc and the SPCN/CDA have similar scalp distributions and that both are larger for lower-field than for upper-field stimuli, consistent with a shared neural generator source. However, McCullough and colleagues (2007) found that the SPCN/CDA had a more parietal focus than the N2pc, suggesting different generator sources for these two components. A magnetoencephalographic study also found that the SPCN/CDA was localized to posterior parietal cortex, which differs from the predominantly occipitotemporal source of the N2pc (Robitaille et al., 2009). Neuroimaging studies have shown that both parietal and occipitotemporal areas exhibit sustained activity during working memory maintenance (Xu & Chun, 2006), and it is therefore possible that the voltage over the broad SPCN/CDA period reflects a combination of activity in the N2pc generator and in other areas.

The N2pc, which is largest over lateral occipitotemporal electrode sites (e.g., PO7 and PO8), is sometimes accompanied by a component with the same time course over central electrode sites (e.g., C3 and C4). This more central component has been labeled N2cc (N2-central-contralateral) by Praamstra and his colleagues (Oostenveld et al., 2003; Praamstra, 2006, 2007; Praamstra & Oostenveld, 2003; Praamstra & Plat, 2001). N2pc and N2cc have overlapping scalp distributions, but it is possible to measure them separately by transforming voltage into current source density, which has a more narrowly focused scalp distribution. As discussed by Praamstra (2006), several sources of evidence indicate that N2cc is not merely volume-conducted voltage from the N2pc generator, but instead reflects a separate source (probably in motor or premotor cortex). N2cc is particularly prominent under conditions in which subjects are instructed to make either a left-hand or right-hand response, depending on the identity of the target presented on a given trial (e.g., left for an upright red T and right for an inverted red T, as in Figure 12.4), leading to the potential for Simon interference when the target appears on one side of the display but its identity indicates that the opposite hand should be used for the response. Praamstra (2006) has suggested that the appearance of a target on one side of the display leads to an automatic preparation of the ipsilateral hand, and that the N2cc reflects the suppression of this preparation so that the response can be made...
Neural Generators of the N2pc Component
Evidence for the neural generator of the N2pc component has come from studies using combined ERP and ERMF (event-related magnetic field) recordings and from studies establishing homologies between the N2pc and single-unit attention effects observed in monkeys. The first ERP/ERMF study of the N2pc used a paradigm much like that shown in Figure 12.3, except that the items were rectangles and the subjects were required to indicate whether the rectangle of the attended color was horizontal or vertical. Figures 12.9A and 12.9B show the observed topography of the electrical N2pc and its magnetic analog, the M2pc, as isolated by means of LVF-target minus RVF-target difference waves (it is not appropriate to perform source localization on contralateral-minus-ipsilateral difference waves because this would artificially cause the voltage to approach zero for electrodes near the midline). The ERP difference waves were positive over the left posterior scalp and negative over the right posterior scalp. The negative voltage over the right hemisphere reflects the negative voltage of the N2pc for the LVF target, and the positive voltage over the left hemisphere reflects the subtraction of the negative voltage for the RVF target. The ERMF maps do not show opposite patterns over the left and right hemispheres, but this is exactly what would be expected from a LVF-minus-RVF ERMF difference wave. A dipole in the right hemisphere pointing downward would produce both a negative voltage over the right hemisphere (corresponding to the N2pc elicited by a LVF target) and a magnetic field that leaves the head medially (denoted by red) and returns into the head laterally (denoted by blue). A dipole in the left hemisphere pointing the opposite direction (because the RVF-target waveforms are subtracted to construct this difference wave) would produce both a positive voltage over the left hemisphere and a magnetic field that leaves the head medially (denoted by red) and returns into the head laterally (denoted by blue). Thus, even though the left-hemisphere and right-hemisphere dipoles point in opposite directions, producing opposite polarity voltages, they produce mirror-image magnetic fields.

Structural magnetic resonance imaging (MRI) data were obtained for each subject, and the minimum norm approach was used to estimate the distribution of current over the cortical surface corresponding to the left-minus-right target difference waves. This source localization approach was applied to the data from each subject individually (with 2400 trials per subject to obtain an adequate signal-to-noise ratio), and it was also applied to the grand average data (using the MRI data from a single subject to constrain the localization). The localization results from the grand average are shown in Figure 12.9C (similar, albeit noisier, results were obtained for the individual subjects). The estimated current distribution was focused over lateral occipitotemporal cortex, consistent with a set of generators in intermediate and/or high levels of the ventral visual processing pathway.

