

Neural Mechanisms of Visual Singleton Detection: Evidence from Human Electrophysiology

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Abstract

It is sometimes necessary to search for visual objects of potential interest that are underspecified (e.g., any illegal item in a suitcase). The search for such an object can be accomplished easily if it possesses a unique feature that makes it stand out from its surrounding. In this case, observers can simply search for the most salient item in the environment (singleton detection). Surprisingly, the neuro-cognitive processes involved in singleton detection are still poorly understood. The overarching aims of this thesis were to reveal neuro-cognitive processes involved in singleton detection using event-related potentials (ERPs) and to address specific questions about the role of attention in singleton-detection tasks. Experiment 1 reexamined the claim that attentional processes associated with an ERP component called the N2pc are absent in singleton detection. The results revealed several ERP components, including the N2pc and a newly discovered component that tracked the time course of singleton detection (the singleton detection positivity; SDP). It was concluded that singleton detection involves some of the same attentional processes as those required for feature-based search. Experiment 2 employed a go/no-go variant of the singleton-detection task to determine whether the attentional processes observed in singleton detection are triggered automatically, as some researchers believe. ERP indices of singleton detection (SDP) and attentional selection (N2pc) were markedly reduced or absent on no-go trials, demonstrating that rapid assessment of task relevancy can prevent salience-driven capture of attention in the singleton-detection task.

Keywords: attention; distraction; individual differences; N2pc; singleton detection; visual search

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List of Acronyms

μV	Microvolt
A-to-D	Analog-to-digital
AF	Midpoint between FP and F (electrode)
Ag/AgCl	Silver/silver chloride
ANOVA	Analysis of variance
C	Central (electrode)
CA	California
CDA	Contralateral delay activity
CI	Confidence interval
cm	Centimeter
DC	Direct current
EEG	Electroencephalography
EOG	Electrooculography
ERP	Event-related potential
F	Frontal (electrode) or false-alarm rate
FINST	Fingers of instantiation
FP	Prefrontal (electrode)
G Ω	Giga-ohm
H	Hit rate
Hz	Hertz
K	Estimate of visual working memory capacity
k Ω	Kiloohm
LCD	Liquid crystal display
LED	Light-emitting diode
M	Mastoid (electrode)
ms	Millisecond
N1	First visual-evoked negativity
N1pc	Posterior-parietal N1
N2	Second visual-evoked negativity
N2b	Posterior N2
N2pc	Posterior-parietal N2
NSERC	Natural Sciences and Engineering Research Council of Canada

O	Occipital (electrode)
P	Parietal (electrode)
P2a	Anterior P2
P3	Third visual-evoked positivity
PCI	Peripheral component interconnect
P _D	Distractor positivity
PO	Parieto-occipital (electrode)
RT	Response time
S	Set size
SDP	Singleton detection positivity
SFU	Simon Fraser University
SOA	Stimulus onset asynchrony
T	Temporal (electrode)
TX	Texas
VCOP	Visual contralateral occipital positivity
vWMC	Visual working memory capacity

Chapter 1. General Introduction

The number of objects in our visual environment often exceeds our capacity to fully process every item at once. To navigate in such a complex environment, the visual system has developed the ability to deal with sensory inputs in a strategic manner, so that objects of interest (those that are related to the task at hand) or of potential interest (those that are physically salient) may be prioritized for processing (Bisley & Goldberg, 2010; Itti & Koch, 2000, 2001; Serences & Yantis, 2006; Wolfe, 1994). For over a century, scholars have used the term *attention* to refer to the various cognitive processes that enable the *selection* of these prioritized objects and the *withdrawal* from other, *unattended* objects in the visual field (e.g., James, 1890). And although attention is hypothesized to enable the conscious perception of, and interaction with, the external world, the precise mechanisms by which attention operates remain poorly understood.

1.1. Visual Search

Several paradigms have been introduced to study attentional processes in well-controlled laboratory variants of real-world tasks. One such paradigm, called visual search, was developed to study how attention is guided across a visual scene as an observer attempts to find an object of interest (called the *target*). Visual search is conducted regularly, from rummaging for keys in a bag to looking for a friend in a crowd. But search is also involved in circumstances where errors may be costly; for example, when examining an x-ray image for presence of pathological abnormalities or monitoring for signs of drowning in a swimming pool. In all these cases, observers are presumed to direct their attention deliberately from one location to another in order to inspect each visual element closely. This type of *serial search* is juxtaposed with *parallel search* processes that are hypothesized to take place throughout the entire visual field (Treisman & Gelade, 1980) or at least the relevant region of the visual field (Theeuwes, 2010). Parallel search occurs when the target is found effortlessly, as if the object “pops out” from the environment, such as locating a bolded word in a page of text.

To help understand the differences between serial search and parallel search, vision scientists theorized that visual processing is broadly comprised of two sequential stages (Desimone & Duncan, 1995; Itti & Koch, 2000, 2001; Julesz, 1986; Neisser,

1967; Theeuwes, 2010; Treisman & Gelade, 1980; Wolfe, 1994). The first is an early, *preattentive* stage, during which the visual system encodes stimuli by their basic visual attributes (e.g., color, orientation, size; herein called *features*) in parallel and computes their salience. This phase is followed by an *attentive* stage, at which point the visual system integrates the various features into individual objects for detailed, perceptual analysis.

From this perspective, serial search takes place when a target is insufficiently salient for the visual system to locate during the preattentive stage, and thus attention must be deployed serially to individual objects in the visual field until the target is found. The serial inspection of each object can be observed directly when participants are permitted to move their eyes during a difficult search task or inferred indirectly on the basis of reaction time (RT) data when eye movements are prevented (i.e., in the study of *covert attention*). In the latter covert-attention studies, participants are instructed to stare at a fixation stimulus and, without moving their eyes, to indicate whether a specific target item is present within each of several search displays that contain varying numbers of items. The time required to determine whether the target is present or absent is affected by several factors, including the similarity between the target and other, nontarget items as well as the number of items in the display (i.e., *set size*; e.g., Wolfe, 1994). When the target cannot be distinguished from nontargets on the basis of one or more simple features (e.g., when looking for a T among Ls, the features of which differ only in the spatial arrangement of lines), researchers have shown that participants are progressively slower to find the target as the set size increased (Bergen & Julesz, 1983; Egeth & Dagenbach, 1991; Kwak, Dagenbach, & Egeth, 1991). Consequently, a positive linear function relating RT to set size (herein called the *search function*) was used as an indicator of serial search.

By comparison, parallel search occurs when the target can be singled out at the early, preattentive stage of visual processing (e.g., based on salience or relevance) so that attention is immediately drawn to the target location. Some researchers have gone further to argue that although the target may trigger a shift in attention, attention is not required to find the target because it is detected preattentively (e.g., Julesz, 1984; Julesz & Bergen, 1983; Treisman & Gelade, 1980). Studies of parallel search show that when participants searched for a unique item such as a red box among green boxes or a vertical line among horizontal lines, the time participants took to detect the target was

independent of set size (e.g., Wolfe, Friedman-Hill, Stewart, & O'Connell, 1992). The search function generated from parallel search is thus characterized by a flat slope.

In addition to the positive and flat search functions hypothesized to reflect serial and parallel search processes, respectively, researchers have also reported a third pattern of results. In their experiment, Bravo and Nakayama (1992) instructed participants to search for the unique stimulus in an array of homogeneous nontargets (i.e., a *singleton* target). To discourage participants from searching for a specific feature, Bravo and Nakayama swapped the feature of the target and that of the nontargets randomly across trials. On any given trial, participants looked for an odd-colored diamond (red or green) with either the left or right vertex cut off situated among other similarly notched diamonds of the other color. Once the color singleton was located, participants indicated the side of the diamond that was missing. Instead of producing a flat search function as expected of parallel-search experiments, Bravo and Nakayama showed that participants were actually faster to respond to the target as set size increased; that is, the slope revealed by the search function was negative rather than positive or flat. By contrast, when the same task was performed with a fixed-feature target, the search function was flat.

Based on this negative search slope, Bravo and Nakayama (1992) hypothesized that the search for a pop-out target can be guided by two different mechanisms: When the precise target feature on a given search display is unpredictable, attention is guided in a purely stimulus-driven manner based on local stimulus contrast (saliency; i.e., *bottom-up* guidance), but when the target feature is fixed across trials, the feature can serve as an additional guiding mechanism (i.e., *top-down* guidance). According to this account, search is guided by the information that leads to the most efficient performance. When the target feature is underspecified, feature-based guidance would require the effortful serial allocation of attention to individual items, whereas saliency-based guidance would enable fast discovery of the target based on the early preattentive stage of processing. When the target feature is known in advance, however, feature-based guidance enables simultaneous inspection of all items for the target feature, so that the speed at which the target is found is unaffected by changes in set size. By comparison, saliency-based guidance in this case would presumably only reach a similar level of search efficiency after the set size becomes sufficiently large.

1.2. Modes of Visual Search

The findings by Bravo and Nakayama (1992) suggest that there are at least two search strategies an observer may adopt, depending on the target's degree of specificity. When the precise features that define the target are known, such as looking for a set of keys on a desk, search is performed by bearing a set of key-related features in mind and then comparing these features with those of the objects on the desk until a match is found (so-called *feature search*; Bacon & Egeth, 1994). When the features of the target are underspecified (e.g., searching x-ray images for any illegal item at a security checkpoint), however, the feature-based search strategy becomes ineffective. Instead, observers must search for *anomalies* by comparing each object in the visual environment with its surrounding until the relevant anomaly (target) is found. The difficulty of searching for a relevant anomaly is greatly reduced if it possesses a unique feature that causes it to stand out from its surrounding, in which case, observers can adopt a strategy to search for the most salient object in the visual environment (so-called *singleton detection*).

1.2.1. Processes Involved in Feature Search

Many contemporary theories of attention have largely focused on the role of features in the guidance of visual attention, and thus the processes involved in feature search mode have been well-documented. Feature search is theorized to begin with the formation of a *target template*, which refers to an internal representation of a set of relevant features that are updated and maintained in visual working memory (Bundesen, 1990; Desimone & Duncan, 1995; Duncan & Humphreys, 1989). The storage of target templates in visual working memory as observers prepare for feature search is corroborated by evidence from monkey single-cell recording and human electrophysiology (Chelazzi, Duncan, Miller, & Desimone, 1998; Chelazzi, Miller, Duncan, & Desimone, 1993; Vogel & Machizawa, 2004; Vogel, McCollough, & Machizawa, 2005). These studies show that neural responses to task-relevant features are sustained throughout a brief waiting period (i.e., memory-retention interval) prior to the onset of a target display.

After observers have established a target template, feature-based attentional mechanisms then highlight objects within the visual field that contain relevant features to

provide a map of likely target locations. Converging evidence from studies using recordings of single-cell activity, event-related potentials (ERPs), and event-related magnetic fields (ERFs) suggests that this process is accomplished by upweighting all relevant features (or feature dimensions; Schubö & Müller, 2009) in *parallel* across the visual field (Bichot & Schall, 1999; Bichot, Rossi, & Desimone, 2005; Eimer & Grubert, 2014; Hopf, Boelmans, Schoenfeld, Luck, & Heinze, 2004; Kiss, Grubert, & Eimer, 2013; Motter, 1994). Taken together, it was found that neural activity simultaneously tracks the locations of objects possessing at least one task-relevant feature in the visual field and that greater activity is elicited by objects possessing multiple relevant features.

This feature-upweighting process is followed by location-based attentional mechanisms that then allocate *spatial attention* to the location in the visual field given the highest relevancy weighting, a process that is often referred to as the covert deployment of attention (Cave, 1999; Treisman & Gelade, 1980; Treisman & Sato, 1990; Wolfe, 1994). Once spatial attention is allocated to the object with the highest relevancy weighting, several processes commence to improve the perceptual analysis at the attended location and reduce interference from objects at other locations. These processes include the binding of features at the attended location into a unitary, visual object (i.e., *object individuation*; Mazza & Caramazza, 2011; Treisman & Gelade, 1980); the suppressing of competing visual inputs from nearby objects to reduce ambiguity in neural encoding of the attended object (i.e., *spatial filtering*; Luck, Girelli, McDermott, & Ford, 1997; Luck & Hillyard, 1994b); the suppressing of other, highly salient objects in the visual field to prevent the misallocation of spatial attention (Gaspar & McDonald, 2014; Hickey, Di Lollo, & McDonald, 2009); and the identifying of the attended object itself (Theeuwes, 2010; Treisman & Gelade, 1980; Wolfe, 1994).

After the attended object is identified, top-down processes then evaluate whether that object is the target by comparing the attended object to the target template stored in working memory. If the attended object matches the template, search is terminated. But if the attended object turns out to not be the target, spatial attention is then redeployed to the location with the next highest relevancy weighting in the visual field. This process is repeated until the target is found or until all the locations deemed likely to contain the target have been searched (Wolfe, 1994; Woodman & Luck, 1999, 2003).

1.2.2. Processes Involved in Singleton Detection

While much is known about the sequence of neuro-cognitive events involved in feature search, less is known about the processes involved in singleton detection. In the first place, *pure* singleton-detection tasks do not permit the storage of a target template because observers do not have sufficient knowledge of the target's identity (due to the unpredictability of its features). Consequently, the feature-search operations that rely on the establishment of a target template cannot occur. Observers can, however, adopt a strategy to search for discontinuities in the visual field that may signal the presence of the target singleton.

In the laboratory, efficient singleton detection has been studied by giving the target a unique feature that causes it to stand out from its surrounding. In doing so, observers can then detect singletons by searching for the most salient object in the visual field. If, however, the singleton possesses a prespecified feature, observers would have the option of adopting the feature search mode, the singleton detection mode, or some unknown combination of bottom-up and top-down guidance strategies. In fact, it has been shown that when both singleton detection and feature search modes are available to the observer, either search strategy can be adopted (Bacon & Egeth, 1994; Leber & Egeth, 2006). Therefore, to ensure that observers are in singleton detection mode, the feature of the target and its surrounding objects are typically swapped randomly on a trial-by-trial basis to discourage feature-based search.

When feature-based search is discouraged by swapping the features of the target and its surrounding objects from trial to trial, it was found that target singletons can be detected effortlessly (e.g., Bravo & Nakayama, 1992). The efficiency with which observers can detect a singleton target is presumably due to a separate group of processes that guide detection in a saliency-based manner. It has been suggested that, similar to having a target template in feature search to map relevant locations in the environment, singleton detection relies on a saliency map that encodes objects in the visual field in terms of conspicuity, so that attention may be deployed to various locations in order of salience until the target is found (Itti & Koch, 2000, 2001; Theeuwes, 2010). By this view, singleton detection differs from feature search not in terms of how visual selection is ultimately achieved (i.e., by focusing attention at the location of the target)

but in terms of *control-level* processes that are used to guide that selection (i.e., relevancy map vs. saliency map).

Role of Attention in Singleton Detection

While it is clear that singleton detection and feature search rely on different control-level processes, it is less clear whether singleton detection relies on the same attentional-selection mechanisms as those involved in feature search. Some researchers argue that all detection processes are accomplished by preattentive mechanisms that identify the location with the greatest saliency activation (e.g., Julesz, 1984; Julesz & Bergen, 1983; Treisman, 1988; Treisman & Gelade, 1980). According to this view, information about the presence of a singleton is available to the observer immediately after the singleton is detected by the visual system, so that judgment of singleton presence can be made without any attentional processing. In other words, this view holds that feature search and singleton detection rely on entirely different search processes, not just at the level of search guidance, because attention is not required for detection.

Consistent with this view, most studies using dual-task paradigms have found that singleton detection does not suffer from the requirement to perform another, more attentionally demanding task (Egeth, Leonard, & Palomares, 2008; Moher, Ashinoff, & Egeth, 2013; Luck & Ford, 1998; but see Joseph, Chun, & Nakayama, 1997). This lack of performance decrement was taken as evidence that singleton detection does not require attention, presumably because the shortage of attentional resources would have otherwise impaired detection performance. It should be noted, however, that these studies used singleton targets that possessed fixed features and so it is possible that the conclusion about preattentive detection of feature singletons may be limited to template-guided search and not generalize to pure singleton detection in the absence of template guidance (i.e., in singleton detection mode).

This unresolved issue demonstrates that the neuro-cognitive processes involved in singleton detection are still poorly understood. Although little research has been focused on the detection of a singleton, many studies have been done on the detection of visual and auditory anomalies (i.e., deviants) in a stream of sequentially presented stimuli. These studies have identified two important electrophysiological correlates involved in such deviancy detection called the mismatch negativity (MMN) and the

novelty P3 (to be further discussed in the following section). Understanding the processes reflected by these correlates may help to inform those involved in singleton detection, given that singleton detection can be viewed as simply the detection of a visual deviant in space rather than in time (for an illustration, see Figure 1.1).

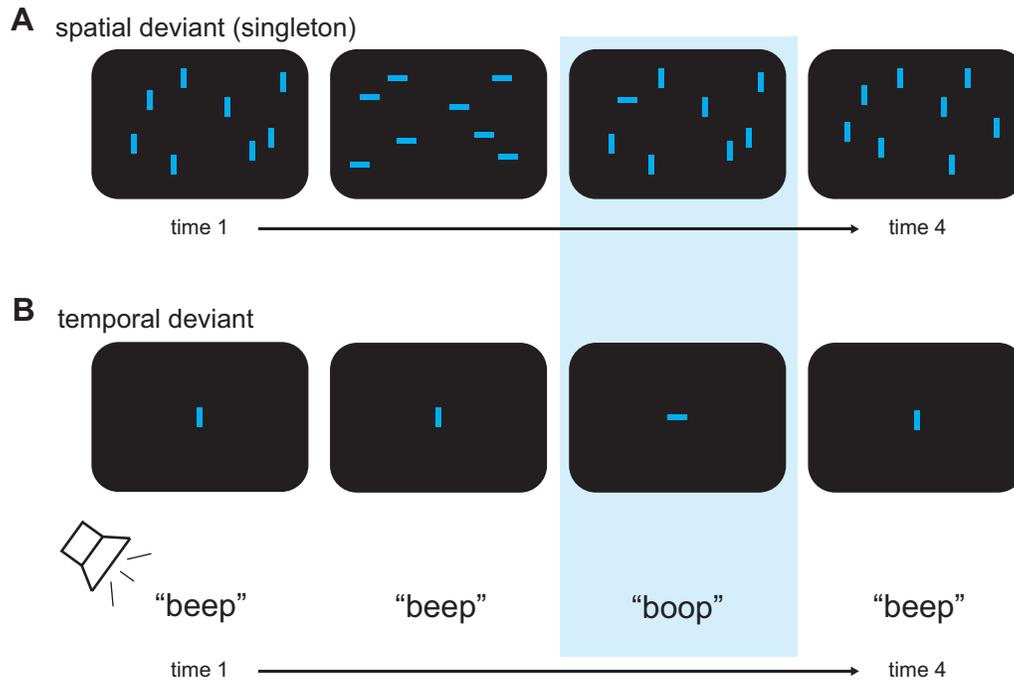


Figure 1.1 Examples of spatial and temporal deviants. The shaded region highlights the presence of a deviant at the third time point. (A) A spatial deviant can appear at any location and is always presented simultaneously with other nondeviants. (B) A temporal deviant is presented by itself and is always preceded by a series of nondeviants. Upper: a visual deviant that differs from preceding nondeviants in its orientation. Lower: an acoustic deviant that differs from preceding nondeviants in its pitch.