Fig. 12.9. Event-related potential and ERMF data from the study of Hopf et al. (2000). (A) Voltage distribution of the N2pc waveform, defined as the difference between trials with a target in the left and right visual fields. (B) Magnetic field distribution for the magnetic analog of the N2pc component, again defined as the difference between trials with a target in the LVF and RVF. (C) Estimated distribution of current density on the cortical surface for the combined electrical and magnetic data.
This study also found evidence for a parietal source during the initial portion of the N2pc (180–200 ms), which could reflect an attentional control signal that is then implemented in lateral occipitotemporal cortex during the main time period of the N2pc. However, follow-up studies have not replicated this parietal source (Hopf et al., 2004, 2006). A transcranial magnetic stimulation (TMS) study found that a TMS pulse over the right posterior parietal cortex 100 ms after stimulus onset, which presumably caused a temporary disruption of processing in that area, led to a delay in the onset of the N2pc (Fuggetta et al., 2006). This could reflect a disruption of the early parietal subcomponent, but it more likely reflects a disruption of parietal control circuitry that must be engaged for the N2pc to be elicited within ventral visual areas.

More precise localization of the N2pc was provided by a study that used a combination of ERPs, ERMFs, structural MRI, and functional MRI (fMRI; Hopf et al., 2006). This study tested the hypothesis that the locus of selection within the visual system depends on the locus of competition between the attended and unattended items. Recordings from monkeys have indicated that attention has much stronger effects on single-unit activity when both a target and a distractor are simultaneously present within the receptive field of the neuron being recorded (Luck et al., 1997a; Moran & Desimone, 1985; Reynolds et al., 1999), presumably because a neuron’s firing rate becomes an ambiguous index of stimulus features when multiple objects are present inside the neuron’s receptive field (Luck et al., 1997b). Because receptive field sizes are small at early stages of the ventral processing stream and become very large at late stages, neurons at late stages will have multiple objects inside the receptive field whenever the display contains multiple objects, whereas neurons at early stages will have multiple objects inside the receptive field only when the objects are very close to each other. Hopf et al. (2006) found that the estimated generator of the N2pc component also varied according to the spatial scale of the display. As illustrated in Figure 12.10, the N2pc was generated primarily in a late anterior region of the ventral stream when the display contained large-scale competition, whereas a more posterior intermediate region also contributed to the N2pc when the display contained small-scale competition. These estimated source locations were confirmed by fMRI data, which showed the same pattern and made it possible to identify the specific posterior and anterior regions (area V4 and the lateral occipital complex, respectively).

Converging evidence for sources in area V4 and the lateral occipital complex comes from homologies between the N2pc and monkey single-unit attention effects observed in visual search tasks in area V4 and in inferotemporal cortex (Chelazzi et al., 1993, 1998, 2001). As shown in Figure 12.11, neurons in these areas initially responded in an attention-independent manner. However, beginning

![Fig. 12.10. Estimated distribution of current density on the cortical surface for the N2pc/M2pc component under conditions of large- or small-scale competition between the target and the distractors (Hopf et al., 2006). Under conditions of large-scale competition, the N2pc/M2pc was confined to the lateral occipital complex (the likely human homologue of macaque inferotemporal cortex). Under conditions of small-scale competition, the N2pc/M2pc was also present in area V4. The identity of these areas was verified using fMRI-based visual field mapping.](Image)
approximately 175 ms after stimulus onset, the neurons began firing differentially, depending on whether the target stimulus or a simultaneous distractor stimulus matched the neuron’s stimulus preferences. The onset latency of this effect is similar to the onset latency of the human N2pc component. Moreover, several experimental manipulations have been shown to have analogous effects on the monkey single-unit attention effect and the N2pc component (Luck et al., 1997b). First, the single-unit effects are larger when the target is a complex image rather than a simple color patch, and the N2pc is also larger for complex multifeature targets than for simple single-feature targets. Second, the single-unit effects are larger when both the target and distractor items fall within the receptive field of the neuron being recorded, and the N2pc is larger when a distractor is located close to the target. Third, the single-unit effects for simple color targets are larger when the monkey is required to make an eye movement to the target rather than to make a simple manual detection response, and the N2pc component is also larger when an eye movement is required. These analogous effects of experimental manipulations across species and recording techniques are consistent with the hypothesis that the N2pc component arises from area V4 and the lateral occipital complex (which is the human homologue of monkey inferotemporal cortex).

**N2pc in Special Populations**

Most N2pc studies have examined the effects of within-subjects manipulations in healthy young adults. However, a few have examined the N2pc across different populations. N2pc amplitude is reduced and N2pc onset and peak latency are increased in older individuals (Lorenzo-Lopez et al., 2008), which is important to keep in mind when groups being compared may differ in age along with some other factor. N2pc onset and peak latency are also delayed in patients with hepatic encephalopathy, a neurodegenerative disorder that is a consequence of liver failure (Schiff et al., 2006). In contrast, no change in N2pc amplitude or latency has been observed in patients with schizophrenia (Luck et al., 2006) or Parkinson’s disease (Praamstra & Plat, 2001) or in athletes with a history of multiple concussions (De Beaumont et al., 2007).

**What Cognitive Process Is Indexed by N2pc?**

The N2pc component is clearly related to attention, because the presence of an N2pc component for a given item depends on the task relevance of that item. However, attention is a broad umbrella term that includes many different types of processes (for reviews, see Luck & Gold, 2008; Luck & Vecera, 2002). Thus, it is important to provide a more specific description of the process reflected by N2pc.

**THE FILTERING HYPOTHESIS**

Luck and Hillyard (1994b) proposed that the N2pc component reflects a filtering process that is used to suppress the processing of distractor items surrounding a given object to reduce interference in the identification of the object of interest. This hypothesis was inspired by single-unit studies in monkeys showing that the effects of attention are much greater when a given neuron’s receptive field contains both a to-be-discriminated target object and distractor objects (Luck et al., 1997b; Moran & Desimone, 1985; Reynolds et al., 1999; Treue & Maunsell, 1996). When multiple objects are present inside a neuron’s receptive field, the neuron’s firing rate no longer reflects the features present in a single object, which can lead to ambiguities in neural coding. If, for example, a red triangle and a blue circle are both present in the receptive field of a red-selective neuron, the neuron will fire at a high rate to indicate the presence of the color red, but it will not be clear whether the color red is present in the triangle or in the circle. Thus, attention may be used to focus a given neuron on the features of a single object, inhibiting inputs to the neuron from other
objects (for an extensive discussion, see Luck et al., 1997b). As described in the influential biased competition model of attention (Desimone & Duncan, 1995), this may be implemented via inhibitory connections between objects: When top-down attentional control signals give a task-relevant object a competitive advantage over the distractor objects, the task-relevant object can inhibit the distractor objects more effectively than the distractor objects can inhibit the task-relevant object. Over a period of tens of milliseconds, these inhibitory interactions lead to a progressive increase in the competitive advantage of the task-relevant object and further inhibition of the distractors. Luck and Hillyard (1994b) proposed that the N2pc component reflects the inhibitory component of this overall scenario.

To test a hypothesis about the relationship between an ERP component and a specific psychological or physiological process, it is necessary to make predictions about how the component will vary as the hypothesized process varies across a range of experimental conditions. However, we rarely know enough about the hypothesized process to make strong predictions about how the ERP component should vary over experimental conditions. Indeed, the reason we wish to establish the link between an ERP component and a psychological or physiological process is that we do not understand the process very well and wish to use ERPs to study it. This leads to a chicken-and-egg problem: we cannot establish the relationship between the ERP component and the internal process unless we know enough about the process to manipulate it and test the effects on the ERP component; however, we need to know the relationship between the ERP component and the internal process to get to the point where we know enough about the process to manipulate it.

Studies of the N2pc component face this problem, because little is known about the filtering process that N2pc is hypothesized to reflect. To address this problem, Luck and Hillyard (1994b) performed a series of experiments in which they used extremely simple and obvious manipulations that must almost certainly influence filtering, even if we do not yet know the details of how the filtering process works. For example, there can be no filtering if there are no distractors to filter, so one experiment tested whether the N2pc was eliminated when the distractors were eliminated. However, even these simple manipulations have been the subject of dispute among researchers, and the relationship between the N2pc component and filtering remains controversial.

The remainder of this chapter will discuss the evidence in favor of the filtering hypothesis, the evidence against this hypothesis, and a variant of the filtering hypothesis that can explain all of the existing evidence.

**EVIDENCE SUPPORTING THE FILTERING HYPOTHESIS**

The first experiment reported by Luck and Hillyard (1994b) tested the more general hypothesis that the N2pc component is related to attention. More specifically, this experiment asked whether the N2pc is observed when a given item must be scrutinized by attention for the observer to determine whether it is the target, but not when the item can be rejected preattentively on the basis of salient features. As illustrated in Figure 12.12, each array could contain a color popout item or an orientation popout item, and each popout item could be either large or small. At the beginning of each trial block, one of the four possible popout stimuli (large color popout, small color popout, large orientation popout, or small orientation popout) was designated the target for that block. The observers were instructed to press one button if the target was present and another button if it was absent.

The color and orientation differences were highly salient, but the size differences were subtle. No matter which popout was the target for a given trial block, one of the nontarget popouts was difficult to discriminate from the target (difficult nontarget) and two of the nontarget popouts were easy to discriminate from the target (easy nontarget). For example, when the small orientation popout was the target, the large orientation popout was the difficult nontarget and the small and large color popouts were the easy nontargets. If the N2pc component reflects the allocation of attention to a given item for the purpose of determining whether it is the target, then it should be present for both targets and difficult nontargets (because it is difficult to know whether these items are targets without focusing attention on them). This is exactly the pattern of results that was obtained: the N2pc was nearly identical for targets and difficult nontargets, but no significant N2pc was observed for easy nontargets.