1.3. Electrophysiology of Deviancy Detection and Selection

Most of the aforementioned studies relied on analyses of manual responses to help inform the role of attention in visual search. Such overt performance measures reflect the summed output of multiple processing stages that may not always reveal information about the specific neuro-cognitive processes of interest. Consequently, noninvasive recordings of human electrophysiology became widely used to help complement the extant behavioral data in the study of attention processes and deviancy detection. Standard electroencephalographic (EEG) methods measure the summed

extracellular activity associated with postsynaptic potentials within the dendrites of neighboring pyramidal neurons (Buzsáki, Anastassiou, & Koch, 2012). Changes in this activity associated with specific sensory, cognitive, or motor events can then be extracted using signal-averaging techniques. The resulting ERPs reflect voltage fluctuations associated with specific neuro-cognitive processes.

Three advantages of the ERP method make it ideal to study the neuro-cognitive processes underlying the detection of deviant stimuli. First, ERPs enable researchers to investigate specific component processes that contribute to behavior and complex mental operations, such as “paying attention”. Second, ERPs can track the timing of these component processes with millisecond precision. Third, ERPs enable measurement of these component processes even under circumstances where no overt behavior is observed. Therefore, the ERP method can help researchers to determine the degree to which attention is involved in deviancy detection and to assess the automaticity of the component processes involved in detection. Three ERP components have thus far been associated with the detection and selection of deviant stimuli, namely, the mismatch negativity (MMN), the novelty P3, and the posterior-contralateral N2 (N2pc).

1.3.1. Mismatch Negativity (MMN)

The MMN is a negative ERP component typically elicited by sudden, infrequent changes (deviants) in the acoustic environment. In MMN studies using the so-called *two-stimulus oddball paradigm*, the deviant stimulus (or oddball) is occasionally presented among a stream of frequently presented stimuli called *standards* (e.g., presenting a high-pitched tone after presenting a series of identical, low-pitched tones). Because the deviant can be any stimulus that breaks from the regularity set by the standard, deviancy detection—like singleton detection—does not require knowledge of the deviant feature.

The MMN is best seen by subtracting the ERPs elicited by the standards from ERPs elicited by the deviants. And depending on the complexity of the regularity that is violated, the MMN can be observed as early as 100-250 ms post deviant onset but can also be later for deviant stimuli that are difficult to detect (Näätänen & Alho, 1995) or break abstract rules (e.g., an ascending tone presented among a series of descending tones; Tervaniemi, Maury, & Näätänen, 1994; see also Paavilainen, Simola, Jaramillo,

Näätänen, & Winkler, 2001; Saarinen, Paavilainen, Schröger, Tervaniemi, & Näätänen, 1992). Critically, contrary to what has been previously argued (Jääskeläinen et al., 2004; May et al., 1999), this latter finding indicates that the MMN does not merely index the release from sensory adaptation of neurons responding to the repeated, standard stimuli but a response triggered by the deviant stimuli (because standard stimuli that follow an abstract rule presumably do not stimulate the same population of neurons).

Based on its frontal and temporal scalp distribution (Sams, Paavilainen, Alho, & Näätänen, 1985), the MMN is theorized to be a product of two functional sources: one in bilateral auditory cortices associated with deviancy detection by comparing the current sensory input with a memory trace of past sensory inputs (Giard, Perrin, Pernier, & Bouchet, 1990), and the other one in the prefrontal cortex associated with the deployment of attention to the deviant sound (Escera, Alho, Winkler, & Näätänen, 1998; Escera, Yago, Corral, Corbera, & Nuñez, 2003) or the amplification of deviancy-detection sensitivity (Opitz, Rinne, Mecklinger, von Cramon, & Schröger, 2002). Interestingly, although deviancy detection seems to trigger a switch of attention to the deviant stimulus, the detection process itself appears to not require attention. In fact, the MMN can sometimes be observed during sleep (Sallinen, Kaartinen, & Lyytinen, 1994) and in comatose patients (Kane, Curry, Butler, & Cummins, 1993). This detection process can, however, be enhanced by attention: The MMN was found to be larger when participants attended to the stream of standard and deviant sounds than when they had to allocate their attention elsewhere, especially when the deviant stimulus is difficult to discriminate from the standard stimulus (Arnott & Alain, 2002; Müller, Achenbach, Oades, Bender, & Schall, 2002).

Using visual variants of the two-stimulus oddball paradigm, a candidate for a similar deviancy-detection mechanism has also been identified in the latency range of the visual-evoked N2 over the posterior scalp, aptly named the visual MMN (Astikainen, Ruusuvirta, Wikgren, & Korhonen, 2004; Czigler, Balázs, & Pató, 2004). Evidence for the detection of temporal anomalies in both audition and vision thus suggests that there may be a detection process for spatial anomalies (e.g., visual singletons) that operates by similar mechanisms.

1.3.2. Novelty P3

The novelty P3 is a positive-going ERP component over the central scalp that sometimes followed the MMN. As its name suggests, this component is elicited by completely novel stimuli (can be visual or acoustic; i.e., an irrelevant deviant with variable features that have not been experienced previously) presented within a stream of standard and deviant stimuli in the so-called *three-stimulus oddball paradigm*, where participants ignored the novel and standard stimuli and responded to the deviant stimuli (Courchesne, Hillyard, & Galambos, 1975; Courchesne, Kilman, Galambos, & Lincoln, 1984). At its discovery, Courchesne et al. (1975) found that the novelty of a stimulus is crucially linked to the novelty P3 because the mechanism underlying this component appears to habituate as novelty wears off, so that presentation of a previously novel stimulus no longer evokes activity of the same magnitude (see also Friedman & Simpson, 1994; Knight, 1984).

Later studies, however, suggest that novelty is sufficient—but not necessary—for eliciting the novelty P3. In one study, Cycowicz and Friedman (1998) made a distinction between familiar and unfamiliar deviants by categorizing novel sounds based on whether participants could identify the sound (i.e., familiarity). It was found that whereas presentation of familiar sounds that were previously novel showed a habituation response, presentation of unfamiliar sounds that were previously novel did not. In another study, Katayama and Polich (1998) found the novelty P3 using a non-novel deviant (nontarget) by having the target deviant closely resemble the standard and the nontarget highly deviate from both the target and the standard, suggesting that novelty is not required for eliciting the novelty P3 but the *distinctiveness* of the eliciting stimulus (i.e., salience; see also Comerchero & Polich, 1998, 1999). In light of these findings, many researchers have equated the novelty P3 with another component called the P3a (Simons, Graham, Miles, & Chen, 2001), resulting in the names of the two components being used interchangeably (Comerchero & Polich, 1998, 1999; Friedman, Cycowicz, & Gaeta, 2001; Katayama & Polich, 1998).

Based on these aforementioned findings, the widely accepted view is that the novelty P3 does not reflect the processing of novel events per se, but a process involved in the involuntary shift of attention to a salient-but-irrelevant deviant following deviancy detection. This *attention-switching hypothesis*, however, is at odds with results from a

study by Woods, Knight, and Scabini (1993). In this study, participants listened to a stream of high-pitched tones in one ear for a longer-lasting, deviant tone (target) while ignoring a stream of low-pitched tones in the other ear. When unexpected novel stimuli were presented in either ear, it was found that novel stimuli presented in the attended stream resulted in a larger novelty P3 and a greater response delay than for novel stimuli presented in the unattended stream. It is argued that if the novelty P3 truly reflects attention-switching, then the novel stimuli in the unattended stream should have elicited the larger novelty P3.

In light of this finding, the novelty P3 has also been associated with another ERP component called the no-go P3 (Goldstein, Spencer, & Donchin, 2002), which has been thought to reflect the inhibition of a target response (Bokura, Yamaguchi, & Kobayashi, 2001; Bruins, Wijers, & van Staveran, 2001). This interpretation of the novelty P3 is consistent with findings from the three-stimulus oddball paradigm because both the novel and target stimuli are deviants, and in order to perform the task accurately, observers must be able to respond to target deviants while suppressing response to nontarget deviants following deviancy detection. This interpretation is also consistent with results from Woods et al. (1993) because attended novel stimuli presumably require greater response inhibition than unattended novel stimuli. This *response-inhibition hypothesis*, however, is challenged by the report of a novelty P3 in a passive, three-stimulus oddball task wherein no response was needed (Jeon & Polich, 2001). While the precise functional significance of the novelty P3 is still unclear, extant data help to show that deviancy detection may additionally involve mechanisms that (a) encode salient stimuli, (b) are enhanced by the allocation of attention, and (c) are subject to some form of perceptual- or response-level inhibitory control.

1.3.3. Posterior-Contralateral N2 (N2pc)

When observers are asked to identify a singleton target that appears in a multi-item visual array, ERPs recorded over the occipital scalp tend to be more negative at electrodes positioned contralateral to the target than at electrodes positioned ipsilateral to the target. This lateralized negativity usually happens in the time range of the N2 peak, and so it has been called the posterior-contralateral N2 (N2pc; for an illustration, see Figure 1.2). The N2pc can be observed in challenging search tasks wherein the target does not necessarily pop out from the rest of the array (e.g., Luck & Hillyard,

1990; Dowdall, Luczak, & Tata, 2012), but it is most often studied in tasks involving fixed-feature singleton targets that are easy to locate.

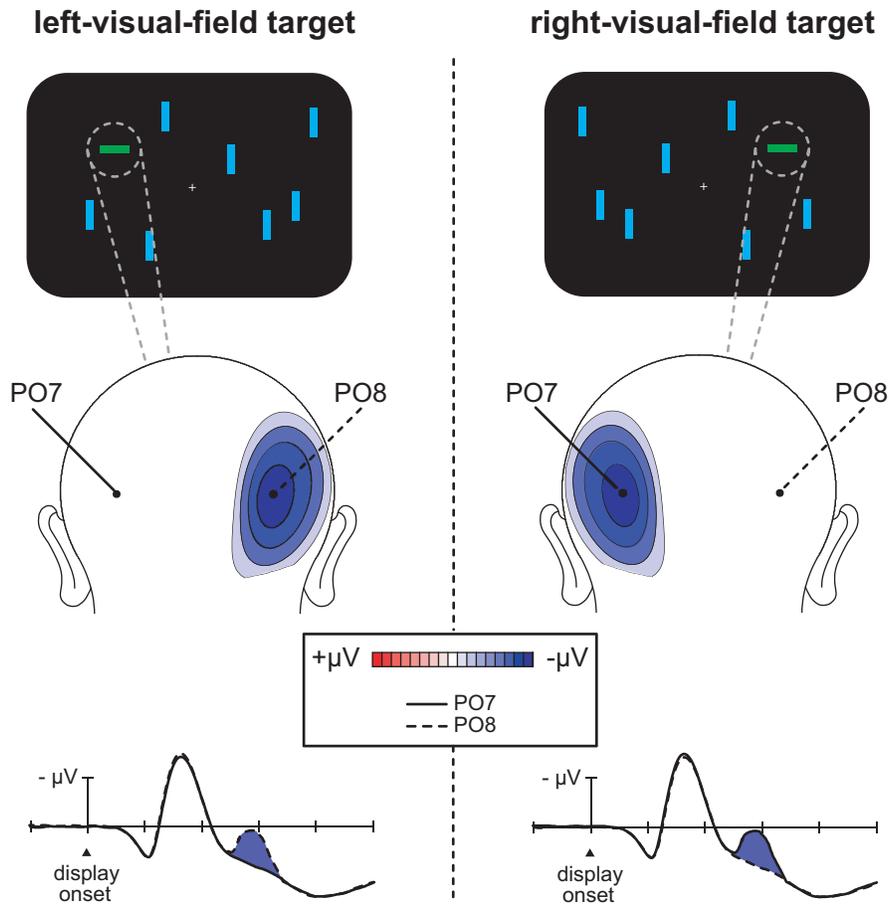


Figure 1.2 Illustration of an idealized N2pc scalp distribution (top) and corresponding ERP recordings over electrode sites PO7 and PO8 (bottom). The contralateral negativity (N2pc; shaded in blue) depicted over the scalp would result from an isolation method that removes the temporally overlapping positive voltage. The gray dashed lines represent the allocation of attention to the singleton (target). When the target is presented in the left visual field, the N2pc is elicited over the right posterior scalp (and vice versa).

In one of the first studies to report on the N2pc, Luck and Hillyard (1994b) presented a singleton that varied in orientation, color, and size across displays that contained seven identical, blue vertical lines in a feature-search task (Figure 1.3). At the start of each experimental block, one of the singletons was designated as the target and the others were designated as nontargets. Participants were informed beforehand the identity of the target singleton (e.g., a small, horizontal, blue bar), so that they were to press a button to indicate target presence whenever the prespecified singleton was

presented and another button to indicate target absence whenever other singletons or no singletons were presented. Luck and Hillyard found that the target singleton always elicited the N2pc, regardless of its actual features. Moreover, they found that nontarget singletons that resembled the target singleton (so-called *difficult nontarget*) also elicited the N2pc (e.g., a small, blue, horizontal bar vs. a large, blue, horizontal bar), whereas easily discriminable nontarget singletons did not (so-called *easy nontargets*, presumably because they could be rejected preattentively; e.g., a large, green, vertical bar).

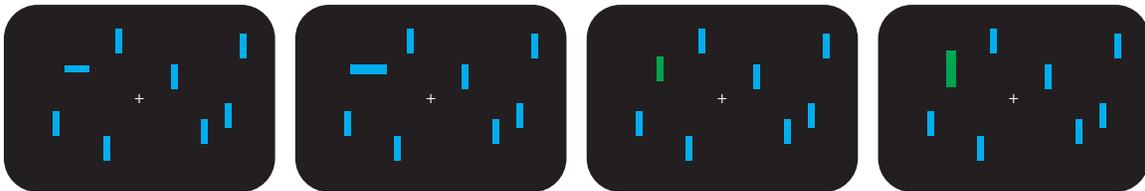


Figure 1.3 The four types of singleton displays used in Luck and Hillyard's (1994b) feature-search experiment. From left to right: When the singleton in the first display is designated as the target, the singleton in the second display would be the difficult nontarget and the ones in the third and fourth displays would be the easy nontargets. Singleton-absent displays (not shown) consist of eight small, vertical, blue bars.

Luck and Hillyard (1994b) reasoned that the N2pc was not tied to response-level processing because both targets and difficult nontargets elicited the N2pc despite requiring different manual responses. The N2pc also could not be attributed to oculomotor activity because trials with eye movements were excluded from ERP analysis. Instead, since the scalp distribution of the N2pc was consistent with the contralateral organization of the geniculostriate visual pathway and with the location of the visual cortex, the N2pc is likely to reflect some visual activity triggered by the target singleton. This visual activity cannot be ascribed to be purely sensory, however, because the same singleton that elicited the N2pc failed to do so when it was designated as the easy nontarget. The failure of the easy nontarget to elicit the N2pc also suggests that this activity arises after the completion of preattentive processing, otherwise preattentive processing of the easy nontarget would also trigger the N2pc. Instead, these results indicate that the N2pc reflects some attentional process that occurs whenever an object requires close scrutiny. Specifically, Luck and Hillyard surmised that the N2pc reflects the suppression of nontarget features in the vicinity of the target (a process called spatial filtering) during the focusing of attention onto an object.

To evaluate their *spatial filtering hypothesis*, Luck and Hillyard (1994b) designed a singleton-detection experiment that discourages filtering. In this experiment, the search display consisted of eight vertical or horizontal lines. On half the trials, the lines presented were either all vertical or all horizontal, and on the other half, one of the lines had the opposite orientation (i.e., an orientation singleton; Figure 2.1). Luck and Hillyard instructed participants to press a button depending on whether an orientation singleton was present. Critically, the four types of displays were randomly intermixed so that participants could not predict the orientation of the singleton. By this design, Luck and Hillyard reasoned that the implementation of a spatial-filtering mechanism in this task would be counterproductive because suppression of items in the search array would impede the process of comparing each item with its surrounding during singleton detection. Consistent with the spatial filtering hypothesis, there was no evidence of the N2pc nor of any visual processes beyond the basic sensory activity elicited by the search display. This null result further suggests that singleton detection does not involve the same selection processes as those found in feature search and that attention may not even be required for singleton detection.

Following the discovery of the N2pc, the results of several studies buttressed Luck and Hillyard's (1994a, 1994b) claim that the N2pc reflects some aspect of attentional selection. Four such lines of evidence are outlined here (for a comprehensive review, see Luck, 2012). First, the amplitude of the N2pc is enhanced when a greater degree of attentional focus is required (e.g., Luck et al., 1997). Second, the N2pc is known to track serial shifts of attention from one side of fixation to another when observers must closely inspect multiple singletons to find a specific target (e.g., Woodman & Luck, 1999, 2003). Third, consistent with the known effect of salience on search guidance (Itti & Koch, 2000, 2001), the N2pc appears earlier for more salient objects (e.g., Gaspar & McDonald, 2014; Luck et al., 2006). Fourth, consistent with the known effect of intertrial priming on search performance (Maljkovic & Nakayama, 1994), the N2pc occurs earlier when the target feature repeats than when they change across consecutive trials (e.g., Christie, Livingstone, & McDonald, 2015; Eimer, Kiss, & Cheung, 2010).

It should be noted, however, that all these N2pc findings likely reveal attentional processing either involved in discriminating a target feature following target detection (in a so-called compound-search task; Duncan, 1985) or involved feature-guided search.

When observers have to discriminate a target's feature following target detection, it is unclear whether the N2pc is triggered by process(es) associated with feature detection or subsequent discrimination. Moreover, many of these studies used multiple-singleton displays, either to balance the sensory energy from the target or to isolate target and distractor processing, and such multiple-singleton displays encourage the adoption of feature search mode because singleton detection would presumably lead to accidental selection of the nontarget singleton on some trials. At the very least, given that (a) all these studies require feature discrimination and that (b) many of these studies permit both feature search and singleton detection, it cannot be determined conclusively whether the N2pc also occurs during singleton detection.