A second experiment tested the filtering hypothesis by changing the task so that filtering would be unnecessary or even counterproductive. As illustrated in Figure 12.13, the nontargets were either
homogeneous arrays of vertical bars or homogeneous arrays of horizontal bars, and the targets were either arrays containing a vertical bar among horizontal bars or a horizontal bar among vertical bars. These different array types were randomly intermixed, so the subjects did not know in advance whether they were looking for a horizontal bar among vertical distractors or a vertical bar among horizontal distractors. Thus, the task required subjects to determine if one bar differed from the surrounding bars rather than identifying the popout bar’s orientation, and filtering the bars surrounding the popout item could actually make it difficult to determine if the popout item differed from the surrounding items. Moreover, behavioral research has shown that tasks like this encourage subjects to adopt a singleton detection mode, in which they try to detect feature discontinuities rather than trying to identify specific target features (Bacon & Egeth, 1994). Thus, filtering should be minimized in this task, and little or no N2pc activity should be observed. Indeed, the observed contralateral-minus-ipsilateral difference was less than 0.2 μV and was not statistically significant (see Figure 12.13, bottom).

A third experiment tested the filtering hypothesis by manipulating the presence or absence of the distractor items. In the multiple-object condition (Figure 12.14A), each array contained a color popout, an orientation popout, a size popout, or no popout, and one of the three popout types was the target for a given block of trials. Subjects pressed one button if the target popout was present and
a different button if it was absent (i.e., if the array contained one of the other two popout features or no popout). Because this task required the subject to identify a specific target item that was surrounded by potentially distracting items, an N2pc component was expected for the target arrays. And because the nontarget popouts could be rejected on the basis of a simple feature, little or no N2pc was expected for the nontarget popout arrays (just as for the easy nontargets in the experiment shown in Figure 12.12). As predicted, a large N2pc was observed for the target popouts in this condition, but little or no N2pc was observed for the nontarget popouts. To isolate target-specific activity and subtract away all other components, the waveforms for the nontarget popouts were subtracted from the waveforms for the target popouts. This yielded a negative voltage from 200 to 300 ms in the contralateral waveform but little or no activity in the ipsilateral waveform (see Figure 12.14A, bottom). As mentioned earlier in this chapter, this is one piece of evidence supporting the claim that the N2pc reflects a negative voltage contralateral to the target rather than a positive voltage ipsilateral to the target.

In the single-object condition of this experiment (Figure 12.14B), the distractors were simply removed but the task remained the same. That is, one of the three items that served as a popout in the multiple-object condition was designated the target at the beginning of each trial block, and the other three
stimuli served as nontargets for that block. If the N2pc reflects filtering of distractors, then it should be eliminated in this condition. Indeed, little or no difference in voltage was observed between the contralateral and ipsilateral waveforms for either the targets or the nontargets. However, lateralized activity was observed in the P1 and N1 latency ranges, as would be expected given that the overall stimulus energy was highly lateralized in this condition. It is possible that a stimulus-evoked contralateral positivity would ordinarily be present in the N2 latency range for these stimuli and that this hypothetical positivity masked the negativity of the N2pc. To address this possibility, target-minus-nontarget difference waves were constructed to subtract away any sensory activity, making it possible to see any remaining target-specific activity (Figure 12.14B, bottom). These difference waves showed very little difference between the contralateral and ipsilateral sites, providing further evidence for the lack of an N2pc component in the single-object condition. In contrast, a substantial contralateral negativity was present in the corresponding subtraction from the multiple-object condition (Figure 12.14A, bottom). Thus, eliminating the distractors eliminated the N2pc component, consistent with the hypothesis that N2pc reflects filtering of the distractors.

An alternative explanation for these results is that both targets and nontargets elicited an N2pc in the single-item condition, because they consisted of lateralized stimuli with sudden onsets, which strongly capture attention under many conditions (see the review by Yantis, 1996). If the N2pc was present for both targets and nontargets, the target-minus-nontarget difference wave may have subtracted away the N2pc along with sensory-evoked activity. Thus, this experiment does not by itself provide definitive evidence for the filtering hypothesis.

The final experiment in this study was designed to rule out this alternative explanation and to provide a further test of the filtering hypothesis. The popout condition of this experiment was just like the multiple-object condition of the previous experiment, except that the entire array was shifted to the LVF or to the RVF (see Figure 12.15A). If a lateralized stimulus automatically attracts attention and elicits an N2pc, regardless of whether it contains any task-relevant features, then no N2pc should be visible in target-minus-nontarget difference waves in this condition. However, the voltage was more negative at contralateral than at ipsilateral scalp sites when the nontarget waveform was subtracted from the target waveform (Figure 12.15A, bottom), demonstrating that the N2pc is specific to arrays containing.

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Fig. 12.15. Stimuli and grand average ERP difference waveforms recorded at posterior temporal electrode sites in the popout condition (A) and the global condition (B) of Experiment 4 in Luck and Hillyard (1994b). In both conditions, each of the four types of stimulus arrays was equiprobable. One of the popout stimuli was designated the target at the beginning of each trial block, and subjects pressed one of two buttons for each stimulus to indicate whether the target was present or absent. Because the stimulus arrays were entirely lateralized, the early sensory responses were lateralized, making it difficult to isolate the N2pc waveform by comparing contralateral and ipsilateral waveforms for the targets. To isolate the N2pc, contralateral-minus-ipsilateral waveforms were constructed (shown here). In the N2pc latency range, the contralateral response was substantially larger than the ipsilateral response in the popout condition but not in the global condition.
relevant features even when the lateralized appearance of the array might be expected to capture attention irrespective of its features. Thus, the lack of a differential N2pc component for targets relative to nontargets in the single-object condition of the previous experiment cannot easily be explained by an automatic capture of attention by both target and lateralized stimuli.

The experiment shown in Figure 12.15 also included a global condition, in which all of the items in each array were identical to each other (Figure 12.15B). As in the popout condition, the items were lateralized to either the LVF or the RVF. However, because the items were all identical to each other in the global condition, there was no need to filter out any of the items in the array. The target-minus-nontarget difference waveforms exhibited little or no difference between the contralateral and ipsilateral sites, providing additional evidence that the N2pc component is observed only under conditions in which filtering is necessary.

If the N2pc component reflects filtering, then it should be larger when the number of to-be-filtered distractors is increased. Two subsequent studies have provided evidence consistent with this prediction, demonstrating that the N2pc is larger when the number of distractors is increased from 1 to 3 (Luck et al., 1997b) or from 3 to 19 (Mazza et al., 2009b). EVIDENCE AGAINST THE FILTERING HYPOTHESIS

Several studies have provided data challenging the filtering hypothesis. First, Eimer (1996) found that an N2pc component could be observed in a task in which each display contained only a target in one hemifield and a single distractor in the opposite hemifield, with no distractors near the target. This is not particularly strong evidence against the filtering hypothesis, because receptive fields at late stages of the ventral visual pathway are very large and bilateral (Gross & Mishkin, 1977). Consequently, both of the stimuli in the Eimer (1996) experiment would have appeared within the receptive field of a typical neuron in inferotemporal cortex, thus leading to the need to filter the distractor. Moreover, although a small N2pc can be observed with a single item in each hemifield, N2pc amplitude is increased if the number of distractors is increased (Luck et al., 1997b; Mazza et al., 2009b), consistent with the filtering hypothesis.

With an isolated target on one side of the display and an isolated distractor on the other side, might we expect to see the N2pc as a negativity contralateral to the distractor rather than contralateral to the target? Although inferotemporal receptive fields are typically bilateral, the response is typically larger for contralateral stimuli than for ipsilateral stimuli. If the purpose of filtering is to reduce interference with the representation of the target, then the filtering might be observed primarily in the hemisphere that most strongly codes the target. Thus, the filtering hypothesis does not predict a reversal of the N2pc when a single distractor is present in the hemifield opposite to the target.

A second challenge to the filtering hypothesis comes from studies by Mazza and colleagues (Mazza et al., 2009a, 2009b), who followed up on the experiment shown in Figure 12.13, in which the target could be either a vertical bar among horizontal distractors or a horizontal bar among vertical distractors. Because the target was defined by being surrounded by items of a different orientation, no filtering of the surrounding items was necessary and no N2pc was observed in this prior experiment. As illustrated in Figure 12.16, Mazza et al. (2009b) used an analogous design but with color rather than orientation as the popout feature. In the constant condition, the popout item was always red among green distractors (or the reverse for half of the subjects). In the variable condition, the popout item could either be red among green distractors or green among red distractors (randomly intermixed from trial to trial). Subjects were required to press one of two buttons on each trial to report whether the popout item contained a missing corner on the left side or the right side. A robust N2pc was observed in both the constant and variable conditions. This is inconsistent with the experiment shown in Figure 12.13, which was analogous to the variable condition of the Mazza et al. study but yielded no significant N2pc. This inconsistency could be explained by the fact that subjects in the Mazza et al. experiment were required to discriminate the shape of the popout item. That is, once the color had been used to locate the target item, it was presumably necessary to filter out surrounding distractors to accurately perceive the shape of this item.

A follow-up study examined this possibility by comparing detection and discrimination variants of the task (Mazza et al., 2009a). In the discrimination version, subjects were again required to report the position of the missing corner on the popout item. In the detection version, subjects were required to report only whether a popout item was present. The waveforms indicated that an N2pc component was present in all conditions, including the variable
condition with the detection task. Unfortunately, the data were not presented in a way that made it possible to determine if the N2pc was smaller for the variable condition than for the constant condition when subjects performed the detection task. Nonetheless, the presence of a substantial N2pc for the variable condition when subjects performed the detection task is a challenge to the filtering hypothesis.