On the Functional Significance of the N2pc

Although researchers agree that N2pc broadly reflects some processes associated with the focusing of attention, they have since found results that are inconsistent with the spatial filtering hypothesis of the N2pc. For example, Eimer (1996) argued that the N2pc reflects target enhancement, not spatial filtering, by showing that an N2pc was found contralateral to the target even though there were no other objects in its vicinity (the only other object was in the opposite visual field; for a similar finding, see Wijers, Lange, Mulder, and Mulder, 1997). Moreover, using analogous singleton-detection and feature-discrimination tasks in the color dimension, Mazza, Turatto, and Caramazza (2009a, 2009b) failed to replicate Luck and Hillyard's (1994b) null result. In these follow-up studies, color singletons were found to elicit the N2pc even when participants should have been in singleton detection mode due to the unpredictable swapping of target and nontarget colors (as in Luck and Hillyard's seminal experiment). In another study involving singleton detection, Schubö et al. (2004) found that whereas no N2pc was observed for displays containing 6 or fewer items, the N2pc was evident for set sizes ranging from 10 to 49. More recently, Tan and Wyble (2015) proposed an alternative hypothesis that the N2pc reflects the process of target localization prior to the deployment of attention. In their study, Tan and Wyble reported that when two targets were rapidly presented at the same location, only one N2pc was observed, but two N2pcs were observed when the two targets were presented in quick succession at different locations.

Despite the debate surrounding its functional significance, the N2pc remains as the gold-standard, electrophysiological marker of visual attention that has greatly contributed to the study of visual search, visual distraction, and attentional impairments. Still, unless the debate on the process that gives rise to the N2pc is resolved, theories on attention and nature of attentional impairments may be misinformed. For example, Luck and Gold (2008) argued that the attentional deficits exhibited by individuals with schizophrenia do not arise from an inability to filter out nontarget items because their N2pc is comparable to that of healthy individuals. By other accounts of the N2pc, however, one might argue instead that individuals with schizophrenia have no deficit in target-enhancement processes or target-localization processes.

When taking into consideration all the aforementioned N2pc findings, it could be tentatively concluded that this ERP component reflects a feature-based, template-matching process. In fact, the N2pc may be a visual-evoked equivalent of another ERP component found in the auditory modality called the processing negativity (Näätänen, 1982), which is theorized to reflect a process of matching the attended sound with an actively maintained, internal representation of the target. This template-matching account of the N2pc is consistent with studies showing objects that partially match the target feature template also elicit the N2pc but at a reduced amplitude (Eimer & Grubert, 2014; Kiss et al., 2013) and with the fact that the N2pc is only consistently observed in tasks that permit feature search or that require feature discrimination and not in pure singleton-detection tasks.

More specifically, the N2pc may reflect the establishment of an *object file* during the template-matching process. According to Kahneman, Treisman, and Gibbs (1992), an object file is a short-term representation of an attended object that stores relevant information of that object. By this view, the template-matching process involves the creation of an object file, accessing of the object file, retrieval of information from the object file, and comparison of said information with that of the target template. This functional interpretation of the N2pc is in line with studies that show an increase in the N2pc amplitude with increase with number of enumerated objects (Ester, Drew, Klee, Vogel, & Awh, 2012; Mazza & Caramazza, 2011; Mazza, Pagano, & Caramazza, 2013; Pagano & Mazza, 2012), presumably because each enumerated object would require its own object file. The object-filing interpretation can also account for the absence of N2pc to the second of two same-location targets in Tan and Wyble's (2015) study because

objects presented in temporal and spatial proximity are likely to be bound to the same object file (Downing & Treisman, 1997).

Although numerous studies support the template-matching account of the N2pc, this account fails to explain reports of the N2pc in a few singleton-detection experiments (e.g., Mazza et al., 2009a, 2009b; Schubö et al., 2004) because searching for a singleton by way of template matching in a pure singleton-detection task is presumed to be counterproductive. The veracity of the singleton-detection N2pc remains equivocal, however, in light of the null N2pc result from Luck and Hillyard's (1994b) singleton-detection experiment. Considering the importance of Luck and Hillyard's negative finding for the functional interpretation of the N2pc and for our understanding of the potential involvement of attention in singleton detection, it is surprising to find that few studies have attempted to verify this result using similar singleton-detection tasks. The study that most closely resembles Luck and Hillyard's singleton-detection experiment thus far is the one conducted by Schubö et al. (2004). In this study, investigators used orientation singletons in a singleton-detection task that varied in set size. It was found that the N2pc was only observable when the set size reaches a sufficiently large number, so that the N2pc was only evident in set sizes ranging from 10 to 49 items and not in displays with 6 or fewer items. Although Schubö et al. suggested that the absence of the N2pc in displays with few items was due to detection being less attentionally demanding at those set sizes, they did not make any conclusion regarding the functional significance of the N2pc. Nevertheless, the positive N2pc result in this study (especially for the 10-item display, which most closely resembles Luck and Hillyard's singleton-detection display) failed to replicate the null result that has been central to Luck and Hillyard's spatial filtering hypothesis.

At first glance, the N2pc found by Schubö et al. (2004) should indicate that it does not reflect spatial filtering, but the different statistical and analytical decisions made between the two studies have led to difficulty in drawing a definite conclusion. In concluding that an N2pc was present in the 10-item display, Schubö et al. may have made a Type I error for two reasons. First, Schubö et al. did not correct for multiple comparisons when testing for presence of an N2pc across the four set sizes (the contralateral negativity observed in the 10-item display had $p = .037$, which does not survive a Bonferroni correction for four ANOVAs). Second, Schubö et al. used a later measurement window of 250-350 ms, instead of Luck and Hillyard's (1994b) original

window of 200-275 ms, to quantify the N2pc but did not provide a clear justification for doing so. Alternatively, in concluding that an N2pc was absent in their singleton-detection experiment, Luck and Hillyard may have made a Type II error. With a sample size of 12 participants in Luck and Hillyard's singleton-detection experiment, the statistical power to detect a medium-sized effect ($d = 0.50$) was only 0.35. Moreover, these authors derived their 200-275-ms measurement window from search tasks in which the target feature is fixed across trials, but the processes involved in the detection of variable-feature targets may result in a later N2pc that is more in line with Schubö et al.'s measurement window. In fact, Eimer et al. (2010) have shown the N2pc to onset 50 ms later in a variable-feature search task when compared with a fixed-feature search task of the same stimuli.

1.4. Aims of this Thesis

The present thesis has four aims. The first general aim is to elucidate some of the neuro-cognitive processes involved in singleton detection, since little is known about such processes (Proulx & Serences, 2006). The second aim is to provide a definitive answer to the longstanding question as to whether attention is involved in the detection of a singleton (specifically, when its defining feature is not known in advance; Chapter 2). Because the N2pc would be measured in pursuit of this second aim, an important third aim is to reassess the functional significance of the N2pc itself. Finally, given the salience-driven nature of singleton detection, the fourth aim is to determine whether processes involved in singleton detection can be overridden by more goal-driven processes associated with task relevance (Chapter 3).

Chapter 2 revisits Luck and Hillyard's (1994b) question of whether the N2pc would be present in a singleton-detection task that prevents feature-guided search and discourages the hypothetical spatial-filtering process that was presumed to drive the N2pc. As it currently stands, the absent N2pc in Luck and Hillyard's seminal singleton-detection task would indicate that spatial attention is not involved in singleton detection, on the grounds that no ERP activity was observed aside from the visual-evoked potentials elicited by the search array. In Chapter 2, I reexamine Luck and Hillyard's claim by replicating their singleton-detection task with five modifications to improve the statistical power. These modifications include (a) increasing the number of trials from 800 to 1,400; (b) testing for the presence of an N2pc elicited by singletons in the lower

visual field, where the N2pc has been observed to be larger (Luck et al., 1997); (c) analyzing ERPs recorded from electrodes PO7 and PO8, where the N2pc is maximally distributed, instead of the average recordings from the four nearby electrodes (O1, O2, P7, and P8); (d) quantifying the N2pc in two additional ways to avoid any potential statistical bias; and (e) increasing the sample size from 12 to 26. If no N2pc is observed following these modifications, then the N2pc reflects, at least in part, the suppression of items near the target. Alternatively, if an N2pc is observed in this task, where filtering activity is presumed to be minimal, then the N2pc reflects some process associated with the attended target itself. In this chapter, I provide evidence that N2pc is, in fact, observable in a singleton-detection task that discourages spatial filtering, demonstrating that spatial attention is involved in the detection of singletons. Functional significance of the N2pc is then discussed in view of extant N2pc findings in other visual-search paradigms. Other findings are also discussed, including a newly discovered ERP component that tracks the time course of singleton detection called the singleton detection positivity (SDP).

Chapter 3 introduces a go/no-go element to the singleton-detection task to investigate whether salient-but-irrelevant singletons automatically trigger the singleton-detection processes observed in Chapter 2 (e.g., the N2pc and SDP) or whether such processes can be prevented by other, higher-level processes associated with the observer's intentions. According to the salience-driven selection hypothesis (Theeuwes, 1991a, 1992, 2004, 2010), (a) the most salient object invariably captures attention and (b) stimulus-driven selection processes must be completed before goal-driven processes can begin. By this account, salient-but-irrelevant singletons would always trigger singleton detection. However, other hypotheses have proposed that goal-driven processes can occur early to prevent salience-driven selection (e.g., Folk, Remington, & Johnston, 1992; Sawaki & Luck, 2010). The singleton-detection task is especially well-suited to evaluate these competing claims for two reasons. First, the singleton is necessarily the most salient stimulus in the singleton-detection display. Second, selection processes elicited by the singleton are necessarily stimulus-driven in singleton-detection mode. Chapter 3 details a singleton-detection experiment similar to that in Chapter 2, except that half of the displays contained yellow lines (instead of cyan) to indicate that responses should be withheld on that trial (i.e., no-go trials; color counterbalanced across participants). In particular, no-go trials were randomly

intermixed with the usual go trials to determine whether participants would terminate visual processing on no-go trials before or after attending to the salient singleton. Because go and no-go displays contained differently colored lines, go and no-go trials were differentiated based on the (global) color of lines throughout the display. I show in Chapter 3 that (a) singletons on no-go trials elicited a markedly reduced SDP and no N2pc and that (b) an ERP component associated with the goal-driven evaluation of stimulus relevance called the P2a emerged prior to the N2pc. These findings run counter to the twin assertions proposed by the salience-driven selection hypothesis and demonstrate that rapid, trial-by-trial assessment of task relevancy can precede and override salience-driven capture of attention. Additionally, I discuss the mechanism by which singleton detection is suppressed along with other findings.

Chapter 2. Experiment 1

The study detailed in this chapter was reported in a recent publication: Tay, D., Harms, V., Hillyard, S. A., & McDonald, J. J. (2019). Electrophysiological correlates of visual singleton detection. *Psychophysiology*, 56(8), e13375.

2.1. Introduction

The primary goal of Experiment 1 was to determine whether a target singleton will elicit the N2pc in a singleton-detection task that prevents the use of a template-matching strategy and discourages the filtering of nontarget items in the display. As illustrated in Figure 2.1, participants viewed search displays containing seven identical nontargets and a target singleton that was rotated 90 degrees (target-present trials) or eight identical nontargets (target-absent trials). The orientations of the target and nontarget were swapped randomly across trials so that observers would not know in advance whether they would be required to search for a horizontal target or a vertical target. As summarized by Luck (2012, p. 349), observers participating in this task would be encouraged “to adopt a *singleton detection mode*, in which they try to detect feature discontinuities rather than trying to identify specific target features” and that “no N2pc activity should be observed” because “filtering should be minimized.” Indeed, as noted in Section 1.3.3, Luck and Hillyard (1994b) reported a statistically nonsignificant N2pc and concluded that there is no N2pc activity when the task discourages filtering. Given the importance of this conclusion to our understanding of the N2pc and the role of attention in singleton detection mode, the present study sought to test the veracity of this null result.

Five methodological changes were made to Luck and Hillyard's (1994b) singleton-detection experiment to improve its statistical power. First, to increase the ERP's signal-to-noise ratio, the experiment contained an additional 600 trials. Second, the effect size of the N2pc was increased by specifically looking at ERPs elicited by singletons in the lower visual field (because it has been shown that N2pc elicited by lower-field targets are larger than those elicited by upper-field targets; Luck et al., 1997). Third, this experiment further increased the effect size by measuring the N2pc from electrodes PO7 and PO8, where the N2pc is found to be maximal, instead of averaging

the ERPs recorded across the four nearby electrodes (O1, O2, P7, and P8). Fourth, in addition to using Luck and Hillyard's (1994b) mean-amplitude measurement window (200-275 ms post stimulus onset), the analysis quantified the N2pc in two other ways: (a) as the mean amplitude in a 250-350-ms time window and (b) as the signed negative area in a 200-350-ms time window. The 250-350-ms measurement window was chosen with the knowledge that an N2pc can be delayed by 50 ms in variable-feature search (Eimer et al., 2010) and to match what was used by Schubö et al. (2004). The 200-350-ms measurement window was selected to encompass both the early and late measurement windows and to avoid *cherry-picking* a biased result based on observed data (Luck, 2012). Lastly, the sample size was increased from 12 to 26, which was determined based on the prediction that the methodological modifications would result in an N2pc equivalent to, at least, a medium-sized effect (i.e., $d \geq 0.50$, power $\geq .72$). This statistical consideration was based on Luck's (2012) revised hypothesis that "*little to no* N2pc activity should be observed" (p. 349) in this task.

Because of the attempt to increase statistical power and the use of the multiple measurement windows, it was decided a priori to base all conclusions on the signed negative area measure obtained from ERPs elicited by lower-field targets using the wide measurement window (200-350 ms). Following this decision, the null hypothesis was that the signed negative area should be no greater than that expected by random noise alone (i.e., by chance). If the null hypothesis were true, it would be concluded that the N2pc reflects suppression of objects near the target and that reduction of filtering eliminated the N2pc in this task. The alternative hypothesis was that the signed negative area would be larger than that expected by random noise alone. This statistical hypothesis was premised on the conceptual hypothesis that the N2pc reflects processes associated with the attended target itself rather than the filtering of nearby objects. Apart from the N2pc analyses, additional analyses were performed to discover other, potential electrophysiological correlates of singleton detection (to be further discussed in the following section).

2.2. Method

The Research Ethics Board at Simon Fraser University (SFU) approved the research protocol. All experimental procedures were performed in accordance with

guidelines and regulations outlined by SFU and the Natural Sciences and Engineering Research Council of Canada (NSERC).

2.2.1. Participants

Thirty-one young adults without history of neurological disorders participated after giving informed consent. Individuals received course credit as part of a departmental research participation system for their participation. All subjects reported normal or corrected-to-normal visual acuity and were tested for normal color vision using Ishihara color plates prior to participation. Data from five participants were excluded from further analyses because more than 25% of trials were contaminated by ocular artifacts (rejection criterion set in advance). Of the remaining 26 participants (mean age: 21.6 years), 15 were female and 11 were right-handed.

2.2.2. Apparatus

The experiment was conducted in a sound-attenuated and electrically shielded chamber dimly illuminated by DC-powered LED lighting. A height-adjustable LCD monitor running at 120 Hz presented visual stimuli. Participants sat in a chair and viewed the monitor at a distance of approximately 57 cm and made their responses using a gamepad. A Windows-based computer controlled stimulus presentation and registered participants' button presses using Presentation (Neurobehavioral Systems, Inc., Albany, CA). A custom software (Acquire) recorded EEG from a second, Windows-based computer, which housed a 64-channel A-to-D board (PCI-6071e, National Instruments, Austin, TX) that connected to an EEG amplifier system with an input impedance of 1 G Ω (SA Instruments, San Diego, CA). The stimulus-control and EEG-acquisition computers were situated outside of the testing chamber.

2.2.3. Stimuli and Procedure

Each stimulus display consisted of a small, white fixation cross ($0.3^\circ \times 0.3^\circ$; 0.3 cd/m^2) positioned at the middle of the display and eight cyan lines ($0.3^\circ \times 1.0^\circ$; $x = .20$, $y = .35$, 17.5 cd/m^2) that appeared within a $10.7^\circ \times 7.9^\circ$ region around fixation (Figure 2.1). The coordinates of the lines were determined randomly, with the restrictions that all displays contain four lines on either side of fixation without crossing the horizontal or

vertical meridians and that no lines connect or overlap. Target-absent displays contained eight horizontal or eight vertical lines. Target-present displays were identical to target-absent displays except one of the eight lines was replaced with a line of an orientation orthogonal to that of the surrounding lines. The four types of displays were randomly intermixed and presented with equal probability. Each display was presented for 750 ms, and the time between stimulus onset (stimulus onset asynchrony; SOA) varied randomly between 1,350 ms and 1,650 ms. Participants pressed either the left or right shoulder button on the gamepad with their index fingers to indicate whether the target orientation singleton was present or absent. The stimulus-response mapping was counterbalanced across participants. Participants maintained eye fixation on the fixation cross and learned the task by completing at least one block of trials as practice prior to the experiment. The entire experiment comprised of 35 blocks of 40 trials for a total of 1,400 trials, with participant-controlled rest periods between blocks.

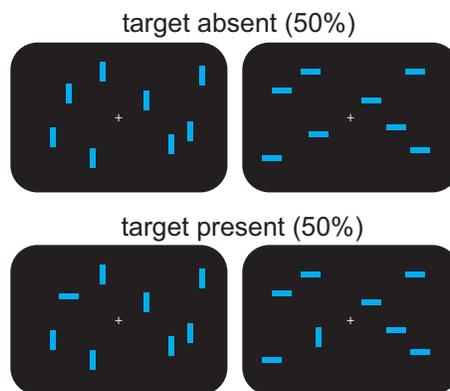


Figure 2.1. Example displays used in Luck and Hillyard's (1994b) singleton-detection experiment and in Experiment 1.

2.2.4. Behavior

Median RTs for target-absent and target-present trials were computed separately for each participant. The analysis excluded trials on which participants responded incorrectly, too quickly (RT < 100 ms), or too slowly (RT > 1,350 ms). The target-present trials were further subdivided into upper-field target and lower-field target trials. Finally, median RTs were derived for subsets of target-present trials based on whether the preceding trial contained a target with the same orientation (i.e., *repeat-orientation trials*) or opposite orientation (i.e., *change-orientation trials*) to determine whether the repeating of a target feature in this singleton-detection task facilitates search (i.e., priming of pop-

out; Maljkovic & Nakayama, 1994). Assessments of statistical significance were performed using paired-sample *t* tests with two tails.