Why might Mazza et al. (2009a) have found an N2pc for color popouts in the variable condition shown in Figure 12.16 even though Luck and Hillyard (1994b) did not find an N2pc for orientation popouts in the analogous experiment shown in Figure 12.13? One possibility is that the color popouts used by Mazza et al. (2009a) were substantially more salient than the orientation popouts used by Luck and Hillyard (1994b). That is, the color popouts may have triggered an automatic shift of attention, yielding an N2pc even though filtering was not needed for the task. Two previous findings make this explanation plausible. First, very salient singletons have been found to elicit an N2pc even when they are nontarget stimuli, including color singletons in the experiment shown in Figure 12.7 and motion singletons in the study of Girelli and Luck (1997). Second, a dual-task experiment demonstrated that an N2pc may be elicited by a popout target in low-load situations in which the subject has nothing better to do with attention, but the N2pc will be eliminated for the same target when a secondary task is used to minimize the availability of free attentional resources. Consequently, the presence of an N2pc for a highly salient popout does not indicate that the process reflected by the N2pc is necessary for performing the popout task.

Mazza et al. (2009a) presented two additional experiments that challenged the filtering hypothesis. Experiment 2 of this study varied the proximity of the distractors to the target. On near trials, two distractors were presented within approximately \(1.25^\circ\) of the target; on far trials, all distractors were at least \(2.5^\circ\) from the target. No significant increase in N2pc amplitude was observed for the near trials (although the later SPCN appeared to be increased). However, the distance between the target and distractors in the far condition may have been close enough that multiple items were still present inside of individual V4 receptive fields. Specifically, Motter (2009) has shown that almost all V4 receptive fields are at least \(2.5^\circ\) in diameter at the eccentricities used in the Mazza et al. (2009a) study, and the \(2.5^\circ\) spacing in the far condition was therefore insufficient to ensure that no distractors were in the same V4 receptive fields as the target. Receptive fields are even larger within the lateral occipital complex, and multiple distractors would have been present within the receptive fields of these neurons in all conditions of this experiment. Thus, equivalent filtering may have been necessary in both the near and far trials.

To provide a valid test of the filtering hypothesis, it would be necessary to test a larger range of target-distractor distances.

In Experiment 3 of Mazza et al. (2009a), a heterogeneous condition was included, in which two different distractor colors were present in each array. Distractor heterogeneity is thought to influence the difficulty of finding the target among the distractors,
not the level of interference produced by the distractors once attention has been directed to the target. Indeed, Mazza et al. (2009a) found that N2pc onset latency was substantially increased in the heterogeneous condition. Thus, this experiment did not really test the filtering hypothesis.

Although it may be possible to explain away the findings of Mazza et al. (2009a), these explanations run the risk of making the filtering hypothesis unfalsifiable. The main difficulty in assessing the evidence for and against the filtering hypothesis is that we do not have an independent means of assessing whether the hypothesized filtering process was present or absent under a given set of experimental conditions. As discussed earlier in this chapter, this is a general problem in linking ERP components with specific cognitive or neural processes: unless we can make very strong predictions about when a particular process will be present or absent, it is difficult to provide very strong tests of the hypothesis that an ERP component reflects this process. Unfortunately, we are not yet at the point where we can know with absolute certainty when filtering will be present or absent, and this makes it difficult to conduct decisive tests of the N2pc filtering hypothesis.

FILTERING AND THE N2PC AND Pd COMPONENTS

Another challenge to the filtering hypothesis was provided by Hickey et al. (2009), who used the paradigm shown in Figure 12.17 to separately assess target processing and distractor suppression. Each stimulus array contained two objects, one located on the vertical midline and the other located to the left or right of fixation. One of the objects was a square or a diamond, and the other was a short or long horizontal line. In Experiment 1 of this study, the subjects’ task was to press one of two buttons to indicate whether a square or a diamond was present; the horizontal line was always a distractor. Because one of the two objects was on the vertical midline, any ERP activity corresponding to this line was neither ipsilateral nor contralateral to a given electrode site, and any lateralized ERP activity must reflect the processing of the lateral stimulus (plus any interactions between the midline and lateral stimuli). Thus, this design made it possible to isolate lateralized processing of the target (when the target was the lateralized stimulus and the distractor was on the midline) and lateralized processing of the distractor (when the distractor was the lateralized stimulus and the target was on the midline). Hickey et al. reasoned that filtering should be seen in the contralateral-versus-ipsilateral comparisons when the distractor was lateralized, whereas target processing should be seen in these comparisons when the target was lateralized.

When the target was lateralized, the presence of lateralized sensory components made it difficult to discern whether an N2pc was present or absent (Figure 12.17A, bottom), just as in the single-item condition of the experiment shown in Figure 12.14. To minimize this sort of lateralized sensory response when the distractor item was lateralized, the distractor was presented at the same luminance as the background (the target, in contrast, was substantially brighter than the background). This substantially reduces P1 and N1 amplitude, which are primarily sensitive to information represented by the magnocellular pathway (see, e.g., Butler et al., 2007). As shown in Figure 12.17B (middle), the P1 and N1 waves were not lateralized when the distractor was lateralized, and the only lateralized effect was a greater positivity at contralateral relative to ipsilateral sites. Thus, distractors appear to elicit a contralateral positivity rather than a contralateral negativity in the N2 latency range. Hickey et al. (2009) called this effect \( P_d \) (distractor positivity), and they speculated that it reflects an active suppression process that is directed to distractors. Experiment 2 of this study demonstrated that the \( P_d \) was eliminated when the task was changed so that subjects simply had to detect the presence of a square or a diamond rather than discriminating its form. Hickey et al. (2009) speculated that the elimination of the \( P_d \) occurred because distractor suppression is unnecessary for a simple detection task.