2.2.5. Electrophysiology

Recording and Preprocessing

EEG signals were recorded from 25 sintered Ag/AgCl electrodes positioned at standard 10-10 sites (FP1, FPz, FP2, F7, F3, Fz, F4, F8, T7, C3, Cz, C4, T8, P7, P3, Pz, P4, P8, PO7, POz, PO8, O1, Oz, O2, M1). During recording, all EEG signals were referenced to an electrode positioned on the right mastoid, and the ground electrode was positioned over the midline frontal scalp at site AFz. To track horizontal eye movements, an additional pair of electrodes placed 1 cm lateral to the external canthus of each eye recorded horizontal electrooculographic (HEOG) activity. Eye blinks were monitored using the FP1 electrode and all electrode impedances were kept below 15 k Ω . EEG and EOG signals were amplified with a gain of 20,000, filtered using a bandpass filter of 0.01-100 Hz (two-pole Butterworth), and digitized at 500 Hz. The EEG signals were stored on a computer for offline averaging. A semiautomated procedure was performed to remove epochs of EEG that were contaminated by horizontal eye movements, blinks, or amplifier blocking (for a detailed description, see Green, Conder, & McDonald, 2008). Artifact-free data were low-pass filtered (half-power cutoff) at 30 Hz to create averaged ERP waveforms. Each EEG channel was digitally rereferenced to the average of the left and right mastoid channels. The grand-averaged event-related HEOG deflection was kept below 2 μ V.

ERPs elicited by displays containing a target in the left or right visual field were combined in such a way as to produce waveforms recorded contralateral and ipsilateral to the target. To isolate the N2pc, ipsilateral ERPs were subtracted from corresponding contralateral ERPs to produce *contralateral-ipsilateral difference waves*. Some additional analyses were performed on *present-absent difference waves*, which were computed by subtracting the target-absent ERPs separately from ERPs elicited by targets in the left and right visual field. Negative voltages were plotted upward by convention.

N2pc Analysis

All N2pc measurements were taken from contralateral-ipsilateral difference waves recorded from electrodes PO7 and PO8. All statistical tests were two-tailed, except for one-sample tests involving signed negative areas because all possible values were necessarily less than or equal to zero. To replicate and extend the measurement approaches taken by Luck and Hillyard (1994b) and Schubö et al. (2004), magnitude of the N2pc was quantified in three ways as noted in Section 2.1: as the mean amplitude within a 200-275-ms time window, as the mean amplitude within a 250-350-ms window, and as the signed negative area within a 200-350-ms window. One-sample *t* tests were conducted on ERPs elicited by all target-present trials to determine whether the mean amplitudes within the early and late measurement windows differed significantly from 0 μ V. Next, contralateral-ipsilateral difference waves elicited by upper- and lower-field targets were separately measured. A paired-sample *t* test was performed to confirm that the N2pc was larger for lower-field targets than for upper-field targets. A one-sample *t* test was also done to determine whether an N2pc was statistically present for lower-field targets. I did not test whether upper-field targets elicited a statistically significant N2pc because (a) there was likely insufficient power to detect the predictably small effect and (b) the result of such a test would not contribute to the goal of the present experiment.

To verify the findings from the mean-amplitude tests, similar tests were conducted using the signed negative area measured within the wide measurement window (200-350 ms). Because measurements of signed negative area are biased to be nonzero even in the absence of a signal, conventional statistical approach of testing observed values against zero was replaced with a nonparametric, permutation approach that estimated the distribution of values generated by noise alone (Sawaki et al, 2012). This process was accomplished by first randomly designating the side (left, right) on which the target appeared in each target-present display to eliminate any lateralized ERP signal, so that the remaining lateralized ERP activity could be estimated as noise. Subsequently, the noise estimation produced for each participant was combined to construct a grand-averaged ERP. This process was repeated 500 times to yield 500 different permuted, grand-averaged ERPs. The signed negative areas obtained from these ERPs were used to provide a distribution of values expected if the null hypothesis were true. In line with the traditional threshold for statistical significance, the observed grand-averaged N2pc was considered statistically present if the measured signed area

fell beyond the 95th percentile of the estimated noise distribution. The p value for this permutation test was calculated using the following equation (Phipson & Smyth, 2010; see also Gaspelin & Luck, 2018a):

$$p = \frac{1 + (\text{number of permuted values} \geq \text{observed area})}{1 + \text{total number of permutations}} \quad (1)$$

Two more sets of analyses were conducted to further verify the N2pc, using paired-sample t tests. The first test examined whether repeat-orientation trials elicited an N2pc earlier than one from change-orientation trials. This prediction was based on behavioral (Maljkovic & Nakayama, 1994) as well as electrophysiological (Christie et al., 2015; Eimer et al., 2010) evidence of intertrial facilitation from repeated targets. Onset latency of N2pc was quantified as the time point at which the N2pc first reaches 50% of its peak amplitude within the 200-350-ms measurement window, using the jackknife approach (Miller, Patterson, & Ulrich, 1998). The second set of analyses compared the amplitude and latency between N2pc waveforms elicited by fast- and slow-response trials, on the hypothesis that the N2pc would be larger or earlier for fast-response trials. The fast- and slow-response trials were computed based on the median RTs of individual participants (i.e., a median split; see McDonald, Green, Jannati, & Di Lollo, 2013). Signed negative area within the 200-350-ms window was used to compare differences in N2pc magnitude and 50% peak amplitude latency was used to assess the timing of N2pc elicited between the fast- and slow-response trials. To establish whether an N2pc is reliably elicited during singleton detection, the split-half reliability of the N2pc signed area measure was estimated by sorting alternating target-present trials into two different averaging bins, constructing contralateral-ipsilateral difference waves for the two halves of trials for each participant, measuring the signed negative area in the 200-350-ms window for each half, and computing the Spearman-Brown coefficient between N2pc areas measured from the split halves.

Additional Analyses

Beyond the N2pc analyses, additional analyses aimed to explore other processes involved in singleton detection, focusing on a lateralized negativity in the time

range of the N1 peak (the so-called N1pc) and an occipital positivity in the time range of the P3b. The N1pc, like the N2pc, is a negativity over the posterior contralateral scalp but in the time range of the N1. The N1pc has been attributed to the reflexive orienting of attention to unilateral stimuli (Wascher & Beste, 2010a, 2010b), as well as the stimulus-driven selection of stimuli during the initial sweep of visual processing (Verleger, & Grajewski, & Jaśkowski, 2012). The N1pc was quantified as the mean amplitude within a 150-200-ms time window, selected based on the conventional time range of the N1. To evaluate whether the N1pc was associated with singleton detection, presence of an N1pc was verified in target-present trials using a one-sample *t* test. A subsequent paired-sample *t* test was performed to compare magnitude of N1pc between upper-field and lower-field targets. Furthermore, one-sample *t* tests were conducted to investigate whether an N1pc was present for repeat- and change-orientation trials as well as fast- and slow-response trials. Additional paired-sample *t* tests were done to see whether N1pc would be larger on repeat-orientation and fast-response trials.

The P3b-like occipital positivity has been previously reported in other studies (Luck & Hillyard, 1990, 1994a; Schubö et al., 2004), and it has been shown to be larger on target-present trials than on target-absent trials. Even though previous studies have equated this positivity to the P3b, and thus measured the positivity in the time range of P3b (350-550 ms), pilot data suggest that this positivity is a separate component that occurs earlier and distributes bilaterally over the occipital scalp (instead of over the midline parietal scalp). To characterize this occipital positivity—herein called the *singleton detection positivity* (SDP)—its timing was measured and subsequently used to determine its appropriate mean-amplitude measurement window.

All SDP measurements were taken from the present-absent difference waves to isolate activity specifically linked to processes associated with the singleton target and to minimize overlap from components like the P3b. Using the jackknife approach, onset latency of the SDP was estimated as the first time point at which SDP reaches 25% of its peak amplitude within a 200-400-ms window. A difference in onset latencies between the ipsilaterally and the contralaterally recorded SDP (presumably driven by the overlapping N2pc) was assessed with a paired-sample *t* test. Moreover, the measured SDP latency was compared with the jackknifed, 25% peak latency of N2pc, using a paired-sample *t* test. The appropriate mean-amplitude measurement window for the SDP was selected by performing one-sample *t* tests of mean amplitudes measured at

consecutive 50-ms time windows, separately at ipsilateral and contralateral electrodes (PO7/8), starting just before the measured onset latency (e.g., the first 50-ms window will be 201-250 ms if measured SDP latency falls within that interval). Following the determination of SDP's mean-amplitude measurement window, the split-half reliability for both the ipsilateral and contralateral SDP was computed. As an added confirmatory measure for presence of the N2pc, N1pc, and SDP, 95% confidence intervals (CIs) were computed for contralateral-ipsilateral difference waves elicited by all targets, upper-field targets, and lower-field targets, as well as for ipsilaterally and contralaterally recorded present-absent difference waves.

A final set of exploratory analyses sought to discover whether select ERP measures of interest linearly correlate with magnitude of N2pc or with RT. Intercomponent correlations were computed using Pearson correlation coefficients, between the signed negative area of N2pc (measured in the 200-350-ms window) and each of the following ERP measures: mean amplitude of P1 (75-125 ms, averaged across electrodes PO7/8), mean amplitude of N1 (150-200 ms, averaged across electrodes PO7/8), mean amplitude of N1pc (150-200 ms), and mean amplitude of ipsilaterally recorded SDP (to avoid issue of N2pc-SDP overlap over the contralateral scalp). Pearson correlation coefficients were also computed between RT and each of the following ERP measures: area of N2pc (as previously measured), onset latency of N2pc (at 25% peak), mean amplitude of SDP (as previously defined), and onset latency of SDP (at 25% peak). Tests for intercomponent correlations and RT correlations were conducted separately across all participants, with each test having a significance threshold at .0125 after correcting for multiple comparisons (per-test $\alpha = .05/4$).

Topographical Mapping

Topographical voltage maps of ERPs were constructed by spherical spline interpolation (Perrin, Pernier, Bertrand, & Echallier, 1989). Contralateral-ipsilateral difference maps were produced by first subtracting the ipsilateral topography from the contralateral topography at corresponding electrode locations, then projecting this difference topography over both sides of the head using the conventional approach (e.g., Green et al., 2008). ERPs elicited by target-present displays were mapped by collapsing over left and right targets and left and right electrodes such that electrodes on the left and right sides were ipsilateral and contralateral to the target, respectively. ERPs elicited

by target-absent displays were mapped using the original electrode montage with left and right electrodes positioned on the left and right sides of the head, respectively.

2.3. Results

2.3.1. Behavior

There was no RT difference between target-present and target-absent trials (536 ms vs. 531 ms, respectively), $t(25) = 0.98$, $p = .335$, or between upper-field targets and lower-field targets (534 ms vs. 538 ms, respectively), $t(25) = 1.38$, $p = .180$. Participants were faster to respond on repeat-orientation than on change-orientation trials (550 ms vs. 569 ms, respectively), $t(23) = 6.78$, $p < .001$, indicating the occurrence of priming of pop-out (Maljkovic & Nakayama, 1994).

2.3.2. Electrophysiology

Figure 2.2 shows the ERPs elicited by the target singleton on target-present trials. The N2pc was statistically absent when measured using Luck and Hillyard's (1994b) early measurement window ($-0.18 \mu\text{V}$), $t(25) = 1.39$, $p = .180$, but present when measured using Schubö et al.'s (2004) late measurement window ($-0.49 \mu\text{V}$), $t(25) = 2.95$, $p = .007$, $d = 0.58$, replicating the findings of the respective studies. Additionally, the signed negative area measured using the wide measurement window yielded a statistically significant result ($-54.9 \mu\text{V}^*\text{ms}$), $p = .002$, confirming Schubö et al.'s positive finding (Figure 2.3A). The residual HEOG deflection in the grand-averaged HEOG waveform was smaller than the N2pc and began approximately 282 ms post stimulus onset, indicating that the observed N2pc was not saccade-induced activity (Figure 2.2B). The preceding N1pc ($-0.16 \mu\text{V}$) was marginally significant, $t(25) = 2.03$, $p = .053$, $d = 0.40$.

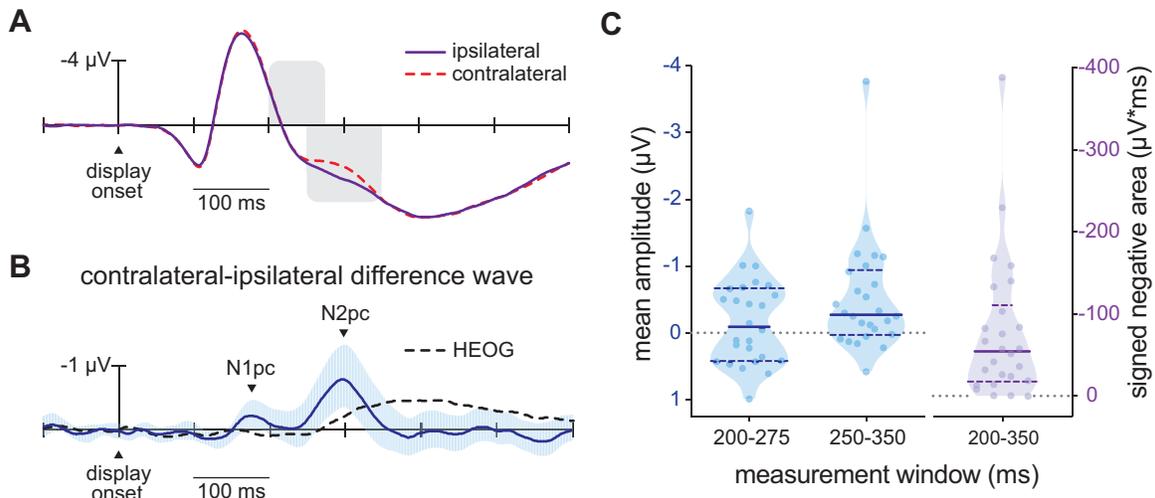


Figure 2.2. Grand-averaged ERPs recorded over the lateral occipital scalp (electrodes PO7, PO8). (A) Waveforms recorded contralateral and ipsilateral to target singletons in all target-present displays. Shaded regions depict the time windows used to measure the N2pc mean amplitude (200-275 ms, 250-350 ms). (B) Contralateral-ipsilateral difference wave corresponding to the waveforms in (A). Blue vertical bars correspond to the 95% CIs at each time point. The residual HEOG deflection is plotted alongside the difference wave to contrast its latency and magnitude with that of the N2pc. (C) Violin plots showing the median, quartiles, and individual-participant data points of N2pc measured in the three measurement windows.

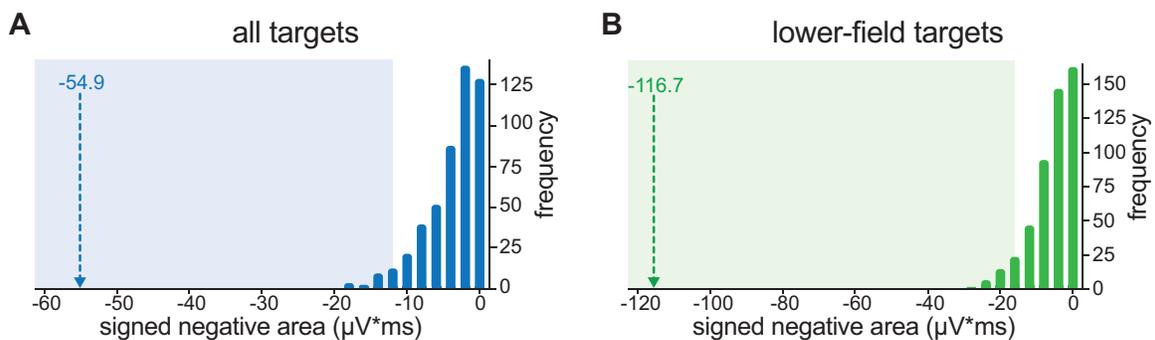


Figure 2.3. Results of permutation tests of the signed negative areas within the time interval of the N2pc (200-350 ms). Vertical bars indicate the distributions of signed negative areas of the scrambled grand averages (i.e., noise distributions). Shaded regions indicate the signed negative areas above the 95th percentile from the noise distributions, and vertical dashed lines indicate the measured signed negative areas from the original, unscrambled data sets. (A) Test result for all target-present trials. (B) Test result for lower-field target trials.

Figure 2.4 shows the ERPs separately elicited by upper-field and lower-field target singletons. As expected, the N2pc was larger for lower-field targets than for

upper-field targets. This difference was found in the early measurement window (upper: 0.16 μV , lower: -0.48 μV), $t(25) = 3.33$, $p = .003$, $d = 0.82$, in the late measurement window (upper: -0.07 μV , lower: -0.89 μV), $t(25) = 4.77$, $p < .001$, $d = 0.88$, and in the wide measurement window (upper: -43.5 $\mu\text{V}\cdot\text{ms}$, lower: -135.1 $\mu\text{V}\cdot\text{ms}$), $t(25) = 4.76$, $p < .001$, $d = 1.01$. The difference in magnitude of N2pc was not driven by difference in saccadic activity because mean amplitude of residual HEOG activity measured in a 350-400 window did not vary between upper-field and lower-field targets (-0.44 μV vs. -0.45 μV , respectively), $t(25) = 0.06$, $p = .955$. For lower-field target displays, an N2pc was observed in the early measurement window, $t(25) = 2.51$, $p = .019$, $d = 0.50$, in the late measurement window, $t(25) = 4.15$, $p < .001$, $d = 0.81$, and in the wide measurement window (-116.7 $\mu\text{V}\cdot\text{ms}$), $p = .002$, demonstrating unequivocally the presence of a sizable N2pc. Moreover, split-half analysis of N2pc from all target-present trials revealed that the N2pc in the present experiment had a high split-half reliability (.96). Topographical mapping of the contralateral-ipsilateral difference wave confirmed that the lateralized negativity was largest at PO7/8 (Figure 2.5), consistent with previous reports of N2pc scalp distribution (Luck, 2012). The N1pc, like the N2pc, was larger for lower-field targets than for upper-field targets (-0.37 μV vs. 0.06 μV , respectively), $t(25) = 2.90$, $p = .008$, $d = 0.79$, and was also statistically present for lower-field targets, $t = 2.74$, $p = .011$, $d = 0.54$.

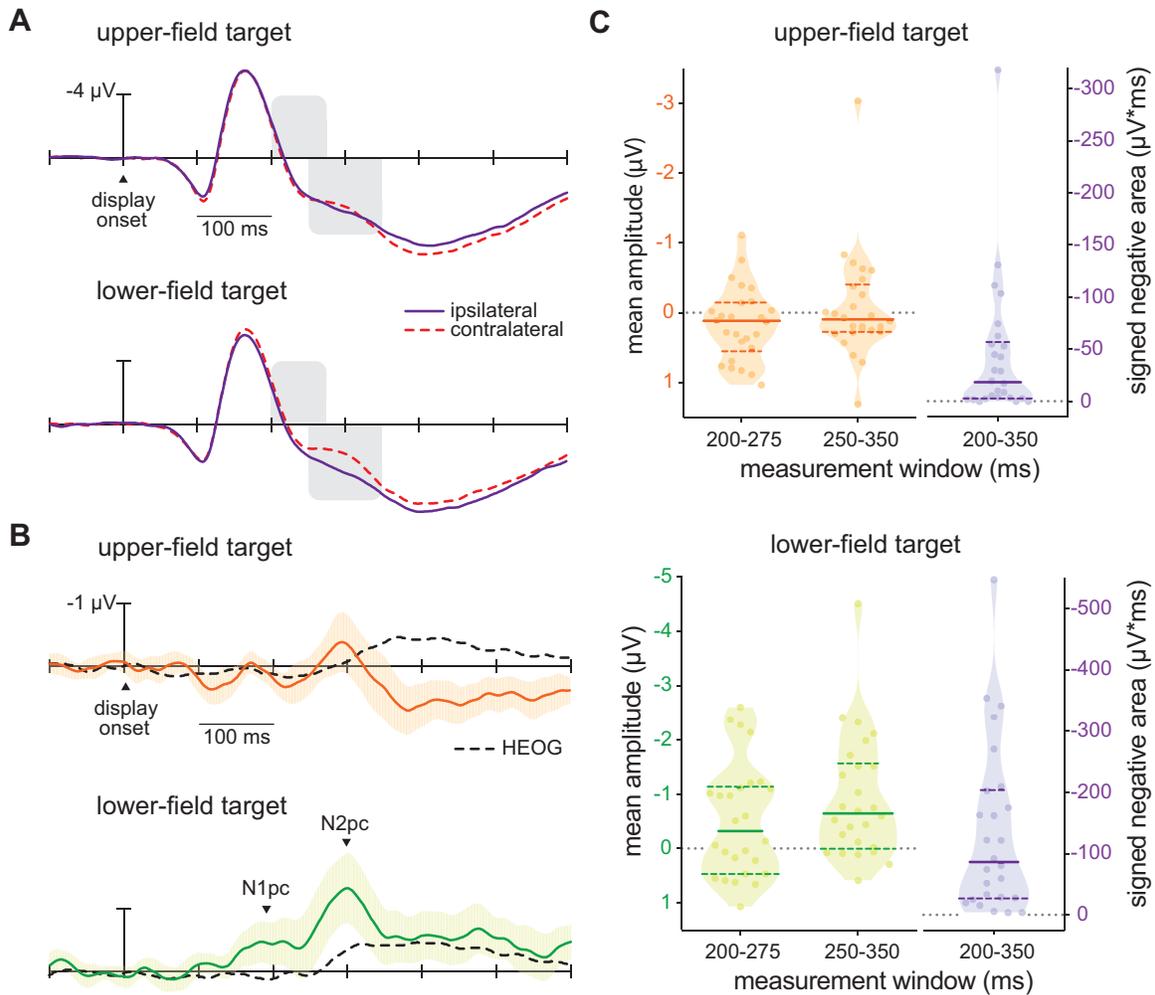


Figure 2.4. Grand-averaged ERPs elicited by upp-field and lower-field targets, recorded over the lateral occipital scalp (electrodes PO7, PO8). (A) Waveforms recorded contralateral and ipsilateral to the target. (B) Contralateral-ipsilateral difference waves corresponding to the ERP waveforms in (A), with vertical bars corresponding to the 95% CIs. The corresponding residual HEOG deflection is plotted alongside the difference waves to contrast its latency and magnitude with that of the N2pc. (C) Violin plots showing the median, quartiles, and individual-participant data points of N2pc measured in the three measurement windows.

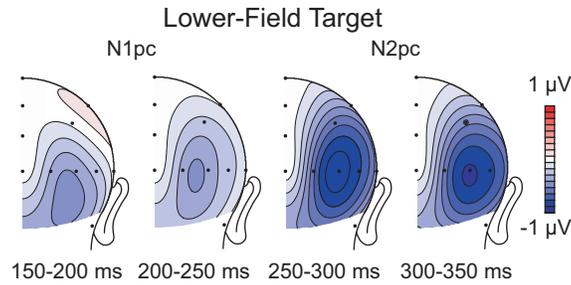


Figure 2.5. Topographical maps of the contralateral-ipsilateral difference wave for lower-field targets. Progression of lateralized activity is shown over the span of 150-350 ms.

Figure 2.6 shows the contralateral-ipsilateral difference waves elicited by repeat-orientation and change-orientation trials as well as fast-response and slow-response trials. Consistent with the RT effect, the N2pc was marginally earlier for repeat-orientation than for change-orientation trials (256 ms vs. 276 ms, respectively), $t(25) = 2.00$, $p = .056$, $d = 0.44$. By contrast, no difference in N2pc area was found (repeat-orientation: $-95.0 \mu\text{V}\cdot\text{ms}$, change-orientation: $-82.2 \mu\text{V}\cdot\text{ms}$), $t(25) = 0.85$, $p = .402$. These results suggest that priming of pop-out facilitated singleton detection in the present experiment. Similarly, RT-based median-split analysis comparing fast- and slow-response trials revealed that fast-response trials had an earlier (253 ms vs. 271 ms, respectively), $t(25) = 2.08$, $p = .048$, $d = 0.39$, but not a larger ($-98.0 \mu\text{V}\cdot\text{ms}$ vs. $-70.1 \mu\text{V}\cdot\text{ms}$, respectively), $t(25) = 1.49$, $p = .150$, N2pc, suggesting that an earlier N2pc facilitated singleton detection in the present experiment. An N1pc was evident on both repeat- and change-orientation trials, $t_s(25) \geq 2.60$, $p_s = \leq .016$, $d_s \geq 0.50$, but no difference in amplitude was found between the two trial types ($-0.52 \mu\text{V}$ vs. $-0.52 \mu\text{V}$, respectively), $t(25) = 0.03$, $p = .973$. An N1pc was also present on fast-response trials ($-0.37 \mu\text{V}$), $t(25) = 2.64$, $p = .014$, $d = 0.56$, but not on slow-response trials ($-0.06 \mu\text{V}$), $t(25) = 0.62$, $p = .539$.

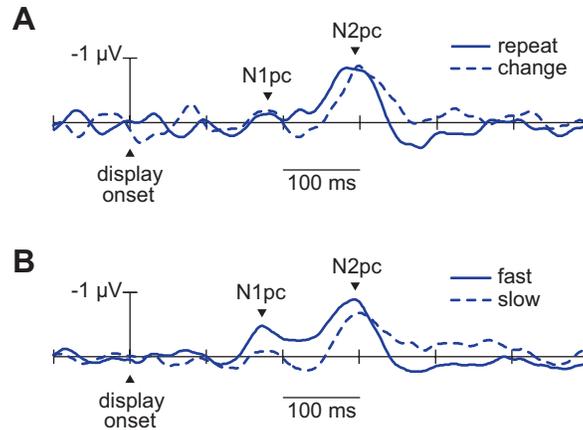


Figure 2.6. Contralateral-ipsilateral difference waves for select subsets of trials. (A) Difference waves for repeat-orientation and change-orientation trials. (B) Difference waves elicited by targets on fast-response and slow-response trials.

Figure 2.7 shows ERPs elicited by target-present and target-absent displays, as well as the difference in activity elicited between the two display types over the occipital scalp. As expected, a P3b was maximally observed over the midline parietal scalp for both target-present and target-absent trials. The P3b appeared larger on target-absent trials than on target-present trials at midline frontal, central, and parietal sites, but a greater positivity was observed over the lateral occipital scalp on target-present trials than on target-absent trials. This difference is herein referred to as the SDP to differentiate it from other components of the P3 family (including the P3b) and isolated by subtracting target-absent ERPs from target-present ERPs (i.e., present-absent difference wave).

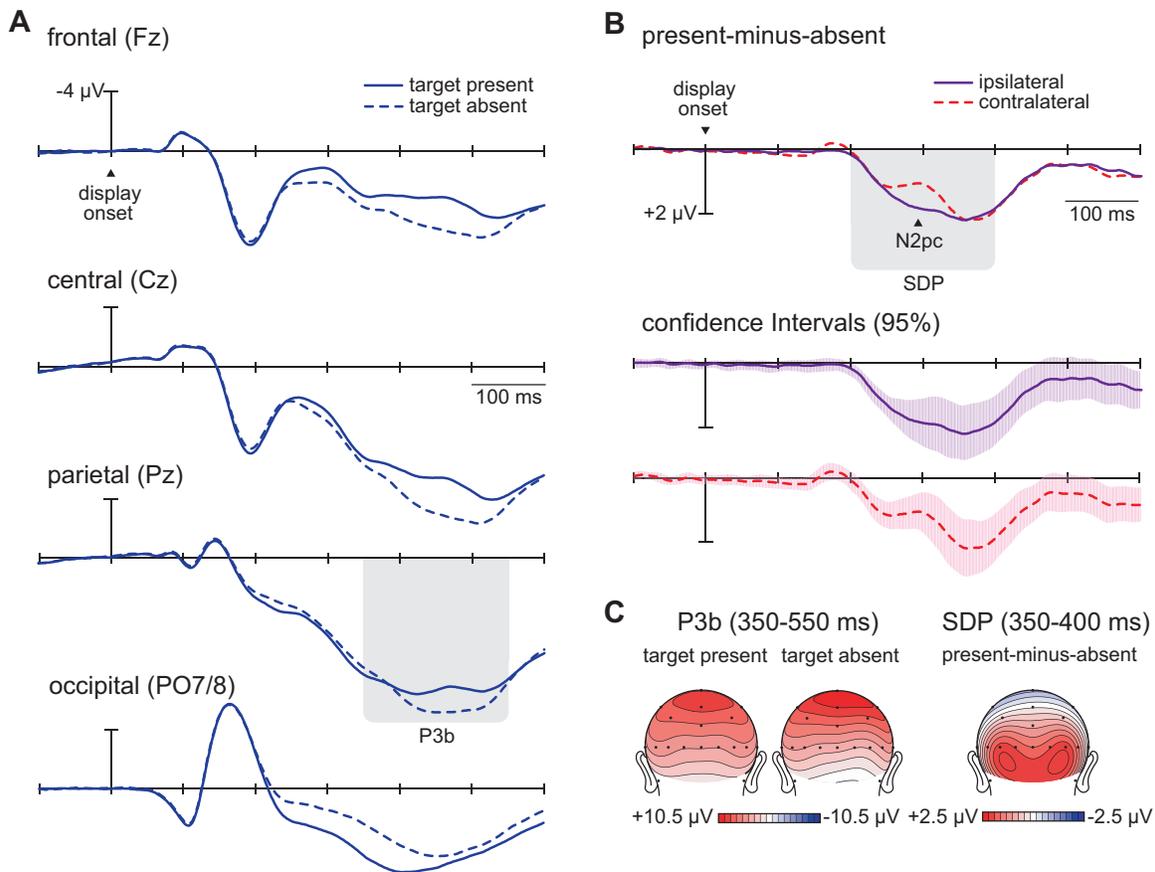


Figure 2.7. Isolation of target-singleton processing. (A) Grand-averaged ERPs elicited by target-present and target-absent displays, recorded over the midline frontal, central, and parietal scalp (electrodes Fz, Cz, Pz), well as the lateral occipital scalp (averaged across electrodes PO7 and PO8). Shaded region denotes the time range and scalp location of maximal P3b activity. (B) Upper: present-absent difference waves recorded over the contralateral and ipsilateral occipital scalp (electrodes PO7, PO8). Shaded region denotes the time range of maximal SDP activity. Lower: same as the waveforms above but separately plotted to show the corresponding 95% CIs of contralateral and ipsilateral SDP (purple and red vertical bars, respectively). (C) Left: topographical maps of the P3b elicited by target-present and target-absent displays. Right: topographical map of the present-absent difference waves.

The bilaterally symmetrical SDP was found to have onsets of 219 ms and 218 ms over the contralateral and ipsilateral scalp, respectively. The SDP latencies over the two hemispheres did not differ, $t(25) = 0.14$, $p = .891$. In comparison with onset latency of the N2pc (252 ms), onset latencies of SDP over the contralateral, $t(25) = 2.28$, $p = .031$, $d = 0.78$, and ipsilateral scalp, $t(25) = 3.27$, $p = .003$, $d = 0.89$, were found to be statistically earlier. Consistent with this finding, 95% CIs around the grand-averaged difference

waves became fully positive at 212 ms and 206 ms over the contralateral and ipsilateral scalp, respectively (Figure 2.7B), whereas those of the N2pc only became fully negative at 262 ms (Figure 2.2B). Furthermore, the CIs showed that both the contralateral (212-464 ms) and ipsilateral (206-458 ms) SDP lasted longer than the N2pc (262-322 ms). Mean amplitudes of SDP were statistically different from 0 μ V in all 50-ms measurement windows (201-250 ms, 251-300 ms, 301-350 ms, 351-400 ms) over the contralateral scalp, $t_s(25) \geq 4.05$, $p_s < .001$, $d_s \geq 0.79$, and over the ipsilateral scalp, $t_s(25) \geq 4.82$, $p_s < .001$, $d_s \geq 0.95$. Split-half reliability of SDP (measured as the mean amplitude over the 200-400 interval) was .92 over both the contralateral and ipsilateral scalp.

As shown in Figure 2.8, magnitude of N2pc correlated positively with magnitudes of the N1, $r(25) = .66$, $p < .001$, and the N1pc, $r(25) = .58$, $p = .002$, as well as marginally with the ipsilateral SDP, $r(25) = .47$, $p = .015$ (the polarities of the signed areas were ignored so that a positive correlation would indicate that, as one component increased in magnitude, so did the other one). These relationships were further visualized in Figure 2.9 by sorting participants into two groups based on the magnitude of their N2pc. Participants with N2pc larger than the median N2pc magnitude were sorted to the large-N2pc group and those with N2pc smaller than the median N2pc magnitude were sorted to the small-N2pc group. ERPs elicited by the two groups were plotted along with the corresponding contralateral-ipsilateral difference waves and present-absent difference waves to help visualize the N2pc-N1 relationship, the N2pc-N1pc relationship, and the N2pc-SDP relationship, respectively. Magnitude of the P1 did not correlate with that of the N2pc, $r(25) = .05$, $p = .797$. RTs were found to correlate with onset latency of the SDP, $r(25) = .55$, $p = .004$, but not with SDP magnitude, N2pc magnitude, or N2pc onset latency, $r_s(25) \leq 0.12$, $p_s \geq .564$.

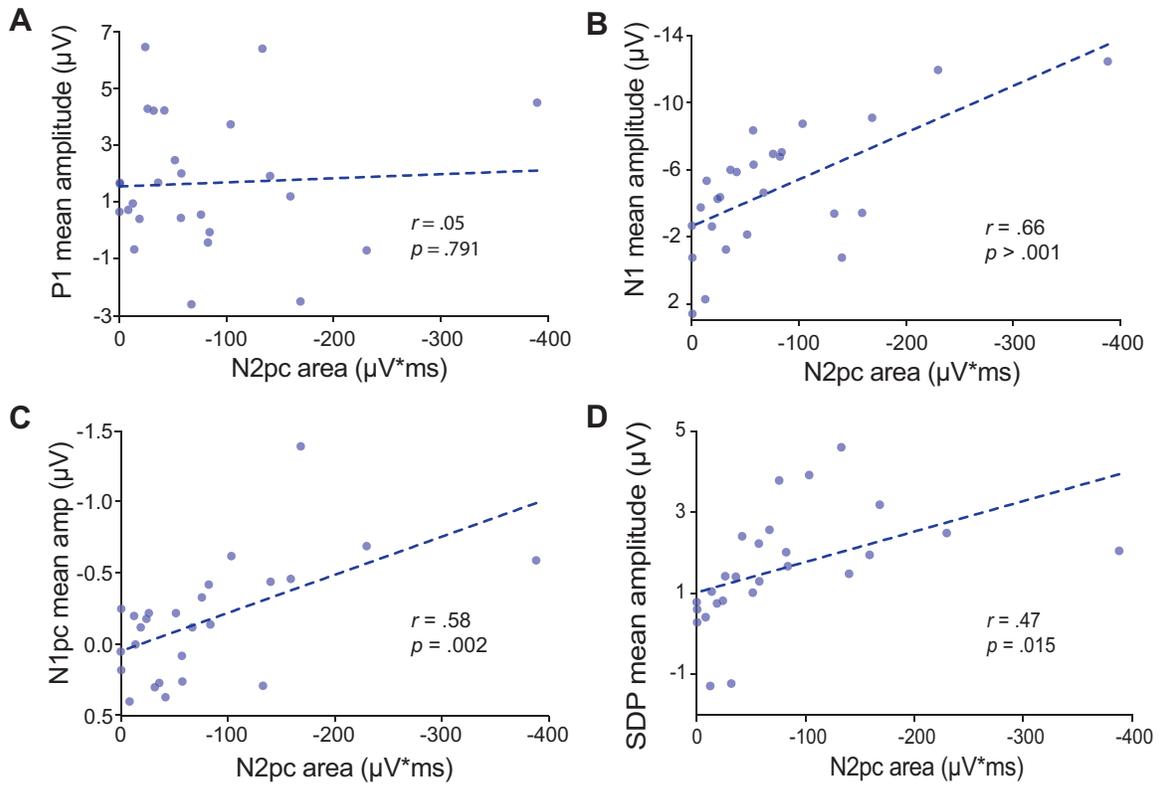


Figure 2.8. Relationships between magnitudes of the N2pc and the P1, N1, N1pc, and SDP. (A) Scatter plot of N2pc area and P1 mean amplitude. (B) Scatter plot of N2pc area and N1 mean amplitude. (C) Scatter plot of N2pc area and N1pc mean amplitude. (D) Scatter plot of N2pc area and SDP mean amplitude.