Additional evidence that the \( P_d \) component reflects suppression was obtained in two recent studies examining the capture of attention by salient color popouts (Eimer & Kiss, 2008; Sawaki & Luck, 2010). When subjects were strongly motivated to restrict attention to form-defined targets, salient irrelevant color popouts did not yield an N2pc component, but instead yielded a \( P_d \) component. Other studies suggest that salient popouts are actively suppressed under these conditions, so the finding of a \( P_d \) component is consistent with the hypothesis that \( P_d \) reflects a suppressive mechanism.

When both the target and the distractors are lateralized, as in a typical N2pc paradigm, the N2pc and \( P_d \) components will presumably combine together. For example, if a visual search display consists of a target in one visual field and a single distractor in the opposite visual field, then the difference in amplitude between the electrodes contralateral
versus ipsilateral to the target will be composed of both the N2pc elicited by the target and the P1 elicited by the distractor. Because the P1 is positive contralateral to the distractor, it will be negative contralateral to the target in this situation, and the N2pc and P1 will sum together. This will create a larger negativity contralateral to the target than would be present if only the target-related N2pc activity were present. However, if multiple identical distractors are present on both sides of the display, then the P1 will presumably be elicited by the distractors on both sides and will largely cancel out when the N2pc is isolated by means of a contralateral minus-ipsilateral difference wave. If the display contains multiple identical distractors, a target that pops out on one side, and a distinctive distractor that pops out on the other side, as in the experiments shown in Figures 12.3 and 12.4, the distinctive distractor may require more suppression than the other distractors. In this case, a substantial P1 may be present contralateral to the distinctive distractor and therefore ipsilateral to the target, and the P1 will again sum together with the target-elicited N2pc component.

In addition to identifying the P1 component, Hickey et al. (2009) tested whether the N2pc component reflects target processing or distractor suppression. In Experiment 4 of this study, the short or long line was the target and the square or diamond was the distractor. The line was again isoluminant with the background, minimizing any lateralized P1 and N1 activity. When the line target was presented laterally, an N2pc component was observed (Figure 12.17). Thus, a lateralized line elicits a contralateral positivity (P1) when it is a distractor but a contralateral negativity (N2pc) when it is a target.

Because the N2pc component was observed contralateral to the target when the distractor was on the vertical midline, Hickey et al. (2009) concluded that N2pc reflects a process that enhances the cortical representation of the target rather than a process
that filters distractors. However, this conclusion was based on the assumption that suppression of a distractor presented on the midline will not lead to lateralized neural activity. This is not necessarily true. As was discussed in the context of Eimer’s (1996) finding that the N2pc was present contralateral to the target when the only distractor was on the opposite side of the display, a distractor relatively far away from the target may still be present within the receptive field of a neuron that codes the target stimulus, and the filtering may therefore be carried out primarily in the hemisphere contralateral to the target. To rigorously test the filtering hypothesis, it would be necessary to present the isoluminant line stimulus at a lateral location without a distractor on the vertical midline. If the N2pc was still present in the complete absence of a distractor, then this would conclusively falsify the filtering hypothesis.

**AN OVERALL APPRAISAL OF THE FILTERING HYPOTHESIS**

As this discussion of the filtering hypothesis illustrates, it is quite difficult to link an ERP component with a specific cognitive or neural process. Unless we have an independent means of determining when a given process is present or absent, it is difficult to provide definitive tests of the relationship between an ERP component and that process. We do not have an independent means of determining when filtering is present or absent, and we do not have a sufficiently well established theory of filtering to make strong predictions about when filtering should be present or absent. Indeed, this is why it would be extremely valuable to have an ERP component that has been definitively linked to filtering.

What, then, can we conclude at this time about the relationship between the N2pc component and filtering? The most direct experiments have addressed the effects of the presence or absence of distractors on the N2pc component, and these experiments have found that (1) the N2pc is present when distractors are present (Luck & Hillyard, 1994a, 1994b); (2) the N2pc is reduced or eliminated when the distractors are removed (Experiments 3 and 4 in Luck & Hillyard, 1994b); and (3) the N2pc becomes larger when the number of distractors is increased (Experiments 1 and 2 in Luck et al., 1997b; Experiment 1 in Mazza et al., 2009b). These findings support the hypothesis that the N2pc component reflects filtering of distractors. The main evidence against this hypothesis is that the N2pc is observed contralateral to the target, even when the only distractor is on the midline or in the opposite visual field (Eimer, 1996; Hickey et al., 2009).