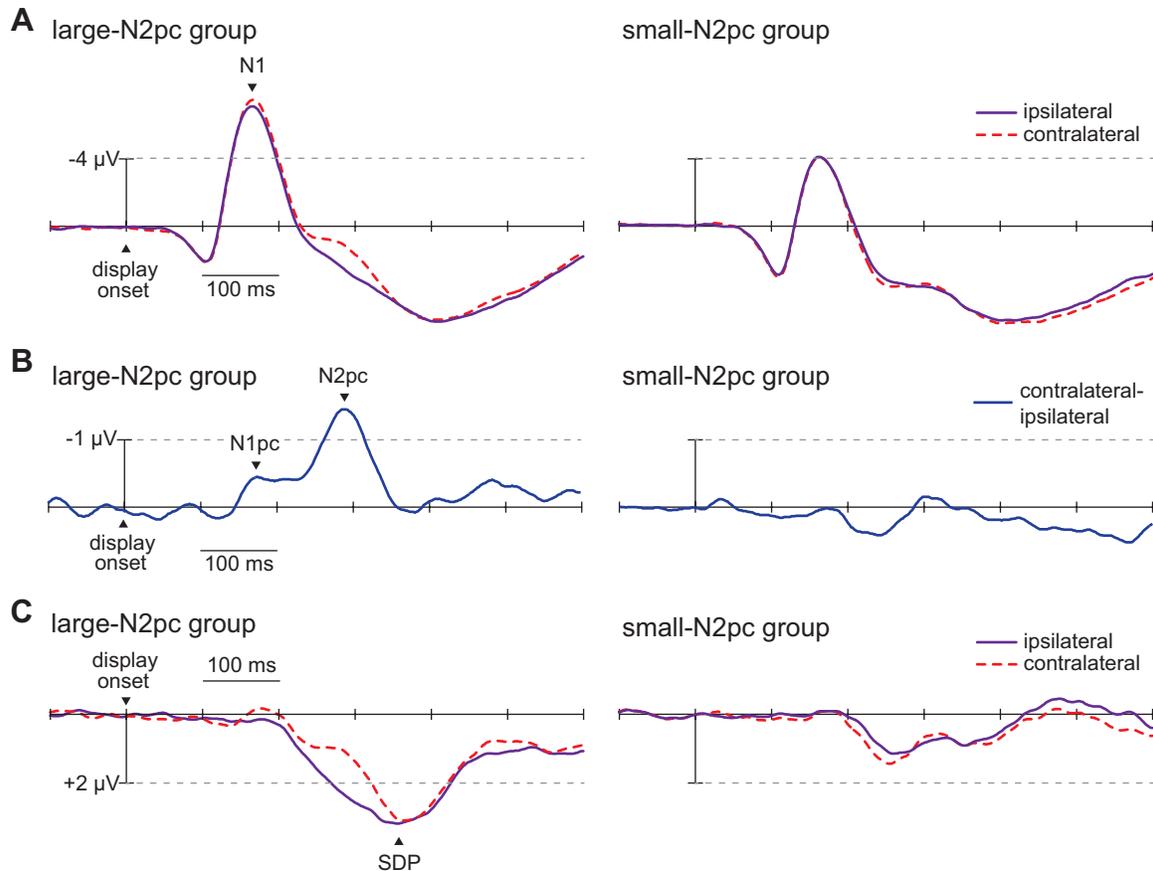


Figure 2.9. ERP visualizations of the intercomponent relationships. (A) ERPs elicited by target-present displays, recorded over the contralateral and ipsilateral scalp (PO7, PO8), separately for the large- and small-N2pc group ($N = 13$ per group). (B) Contralateral-ipsilateral difference waves corresponding to the ERPs in (A). (C) Present-absent difference waves plotted separately for the large- and small-N2pc group.

2.4. Discussion

When the N2pc was first discovered by Luck and Hillyard (1994b), they surmised that it reflects a spatial-filtering mechanism that suppresses irrelevant items near the attended object. This hypothesis was supported by the absence of an N2pc in a singleton-detection task where filtering would presumably interfere with search. A subsequent study by Schubö et al. (2004), however, failed to replicate Luck and Hillyard's null result in a similar singleton-detection task. Although the functional significance of the N2pc was not addressed by Schubö et al., their finding nevertheless contradicts the spatial filtering hypothesis. A resolution to this inconsistency would enable a better understanding of the neuro-cognitive process(es) giving rise to the N2pc,

the role of attention in singleton detection, and the nature of attention deficits indicated by an altered N2pc.

The present experiment aimed to resolve the debate surrounding the functional significance of the N2pc by replicating Luck and Hillyard's (1994b) singleton-detection task with modifications to improve statistical power. If N2pc reflects a spatial-filtering process, then an N2pc should be absent in singleton-detection tasks that discourage feature-based search strategies such as spatial filtering and target template matching. A positive finding, however, would cast doubt on the spatial filtering hypothesis. Contrary to the spatial filtering hypothesis, the present results showed that the N2pc was observable even when filtering was discouraged. Consistent with previous findings on the N2pc, the presently observed N2pc was maximal at electrodes PO7/8 (Luck, 2012), larger for lower-field targets (Luck et al., 1997), earlier on repeat-orientation trials (Christie et al., 2015; Eimer et al., 2010), and earlier on fast-response trials (McDonald et al., 2013). Critically, the earlier N2pc on fast-response trials runs counter to Luck and Hillyard's prediction: If N2pc reflects filtering, the N2pc should be larger on slow-response trials and smaller on fast-response trials in a task where suppression presumably interferes with search.

Luck and Hillyard (1994b) interpreted their null result as evidence for the spatial filtering hypothesis (see also Luck, 2012). By the same rationale, it would appear that the present N2pc results disconfirm the spatial filtering hypothesis. Certainly, the spatial filtering hypothesis could be revised to permit some filtering to occur during singleton detection in order to explain the smaller singleton-detection N2pc, despite the presumed performance impairment that would result from filtering. Even with this revised filtering hypothesis, it is unclear why filtering would occur later in singleton-detection tasks than in feature-search tasks or why earlier filtering activity is associated with faster singleton detection. As a result, greater modification would be required to account for this new set of data, yet it has been cautioned that continued attempts to revise the filtering hypothesis to explain new data would "run the risk of making the filtering hypothesis unfalsifiable" (Luck, 2012, p. 354). Therefore, at present, there seems to be no reason to abandon the rationale of Luck and Hillyard's original singleton-detection experiment for this post-hoc assertion.

If the N2pc does not arise from the filtering of (unattended) nontarget items in the vicinity of the target, what might it reflect? The N2pc is unlikely to reflect a template-matching process (Section 1.3.3) because such a feature-based search strategy would interfere with singleton detection. Here I surmise that the N2pc reflects some process(es) associated with the selection of the attended object itself, which may include some or all of the following processes: (a) the localization of to-be-attended objects prior to the deployment of attention (Tan & Wyble, 2015), (b) the spatially selective processing of task-relevant features following the deployment of attention (Eimer, 1996), (c) and the binding of features to a location in space (object individuation; Mazza & Caramazza, 2011).

The present findings also shed light on the neuro-cognitive processes involved in the different search modes. Whereas Luck and Hillyard's (1994b) findings on the N2pc would suggest that feature-search tasks (where an N2pc was observed) and singleton-detection tasks (where an N2pc was ostensibly absent) involve different processes of visual selection, the current results suggest that the same selection processes are implemented in feature search and singleton detection and that differences between the two search modes likely stem from processes at the control level rather than at the implementation level. The N2pc finding also suggests that attention is involved in singleton detection. At present, it is unclear whether attention is required for detection to take place or whether detection occurs preattentively but then reflexively initiates attentional selection of the singleton so that the item is consciously perceived and remembered.

It should be noted that N2pc waveforms observed in other feature-search experiments were earlier and larger than the N2pc elicited in the present singleton-detection task, but there are many possible reasons for this difference (hence the inclusion of a feature-search condition would not be informative in the present experiment). One reason is that having an attentional set for a specific feature, combined with a history of selecting the same feature across all trials, would greatly enhance the perceived salience of a fixed-orientation target compared to that of variable-orientation target. This explanation is consistent with known effects of salience on N2pc magnitude and latency (e.g., see figure 5 of Gaspar & McDonald, 2014). Another reason is that the N2pc may be comprised of two subcomponents: an early portion that enhances all task-relevant features in in the visual field, and a later portion that binds the

target features to a location in space (Eimer & Grubert, 2014; Kiss, Grubert, & Eimer, 2013). And since the present task discourages the adoption of an attentional set for a specific feature, the early portion of the N2pc would not be elicited, resulting in a smaller and later N2pc.

An unexpected finding in the present experiment is that, although the N2pc was unambiguously observed in the singleton-detection task, there was considerable variability in N2pc magnitude across individual participants; roughly a quarter of participants showed no N2pc (see Figures 2.2C, 2.4C). The underlying cause for this variability is unclear. Past research has shown that magnitude of N2pc increases as the number of to-be-enumerated objects increased in a display, until about three to four objects (Ester et al., 2012), which coincides with previous estimates of one's short-term, *visual working memory capacity* (vWMC; Luck & Vogel, 1997; Sperling, 1960). Thus, it is possible that the observed variability in N2pc magnitude is in part contributed by individual differences in vWMC. This possibility is addressed in Experiment 2 (Chapter 3) of this thesis.

The present exploratory analyses revealed three key findings. First, the N1pc, which has been hypothesized to reflect stimulus-driven attention (Wascher & Beste, 2010a, 2010b), is observable in the singleton-detection task, especially for lower-field targets and on fast-response trials (Figures 2.4B, 2.5B). Second, the SDP was observed with maxima over both the contralateral and ipsilateral occipital scalp. This positivity was isolated by subtracting ERPs elicited on target-absent trials from ERPs elicited on target-present trials. The subtraction revealed that the SDP, compared to the P3b, was more posteriorly and bilaterally distributed, had an earlier peak, and was shorter in duration. The absence of visual-evoked potentials, particularly the P1, in the present-absent difference wave suggests that processes underlying the SDP do not reflect mere sensory activity from the extrastriate visual cortex. Furthermore, because the SDP begins 33-34 ms prior to the deployment of attention (as indexed by the N2pc) and earlier among individuals with shorter RTs, the SDP likely reflects a multi-stage process that begins with the preattentive detection of a singleton by the visual system. And as the accrual of evidence for the presence of a singleton reaches a critical threshold, attention is then deployed (as indexed by the N2pc) to the target singleton, enabling conscious processing and identification of the singleton. Third, magnitude of the N2pc

linearly correlated with that of the N1, N1pc, and SDP, so that individuals were more likely to have a large N2pc if at least one of these earlier components was large.

Chapter 3. Experiment 2

3.1. Introduction

In addition to having implications for our interpretation of the N2pc component, the results of Experiment 1 (Chapter 2) shed light on the neuro-cognitive processes involved in singleton detection and demonstrate that detection of a salient visual singleton with unpredictable features involves the same attentional-selection process as those involved in feature search (as indexed by the N2pc). In this chapter, I consider the automaticity of singleton detection, with a focus on the attentional-selection process reflected by the N2pc.

Prior research has highlighted three properties that differentiate automatic and controlled processes (e.g., Hasher & Zacks, 1979; Logan, 1978; Regan, 1981; Shiffrin & Schneider, 1977). These properties are (a) the degree to which a process is sensitive to concurrent informational load, (b) the degree to which a process is influenced by an observer's intentions (e.g., goals, strategies, expectations, etc.), and (c) whether a process requires, or at least benefits from, attention. By these criteria, a cognitive operation is considered to be automatic if it is unhindered by perceptual or cognitive load, outside of the observer's voluntary control, and occurs independently of the observer's attention. A cognitive operation was considered to be *strongly* automatic if it satisfied all three criteria, and it was considered to be at most *partially* or *occasionally* automatic if at least one of the criteria was sometimes violated or if the focusing of attention improved said process (Kahneman & Chajczyk, 1983; Yantis & Jonides, 1990).

Research on automaticity evolved beyond determining whether a given cognitive process is strongly automatic after it was learned that attention influences performance in the majority of perceptual and cognitive tasks. The involuntary reading of words, for example, was once thought to be strongly automatic (e.g., Stroop, 1935), but Kahneman and Chajczyk (1983) showed that the degree to which involuntary reading interferes with the task at hand was modulated by attention. Similarly, location cueing studies revealed that detection of salient visual targets can be facilitated by precueing the target's location so that an observer can orient attention to that location in advance (e.g., Posner, 1980). Consequently, researchers began to ask whether the cognitive operation under investigation engages attention automatically. By this perspective, a cognitive operation

is considered to be more or less automatic depending on the degree to which said operation engages an observer’s attention against their will, so that fully automatic processes always engage attention irrespective of the task at hand.

Along these lines, researchers have debated the extent to which salient visual stimuli (e.g., singletons, abrupt visual onsets) capture attention automatically. Figure 3.1 positions several emerging perspectives on an “automaticity continuum” that ranges from fully controlled (left end) to fully automatic (right end). As illustrated in the figure, the salience-driven selection hypothesis proposes that attention capture by salient stimuli is highly automatic (Theeuwes, 1991a, 1992, 2004, 2010). This theoretical perspective is broadly comprised of two related tenets. First, the most salient stimulus within the monitored region of the visual field (the so-called *attentional window*) invariably captures attention. Second, stimulus-driven selection processes must be completed before goal-driven processes can begin. By this view, salient stimuli automatically capture attention unless they fall outside of an observer’s attentional window (because salience is not computed outside of this window). Accordingly, an observer can prevent salience-driven distraction only by restricting the size of their attentional window in advance so that a salient distractor appears outside of the window (Belopolsky & Theeuwes, 2010; Belopolsky, Zwaan, & Theeuwes, 2007).

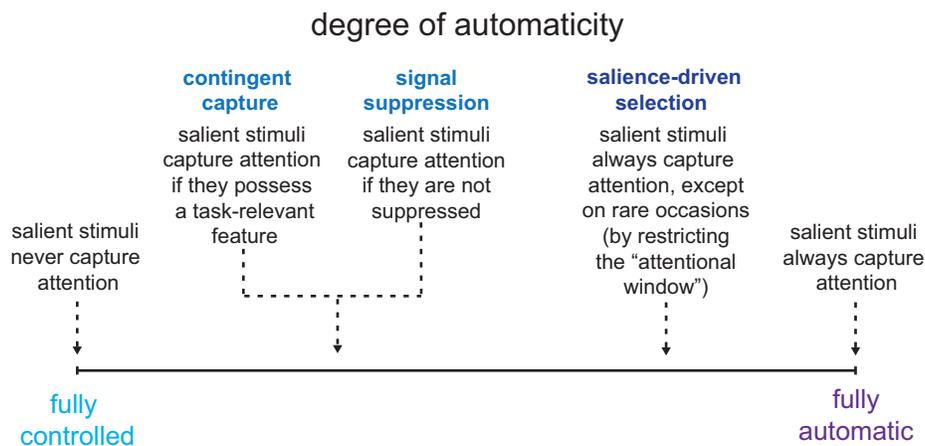


Figure 3.1 Visualization of the various hypotheses on the automaticity of attention capture along a continuum from attention being fully controlled (left) to fully automatic (right).

Other theoretical perspectives allow for considerably more top-down control of selection (e.g., Folk et al., 1992; Sawaki & Luck, 2010). Such control is hypothesized to prevent distraction by salient-but-irrelevant visual stimuli and to keep observers’

attention engaged on stimuli that are relevant to the task at hand. According to these latter perspectives, salience-driven capture is a process that occurs in much more limited circumstances, such as when an observer adopts a strategy to search for differences in local features rather than for a specific feature (i.e., in singleton detection mode). In feature search mode, by contrast, salience-driven distraction might be prevented primarily by up-weighting relevant features or down-weighting irrelevant features.

Figure 3.1 highlights two perspectives that are toward the “fully controlled” end of the automaticity continuum. According to the *contingent capture hypothesis*, salience-driven distraction is prevented by selectively up-weighting the features that are relevant to the task at hand (Folk et al., 1992). By this view, salient-but-irrelevant stimuli capture attention only when they possess an up-weighted feature (i.e., when one of the features of the distractor happens to also be a feature of the target). According to the *signal suppression hypothesis*, salience-driven distraction is prevented by selectively down-weighting salient-but-irrelevant features (Sawaki and Luck, 2010). This down-weighting process is thought to be accomplished by the suppression of objects with a salient, predictable feature (Gaspelin & Luck, 2018b).

Electrophysiological support for these controlled-attention perspectives has come from several different feature-search paradigms. First, when searching for a singleton defined by one specific feature, displays containing other singletons (that is, defined by other features) fail to elicit the N2pc (Luck & Hillyard, 1994b; see also Schubö & Müller, 2009). Second, in a modified cueing task developed to assess contingent capture, distractor singletons in the cue display elicit an N2pc only if they are defined by the same feature as the target (e.g., Eimer & Kiss, 2008). Third, in the additional singleton paradigm, a salient distractor that appears in the same search display as a fixed-feature target fails to elicit an N2pc and often elicits an ERP component associated with suppression called the distractor positivity (P_D ; Hickey, Di Lollo, & McDonald, 2009; e.g., Gaspar, Christie, Prime, Jolicœur, & McDonald, 2016; Gaspar & McDonald, 2014; Gaspelin & Luck, 2018a; Jannati, Gaspar, & McDonald, 2013). Based on these converging lines of evidence, it is reasonable to conclude that singletons do not capture attention automatically in feature search mode. Less is known about whether capture by singletons can be prevented when participants adopt a singleton-detection strategy, but it has been proposed that observers will attend to any singleton regardless of its

relevance in singleton detection mode (Bacon & Egeth, 1994). Some ERP evidence obtained from the additional singleton paradigm suggests that this might be the case (Hickey, McDonald, & Theeuwes, 2006; but see McDonald et al., 2013).

In Experiment 2 of this thesis, a go/no-go element was incorporated into a pure singleton-detection task. This *go/no-go singleton-detection task* was developed to determine whether the detection (and selection) of a singleton could be prevented. In this task, participants were instructed to detect the presence of an orientation singleton when all items in the display were cyan (go trials) and to withhold responses when all items were yellow (no-go trials; note: the go and no-go colors were counterbalanced across participants; Figure 3.2B). The go and no-go displays were randomly intermixed across trials so that the participants would have to react to the display color on a trial-by-trial basis. Similar to Experiment 1, vertical and horizontal line stimuli were used create singleton-absent and singleton-present displays for both go and no-go trials. Singleton-absent displays consisted of all vertical or all horizontal lines. Singleton-present displays consisted of a vertical line situated among horizontal lines or a horizontal line situated among vertical lines so that participants could not detect the presence of a singleton based on a particular line orientation. The number of items in each display was changed from 8 (in Experiment 1) to 16 to increase salience of the singletons on both go and no-go trials and thus improve, if possible, the efficiency of saliency-based selection mechanisms.

The theoretical perspectives outlined in Figure 3.1 would lead to different predictions about the sequence of neuro-cognitive processes that would take place on go and no-go trials. Because there was no requirement to bring attention into a narrowly focused state at the start of each trial, it could be assumed that the attentional window would remain wide throughout each trial of the experiment. Thus, according to the saliency-driven selection perspective, the singleton should capture attention at the outset of each trial, thereby giving rise to an N2pc on both go and no-go trials. Furthermore, because this perspective asserts that spatial attention is required to make any decision about visual input (Theeuwes, 2010), the color of the display would be identified only after attention is deployed to the singleton's location. By this account, observers would be able to implement top-down control to withhold responses on no-go trials, but only after the singleton captured attention. In contrast, from the two controlled-attention perspectives, one could envisage observers adopting a strategy to process the

global display color first and to orient attention to the singleton only when necessary (on go trials). In this case, the singleton would be predicted to elicit the N2pc only on go trials. One might also predict the singleton to elicit a P_D on no-go trials, because, according to the signal-suppression account, salient stimuli generate attend-to-me signals that must be suppressed to prevent capture.

In addition to isolating lateralized ERP waveforms to look for the N2pc and the P_D, I planned to compare directly the ERPs elicited on go and no-go trials to (a) estimate the earliest time at which go and no-go colors had been differentiated and (b) ensure that the go/no-go manipulation was successful. This examination focused on the *anterior P2* (P2a) and the *no-go P3*. The P2a is an enhanced positivity found over the prefrontal scalp approximately 180-300 ms post stimulus onset and is typically elicited by task-relevant stimuli, especially when observers must evaluate whether a stimulus is relevant to the task at hand (Potts, 2004; Potts, Liotti, Tucker, & Posner, 1996). The onset latency of the P2a therefore provides an upper-bound estimate for the earliest goal-driven activity, and this estimate would then enable me to evaluate the assertion by the salience-driven selection hypothesis that goal-driven processes cannot occur prior to completion of the stimulus-driven selection process. This assessment was done by comparing the onset latencies of the P2a and the N2pc elicited by target singletons. If goal-driven processes occur only after attentional selection, then there should be no P2a before the onset of the N2pc. Conversely, if goal-driven processes can precede salience-driven selection, then the P2a should have an earlier onset than that of the N2pc.

The no-go P3 is an enhanced positivity found over the frontocentral scalp approximately 200-500 ms post stimulus onset (Eimer, 1993; Kok, 1986; Roberts, Rau, Lutzenberger, & Birbaumer, 1994; Schröger, 1993; Simson, Vaughan, & Ritter, 1977), and it is thought to originate from the *anterior cingulate cortex* (Fallgatter, Bartsch, & Herrmann, 2002). As the name suggests, this positivity is elicited by no-go trials in a wide variety of go/no-go tasks, and it is thought to reflect the competition between a go and a no-go decision (Donkers & van Boxtel, 2004; Smith, Smith, Provost, & Heathcote, 2010) or the inhibition of a go response (Bokura et al., 2001; Bruin et al., 2001). Therefore, the presence of this component in the current experiment would help to confirm that participants performed the go/no-go task as intended.

Another objective of the present experiment was to follow up on three specific findings from Chapter 2. The first finding was that of the SDP component, which was hypothesized to reflect processes associated with the detection of a singleton. In Experiment 2, I asked whether the singleton-detection processes reflected by the SDP are exclusively stimulus-driven or whether they can be modulated by task relevance. If singleton detection is automatic, then target and distractor singletons should elicit comparable SDP waveforms. Alternatively, if singleton detection can be modulated by relevance, then distractor singletons should elicit a reduced SDP or no SDP at all.

The second finding was the marked variability in N2pc magnitude across individuals. As illustrated in Figure 2.4, roughly one quarter of the participants showed little to no N2pc. The third finding was that this variability in N2pc magnitude was also observed to correlate with the magnitudes of the earlier-onsetting N1, N1pc, and SDP. Here, I investigate whether N2pc variability is associated with individual differences in vWMC. Numerous studies have shown higher vWMC is associated with larger P_D (Feldmann-Wüstefeld & Vogel, 2019; Gaspar et al., 2016) and contralateral delay activity (CDA) observed in memory-retention intervals (Vogel & Machizawa, 2004). In fact, there is also evidence to suspect a relationship between vWMC and N2pc because higher subitizing capacity is associated with larger N2pc (Ester et al., 2012), and this capacity has been shown to correlate positively with vWMC (Piazza, Fumarola, Chinello, & Melcher, 2011). Therefore, in light of the findings from Experiment 1 and past studies, I sought to (a) compute correlations between vWMC and magnitudes of ERPs associated with singleton detection, selection, and suppression (SDP, N2pc, and distractor-elicited P_D , respectively) and (b) intercomponent correlations.

3.2. Method

The Research Ethics Board at SFU approved the research protocol. All experimental procedures were performed in accordance with guidelines and regulations outlined by SFU and NSERC.

3.2.1. Participants

Twenty-four young adults without history of neurological disorders participated after giving informed consent. For their participation, individuals received either \$20 or

course credit as part of a departmental research participation system. All subjects reported normal or corrected-to-normal visual acuity and were tested for normal color vision using Ishihara color plates prior to participation. Data from two participants were excluded from further analyses because more than 25% of trials were contaminated by ocular artifacts (rejection criterion set in advance). Of the remaining 22 participants (mean age: 22.0 years), 12 were female and 20 were right-handed.

3.2.2. Apparatus

The apparatus was identical to that in Chapter 2.

3.2.3. Stimuli and Procedure

Change-Detection Task

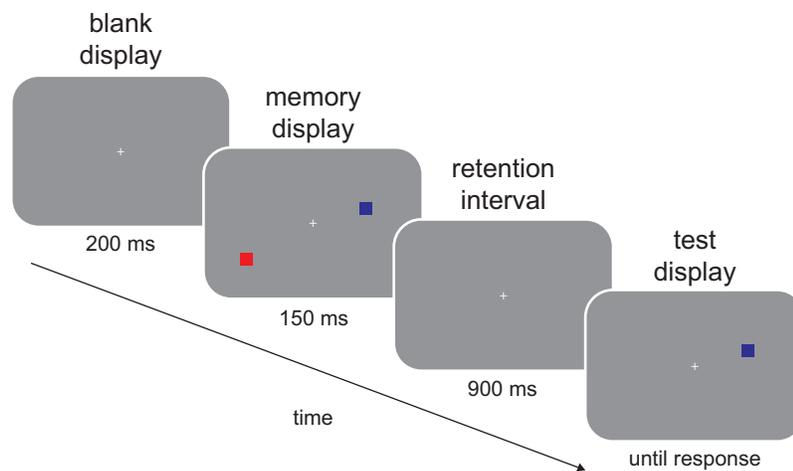
Participants first completed a *change-detection task* that assessed their vWMC (Figure 3.2). All stimuli and procedure for this task were identical to those used by Gaspar et al. (2016). Briefly, participants viewed a sequence of displays on each trial, starting with a memory display lasting 150 ms. In the memory display, colored squares of varying set sizes (two, four, six, eight) appeared in one of 36 possible locations (nine in each quadrant), the coordinates of which formed a regular grid. This display was followed by a 900-ms retention interval, during which only a fixation cross was presented at the center of the display. Following this interval, a test display presented a colored square at one of the locations previously occupied in the memory display. Participants pressed a button to indicate whether the square occupying that location changed in color across the two displays. Each participant completed a total of 120 trials.

Go/No-Go Singleton-Detection Task

Following the change-detection task, participants took part in the *go/no-go singleton-detection task*. The stimuli and procedure in this task were identical to the singleton-detection task in Chapter 2 except as follows. To increase the salience of the orientation singleton, the number of lines contained in each stimulus display was increased from 8 to 16. All lines appeared within a $11.1^\circ \times 8.3^\circ$ region around fixation. Half the displays contained cyan lines and the other half contained yellow lines ($x = .37$, $y = .57$, 28.0 cd/m^2). The color of the lines indicated whether a given trial was go or no-

go. The go trials contained cyan lines for half the participants and yellow lines for the other half. On go trials, participants pressed either the left or right shoulder buttons on a gamepad using their index fingers, depending on the presence of an orientation singleton. The stimulus-response mapping was counterbalanced across participants. On no-go trials, participants simply waited for the trial to end without providing a response. Go and no-go trials were randomly intermixed within each block of trials so that participants could not predict whether singleton detection was required on any given trial. Each participant completed 40 blocks of 40 trials, yielding a total of 1,600 trials.

A change detection task



B go/no-go singleton-detection task

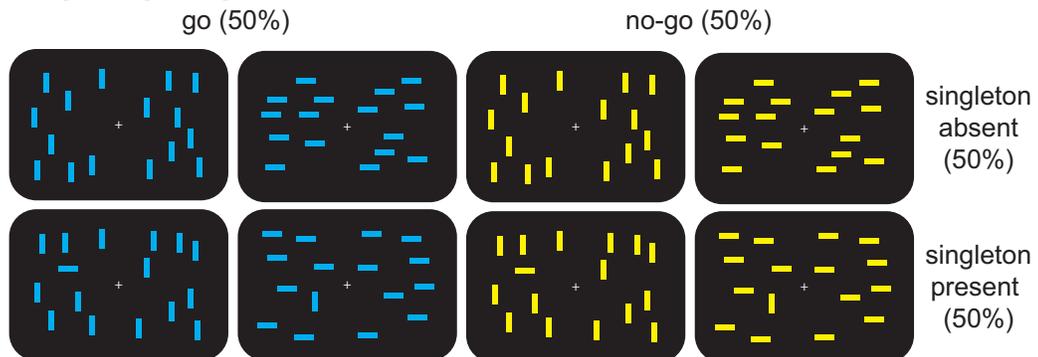


Figure 3.2. Example stimulus displays used in the change-detection task (A) and in the go/no-go singleton-detection task (B).

3.2.4. Behavior

Change-Detection Task

Individual participant's vWMC was estimated using the following equation (Cowan, 2001; see also Pashler, 1988b):

$$K = S(H - F), \quad (2)$$

where K is the vWMC, S is the set size, H is the hit rate, and F is the false-alarm rate. This equation yielded four K values for each individual, corresponding to each of the four set sizes presented in the change-detection task. These values were then averaged to produce a mean K value to represent each participant's vWMC.

Go/No-Go Singleton-Detection Task

The behavioral analysis performed on go trials was identical to that in Chapter 2 except as follows. Correlation between RT and K was assessed, separately for target-present and target-absent trials. Priming of pop-out was not assessed here because there were insufficient repeat- and change-orientation trials to yield meaningful results.

3.2.5. Electrophysiology

Recording and Preprocessing

The method of EEG recording and preprocessing was identical to that in Chapter 2.

ERP Analyses

The method of ERP analysis was identical to that in Chapter 2 except as follows.

N2pc and SDP

The magnitude of the N2pc was strictly quantified as the mean amplitude within a 50-ms window (275-325 ms post stimulus) elicited by lower-field singletons. This analytical decision was made on the grounds that (a) pilot studies from the laboratory suggest that the addition of a go/no-go element to the task delays N2pc onset latency and (b) that mean-amplitude measures are less susceptible to noise fluctuations in the waveform compared to signed-area measures (because the calculation of means

averages out positive and negative noise fluctuations, whereas signed-area measures do not). Having an increased signal-to-noise ratio, and therefore an increased effect size and statistical power, would provide more accurate assessments later on, especially in testing of a linear relationship between magnitude of N2pc and vWMC (K). One-sample t tests against $0 \mu\text{V}$ was conducted to assess the presence of an N2pc, separately for go and no-go trials containing a singleton in the lower visual field, where N2pc waveforms are known to be larger (Luck et al., 1997). Magnitude of the N2pc was then compared between go and no-go trials using a paired-sample t test.

Magnitude of the SDP was strictly quantified as the mean amplitude over the ipsilateral scalp (to avoid overlap with the N2pc over the contralateral scalp) in a 200-400-ms window (as established in Chapter 2). Presence of the SDP was tested using one-sample t tests against $0 \mu\text{V}$, separately for go and no-go trials. Difference in magnitude of the SDP on go and no-go trials was then assessed using a paired-sample t test. Onset latencies of the SDP and N2pc were quantified as the time at which each component reached 25% of its peak amplitude, using a standard jackknife approach (Miller et al., 1998). Differences in the onset latencies of each component across go and no-go trials were assessed using a paired-sample t test.

P_D

The magnitude of the P_D was quantified as the signed positive area elicited by upper-field singletons 200-500 ms post stimulus onset. Measurement was based on upper-field stimuli because such stimuli are known to elicit larger P_D components (Hickey et al., 2009) and smaller N2pc components (Luck et al., 1997) that might otherwise obscure P_D measurement. The signed-area approach was used instead of a mean-amplitude approach because the timing of the P_D is quite variable and thus is unknown a priori (Sawaki et al., 2012). Because signed-area measures are necessarily biased by noise, the presence of the P_D was assessed using the nonparametric approach described in Chapter 2, separately for go and no-go trials containing a singleton in the upper visual field. A paired-sample t test was then conducted to compare the magnitude of the P_D elicited by singletons in the upper visual field between go and no-go trials. To verify that the P_D was indeed larger for upper-field stimuli in the present experiment, a difference in P_D magnitude elicited by upper- and lower-field singletons on no-go trials was assessed using a paired-sample t test. The same test was not performed for upper-

and lower-field singletons on go trials because even if such a visual-field effect were present on go trials, it would remain unclear whether this difference is contributed by a larger upper-field P_D or simply due to a larger overlapping, lower-field N2pc (as was observed in Experiment 1 and by Luck et al., 1997).

Other ERP Components

Additional analyses were performed on the N1, N1pc, P2a, and no-go P3. Threshold of statistical significance for all assessments involving multiple comparisons was adjusted based on the number of comparisons using Bonferroni correction (per-test $\alpha = .05/\text{number of comparisons}$).

As in Chapter 2, magnitude of the N1 was quantified as the mean amplitude within a 150-200-ms window, averaged across electrodes PO7 and PO8. N1 magnitude was measured separately for singleton-present go trials, singleton-absent go trials, singleton-present no-go trials, and singleton-absent no-go trials. These N1 magnitudes were assessed using a repeated-measures ANOVA with a factor of trial type (go vs. no-go) and a second factor of singleton presence (present vs. absent) to determine whether the N1 is associated with the processing of global display color or detection of a singleton.

It is possible that the target and distractor singletons would elicit the N1pc prior to or in absence of the N2pc, which would still indicate that some early form of stimulus-driven attention has occurred. Therefore, one-sample *t* tests against 0 μV were conducted to assess the presence of an N1pc (mean amplitude within a 150-200-ms interval, as previously defined in Chapter 2), separately for go and no-go trials containing a singleton in the lower visual field, where N1pc was previously confirmed to be larger (see Figure 2.4B).

To isolate the P2a and no-go P3, ERPs elicited by no-go trials were subtracted from those elicited by go trials to produce the *go-no-go difference waves*, so that the P2a would appear as a positive deflection and the no-go P3 would appear as a *negative* deflection. The P2a was isolated to establish an upper-bound estimate of the earliest goal-driven activity, which enables me to evaluate the assertion by the salience-driven selection hypothesis that goal-driven processes cannot occur prior to the completion of the stimulus-driven selection process. This evaluation was done by comparing the onset

latency between the P2a and the N2pc elicited on go trials. In particular, because task-relevance cannot influence selection according to the salience-driven selection hypothesis, the N2pc elicited on go trials is also stimulus-driven and can thus be used as a lower-bound estimate for the completion of the stimulus-driven selection process. Presence of the P2a was first confirmed by comparing the mean amplitude within the 180-230-ms at electrode FPz against 0 μ V using a one-sample *t* test. Onset latency of the P2a was measured as the time point at which P2a first reaches 25% of its peak amplitude, using the jackknife approach. This latency was then compared with that of the N2pc using a paired-sample *t* test. The no-go P3 was isolated to provide added confirmation that participants were performing the go/no-go task as intended. Magnitude of the no-go P3 was quantified as the mean amplitude measured at electrode Cz within a 250-350-ms window. Presence of the no-go P3 was also assessed using a one-sample *t* test against 0 μ V.

Correlational Analyses

A linear relationship between magnitude of the N2pc and magnitudes of the target-elicited N1 and SDP were assessed by computing Pearson correlation coefficients, as in Chapter 2. The magnitudes of these components were quantified in the manner as previously described. A relationship between magnitudes of the N2pc and N1pc was not assessed because no N1pc was observed in the present experiment. A post-hoc correlational analysis was done to assess the linear relationship between the P_D elicited on go and no-go trials, after it was determined that a go-trial P_D (i.e., a *target-elicited P_D*) was present. A positive linear correlation would be consistent with the claim that these components reflect a common suppression mechanism (Sawaki et al., 2012).

Pearson correlation coefficients were computed to assess linear relationships between *K* and the magnitudes of several ERP components. Computations were done in four sets of tests that focused on (a) singleton processing on go trials (as measured by magnitudes of N1, SDP, and lower-field N2pc), (b) singleton processing on no-go trials (as measured by magnitudes of the same three ERP components), (c) processing associated with go/no-go discrimination (as measured by magnitudes of the P2a and no-go P3), and (d) singleton suppression on go and no-go trials (as measured by magnitudes of the upper-field target- and distractor-elicited P_D , respectively).

Topographical Mapping

The method of topographical mapping is identical to that in Chapter 2.

3.3. Results

3.3.1. Behavior

Change-Detection Task

The average vWMC estimate was 2.72, with scores ranging from 1.43 to 3.77. These values were consistent with previous estimates of vWMC (Luck & Vogel, 1997; Sperling, 1960).

Go/No-Go Singleton-Detection Task

There was no RT difference between target-present (610 ms) and target-absent (611 ms) trials, $t(21) = 0.35$, $p = .734$, or between upper-field targets (608 ms) and lower-field targets (611 ms), $t(21) = 0.84$, $p = .412$. Neither RT on target-present or target-absent trials correlated with K , $r_s(21) \geq -.125$, $p_s \geq .579$.