Although it is possible to explain away some of these results, a somewhat broader hypothesis could accommodate all of the existing results. Specifically, the N2pc may reflect a process that is applied to the representation of the target stimulus, but only under conditions of competition from simultaneous distractors. Indeed, Luck and Hillyard (1994a) noted that “the filtering process may be accomplished by activating the neural representation of the object undergoing identification rather than by inhibiting the distractor items, as long as this selection process is assumed to be necessary only when competing distractor items are present” (p. 1010). However, the term filtering tends to imply an operation that is applied to the distractors, and it may be more appropriate to say that the N2pc component reflects a process that resolves competition between the attended item and the distractor items. We call this the competition resolution hypothesis of the N2pc component. This hypothesis is explicitly agnostic about whether the competition resolution hypothesis acts directly on the representation of the target, directly on the representations of the distractors, or on interneurons that mediate the competition between the target and distractor representations. However, it proposes that the computational function of the process is to enhance the representation of the target by minimizing interference from simultaneous distractor items. This hypothesis appears to be fully compatible with all existing evidence.

**LINKS TO THEORIES OF ATTENTION**

The competition resolution hypothesis is closely related to the biased competition model of Desimone and Duncan (1995), which specifies that the main role of attention is to resolve competition between neural representations. It is also closely related to Treisman’s feature integration theory (Treisman, 1988, 1999; Treisman & Gelade, 1980), which proposes that attention is needed to prevent features from different objects from combining together. Luck et al. (1997b) proposed an ambiguity resolution theory, which combines elements of these two theories. The ambiguity resolution theory proposes that the output of a neuron becomes ambiguous when multiple objects are present in the neuron’s receptive field, because it is not clear which of the objects contains the feature that is represented by the neuron. As noted previously, if a red triangle and a blue circle are both present in the receptive field of a red-selective neuron, the neuron will fire at
a high rate to indicate the presence of the color red, but it will not be clear whether the triangle or the circle is the red item. Attention can resolve this ambiguity by limiting processing to a single object at any time; when attention is focused on a single object, all of the remaining neural activity reflects the features present in the attended object. This is the type of attentional mechanism that the N2pc component appears to reflect.

A key prediction of feature integration theory and the ambiguity resolution theory is that this variety of attention should be unnecessary when the target is defined by the presence of a single feature (although other types of attentional mechanisms will obviously be necessary to implement the rules of the task). If, for example, the observer’s task is to detect the color red, then the output of a red-selective neuron will be sufficient to perform this task even if non-red items are present along with a red item in a given neuron’s receptive field. Consistent with this prediction, the N2pc component is larger for tasks that require subjects to combine multiple features than for tasks that require the mere detection of a simple feature (Luck & Ford, 1998; Luck et al., 1997b). However, a substantial N2pc is often present for simple feature-detection tasks (see, e.g., Figures 12.5, 12.14A, and 12.15A).

How can the presence of a substantial N2pc for simple feature targets be reconciled with the proposal that the variety of attention reflected by the N2pc component is not necessary for the detection of simple features? The answer to this question provides an important principle that is often overlooked in studies that attempt to link ERP components with neural or cognitive processes. Specifically, a given neural or cognitive process may be active in a laboratory experiment even though it is not strictly necessary for task performance. Most ERP experiments are long and boring, and they do not typically push subjects to the limits of their abilities. Consequently, a given process may occur not because it is necessary for task performance, but because there is no disincentive for using this process and because this process may ordinarily be necessary in natural task situations. In the case of the process reflected by the N2pc component, it may not be necessary for the detection of simple features, but most feature detection tasks are extremely simple and provide no disincentive for allocating attention to the target. Subjects may focus attention on the target because they have nothing else to do or because most real-world situations require the focusing of attention onto relevant objects.

To test this hypothesis, Luck and Ford (1998) performed a dual-task experiment in which subjects performed a visual search task simultaneously with a demanding task that required determining whether a degraded letter presented at fixation was a consonant or a vowel. In one set of conditions, the visual search task required subjects to merely report the presence or absence of a specific color in an array of colored squares. When this task was performed alone, an N2pc component was observed contralateral to the target color. However, when this task was performed simultaneously with the demanding central task, the N2pc component was eliminated. Subjects were still highly accurate at performing the visual search task, indicating that the process reflected by the N2pc component is not necessary for the detection of simple features. In a second set of conditions, the visual search task required the subject to report a conjunction of color and orientation. When this task was performed alone, a large N2pc component was observed. When it was performed simultaneously with the central task, the N2pc component was delayed rather than being eliminated. Thus, subjects could not perform a conjunction task without the process reflected by the N2pc component.

These results provide further support for the hypothesis that the N2pc component reflects a competition resolution process. They also provide a cautionary note about experiments that attempt to link an ERP component with a neural or cognitive process. That is, an ERP component that reflects a given neural or cognitive process may be observed under conditions in which that process is not necessary. Thus, even when a good theory of a process already exists, caution is needed in using the theory to predict the absence of the component under conditions in which the theory specifies that the process is not necessary.

References