3.3.2. Electrophysiology

N2pc and SDP

Presence of the N2pc was assessed in the contralateral-ipsilateral difference waves elicited by lower-field singletons on go and no-go trials to determine whether the singletons captured attention reflexively, as predicted by the salience-driven selection hypothesis. As illustrated by Figure 3.3, the N2pc was present on go trials ($-1.11 \mu\text{V}$), $t(21) = 4.83$, $p < .001$, $d = 1.06$, but not on no-go trials ($-0.20 \mu\text{V}$), $t(21) = 1.22$, $p = .237$. Moreover, the difference in N2pc magnitudes across go and no-go trials was significant, $t(21) = 4.16$, $p < .001$, $d = 0.90$. In line with this finding, 95% CIs around the grand-averaged difference waves elicited by all singletons on go trials became fully negative at 270 ms until 318 ms whereas those of no-go trials never became fully negative. These results indicate that whereas singletons were attended on go trials, singletons on no-go trials did not capture attention, disconfirming the salience-driven selection hypothesis.

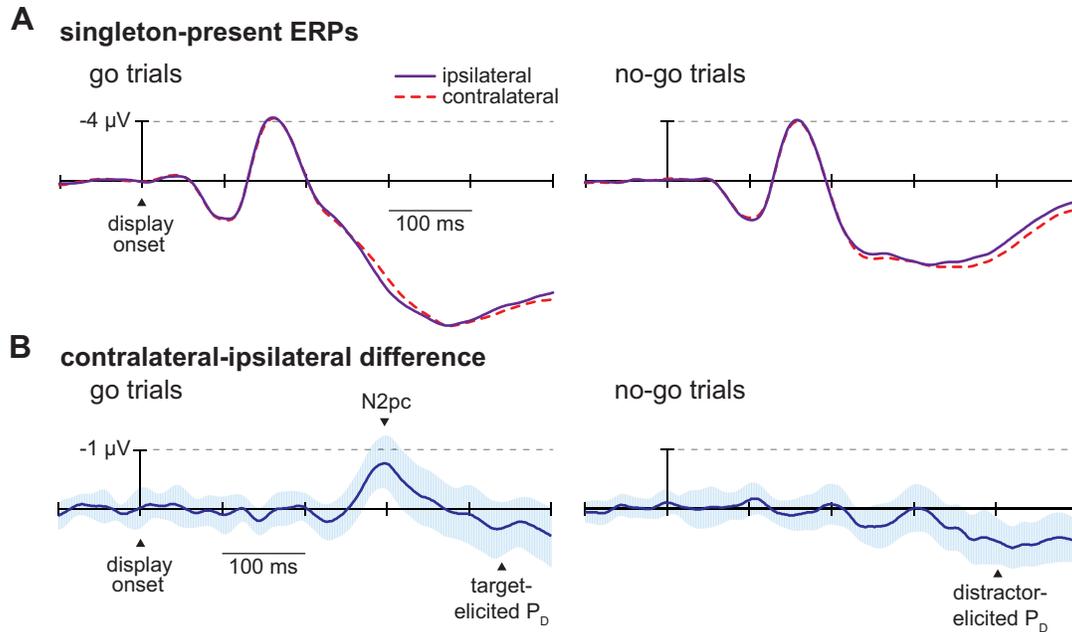


Figure 3.3. Grand-averaged singleton-present ERPs recorded over the lateral occipital scalp (electrodes PO7, PO8). (A) Left: waveforms recorded contralateral and ipsilateral to singletons on all singleton-present go trials. Right: waveforms recorded contralateral and ipsilateral to singletons on all singleton-present no-go trials. (B) Contralateral-ipsilateral difference waves corresponding to the waveforms in (A). Vertical bars correspond to the 95% CIs at each time point.

Next, to evaluate whether the singleton-detection processes reflected by the SDP are strongly stimulus-driven or governed by task relevance, the SDP was measured from the present-absent difference waves, separately for go trials and no-go trials (Figure 3.4B). The SDP was present on go trials ($2.25 \mu\text{V}$), $t(21) = 9.93$, $p < .001$, $d = 2.18$, and on no-go trials ($0.44 \mu\text{V}$), $t(21) = 2.61$, $p = .016$, $d = 0.49$, but was markedly reduced on no-go trials, $t(21) = 7.97$, $p < .001$, $d = 1.94$. The dramatic reduction of SDP on no-go trials indicates that the process underlying the SDP is largely driven by stimulus relevance rather than stimulus salience. Presence of the SDP was corroborated by the 95% CIs, which became fully positive at 206 ms on go trials and at 230 ms on no-go trials. As was found in Experiment 1 (Chapter 2), the SDP preceded the N2pc (236 ms vs. 262 ms, respectively), $t(21) = 2.47$, $p = .022$, $d = 0.54$.

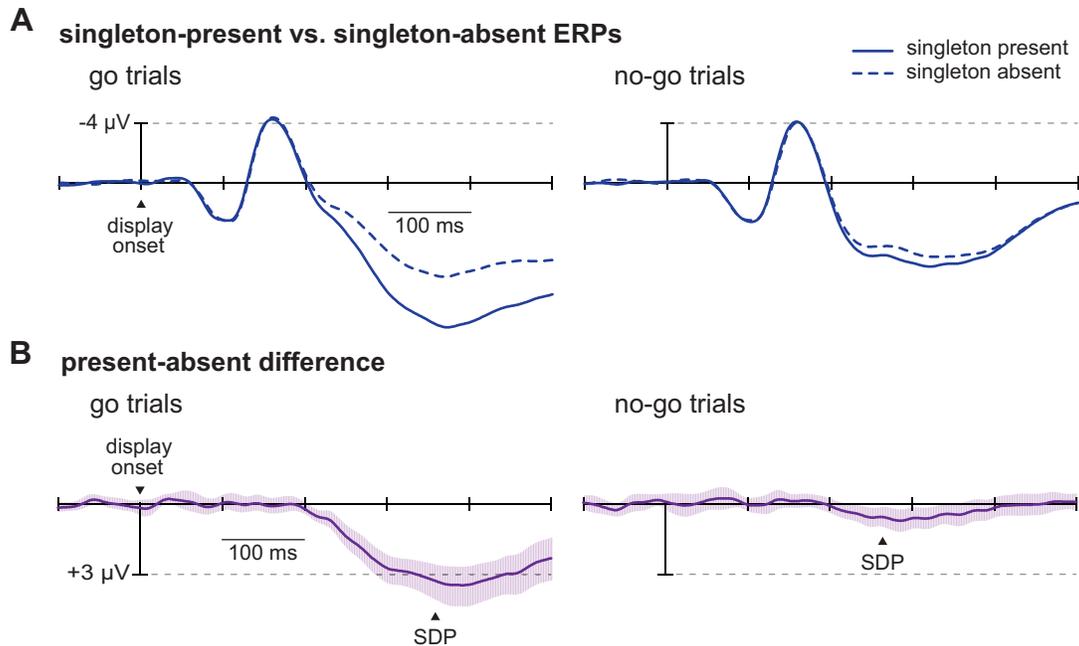


Figure 3.4 Comparison of grand-averaged singleton-present and singleton-absent ERPs. (A) Waveforms of singleton-present (ipsilateral PO7/8) and singleton-absent trials (combined PO7/8). (B) Present-absent difference waves recorded over the ipsilateral scalp constructed by subtracting the singleton-absent ERPs from the corresponding singleton-present ERPs in (A). Vertical bars correspond to the 95% CIs at each time point.

P_D

Presence of the P_D was assessed in the contralateral-ipsilateral difference waves elicited by upper-field singletons to determine whether selective processing of the singleton was actively terminated (on go trials; see Sawaki et al., 2012) or prevented by suppression (on no-go trials; as predicted by the signal suppression hypothesis). Figure 3.5A shows the results of the permutation tests performed to assess presence of the P_D , separately for go and no-go trials. A contralateral positivity was elicited by singletons on both go and no-go trials, $p_s = .002$ (Figure 3.5B, see also Figure 3.2B), and the positivities were statistically indistinguishable between the two trial types (211.1 μ V*ms vs. 218.7 μ V*ms, respectively; Figure 3.5C), $t(21) = 0.25$, $p = .802$. These observations suggest that singletons on go trials also elicited a P_D . A target-elicited P_D has been previously proposed to reflect a suppression mechanism that terminates the allocation of attention after attentional processing is complete (Sawaki et al., 2012). The P_D was verified to be marginally larger for upper-field than for lower-field singletons on no-go

trials (Figure 3.5D; 218.7 $\mu\text{V}\cdot\text{ms}$ vs. 141.9 $\mu\text{V}\cdot\text{ms}$, respectively), $t(21) = 1.96$, $p = .063$, $d = 0.49$.

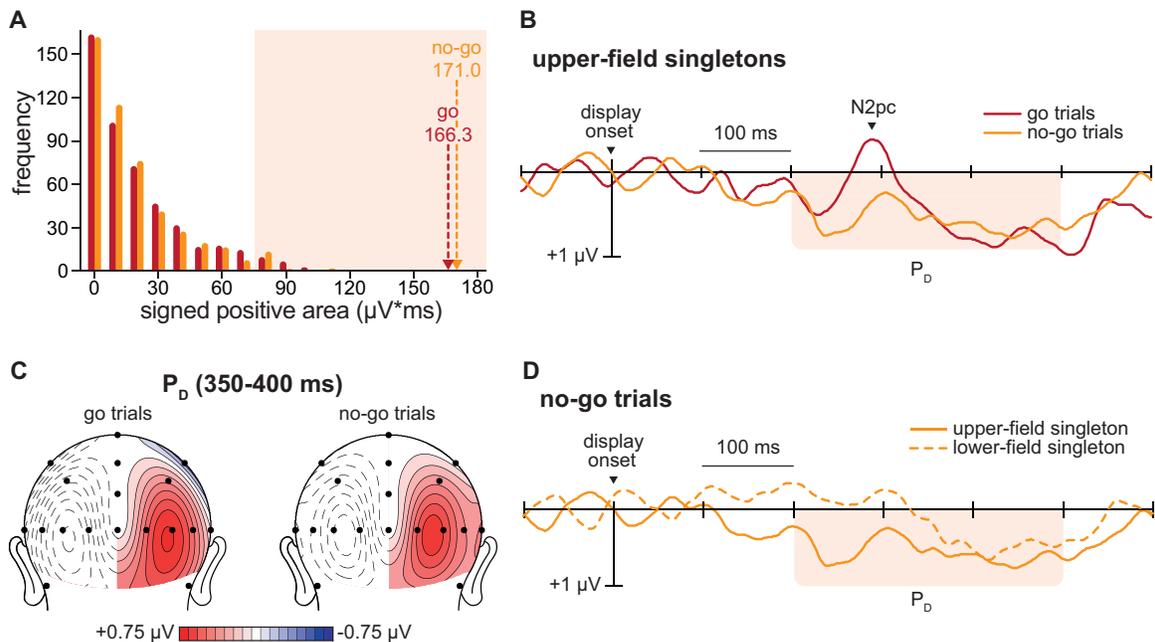


Figure 3.5. Visualization of suppression activity. (A) Results of permutation tests of the signed positive areas within the time interval of the P_D (200-500 ms). Red (go trials) and orange (no-go trials) vertical bars indicate the distribution of signed positive areas of the scrambled grand averages (i.e., noise distributions). Shaded region indicates the signed positive areas above the 95th percentile from the noise distributions, and vertical dashed lines indicate the measured signed positive areas from the original, unscrambled data sets. (B) Contralateral-ipsilateral difference waves elicited by upper-field singletons on go and no-go trials, recorded over the lateral occipital scalp (electrodes PO7, PO8). (C) Topographical maps corresponding to the waveforms plotted in (B). (D) Contralateral-ipsilateral difference waves elicited by no-go displays containing a singleton in the upper and lower visual field, recorded over the lateral occipital scalp (electrodes PO7, PO8).

Other ERP Components

N1

A two-way, repeated-measures ANOVA was conducted to assess whether the N1 is associated with the processing of global color (i.e., trial type; go vs. no-go) or detection of a singleton (i.e., singleton presence; present vs. absent) by measuring the mean amplitude within a 150-200-ms window of the averaged ERP waveform recorded from PO7 and PO8. This test revealed a main effect of trial type (go: $-3.02 \mu\text{V}$; no-go: -

2.29 μV), $F(1, 21) = 15.53$, $p < .001$, $\eta_p^2 = .43$, but no main effect of singleton presence (present: -2.66 μV ; absent: -2.64 μV), $F(1, 21) = 0.11$, $p = .744$. There was also no interaction between trial type and singleton presence, $F(1, 21) = 1.26$, $p = 0.275$. Based on these results, it could be tentatively concluded that early visual processing reflected by the N1 indexes global color processing and that this global processing is enhanced for task-relevant features. However, the difference in mean N1 amplitudes might have been caused by an earlier termination of N1 due to the subsequent positive-going waveform.

N1pc

It is possible that despite the absence of an N2pc, the singletons nevertheless elicited the N1pc, which might suggest that some form of early stimulus-driven shifts of attention have nevertheless occurred. To determine the presence of the N1pc, contralateral-ipsilateral difference waves elicited by lower-field singletons on go and no-go trials were assessed. The N1pc was statistically absent for both go trials (-0.13 μV), $t(21) = 1.05$, $p = .307$, and no-go trials (-0.26 μV), $t(21) = 1.55$, $p = .136$ (Figure 3.2B). These results suggest that processes associated with go/no-go evaluation prevented the singletons from triggering early shifts of stimulus-driven attention.

P2a and no-go P3

The assertion by the salience-driven selection that processes informed by top-down knowledge cannot commence until after the completion of bottom-up selection was assessed in the go-no-go difference wave. The assessment was done by using the P2a in the present experiment as the upper-bound estimate for the earliest goal-driven activity and the target-elicited N2pc as the lower-bound estimate for the latest stimulus-driven selection activity. The P2a was confirmed to be statistically present (4.12 μV), $t(21) = 12.09$, $p < .001$, $d = 3.09$, over the midline frontal scalp (Figure 3.6). A paired-sample t test revealed that the onset latency of the P2a was significantly shorter than that of the N2pc (159 ms vs. 262 ms, respectively), $t(21) = 8.34$, $p < .001$, $d = 2.63$, demonstrating that processes driven by relevance can, in fact, take place prior to salience-driven selection processes. And as expected, the no-go P3 was observed on no-go trials (-2.16 μV), $t(21) = 3.70$, $p = .001$, $d = 1.04$, indicating that participants inhibited their responses on no-go trials (see, e.g., Bokura et al., 2001).

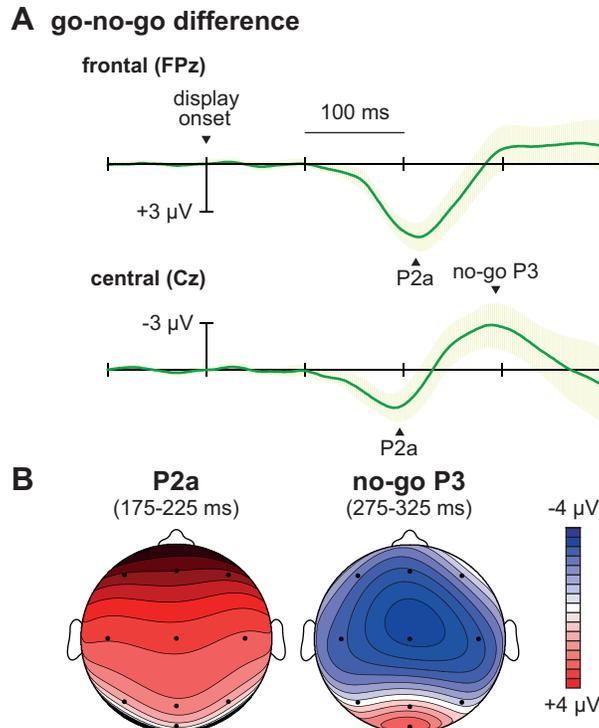


Figure 3.6. Visualization of P2a and no-go P3 activity. (A) Grand-averaged, go-no-go difference waves recorded over the midline frontal and central scalp (FPz and Cz, respectively) isolated by subtracting ERPs elicited by no-go trials from those elicited by go trials. Vertical bars correspond to the 95% CIs at each time point. (B) Topographical maps corresponding to the waveforms plotted in (A).

Correlations

Linear relationships between N2pc magnitude and magnitudes of the target-elicited N1 and SDP (on go trials) were assessed to determine whether the same relationships observed in Chapter 2 would be observed in the present experiment. Interestingly, the N1 magnitude did not predict N2pc magnitude in this experiment, $r(21) = -.13$, $p = .579$. However, SDP magnitude was found to predict N2pc magnitude once more, $r(21) = .53$, $p = .012$ (polarities of the components were ignored, so a positive correlation indicates that N2pc magnitude increased along with increases in SDP magnitude). These results further suggest that the N1 was associated with global color processing, rather than singleton processing, in the current task, and that the SDP was associated with the detection of the singleton itself. In addition to these planned analyses, a post-hoc analysis was performed to determine whether the predicted P_D on no-go trials correlated to the somewhat unexpected contralateral positivity observed on go trials. A significant correlation was found, $r(21) = 0.64$, $p = .001$, suggesting that the

positivity on go trials was a target-elicited P_D that likely reflected active termination of attentional processing (see Sawaki et al., 2012).

Linear relationships between each ERP component and the vWMC capacity estimate (K) were then assessed to determine which component processes predict individual differences in vWMC. The first set of tests focused on go trials. As shown in Figure 3.7, K correlated positively with SDP amplitude, $r(21) = .67$, $p < .001$ and N2pc amplitude, $r(21) = .51$, $p = .016$, (the polarities of the amplitude measures were ignored so that a positive correlation would indicate that, as one component increased in magnitude, so did K). By contrast, there was no correlation between K and magnitude of N1 elicited by target singletons, $r(21) = .07$, $p = .768$.

The second set of tests focused on no-go trials. These tests revealed that there was no correlation between K and amplitudes of the N1, SDP, or N2pc, $r_s(21) \geq -.03$, $p_s \geq .878$ (note that the N2pc was found to be absent on no-go trials, so amplitude of the N2pc here simply reflected the mean amplitude obtained in the prespecified N2pc measurement interval). Together, the results of these first two sets of tests suggest that high- and low-capacity individuals were equally adept at preventing singleton detection on no-go trials, but low-capacity individuals showed diminished singleton-detection activity on go trials in comparison with high-capacity individuals.

The third set of tests focused on ERPs associated with go/no-go processing. The results showed that K did not correlate with P2a amplitude or no-go P3 amplitude, $r_s(21) \leq .17$, $p_s \geq .450$. These results suggest that there was no difference in ability to distinguish a go from a no-go display nor ability to adhere to the task instruction between high- and low-capacity individuals.

The final set of tests focused on ERPs associated with suppression on go and no-go trials. The results showed that K correlated positively with magnitude of the target-elicited P_D on go trials, $r(21) = .55$, $p = .008$, and marginally so with magnitude of the distractor-elicited P_D on no-go trials, $r(21) = .42$, $p = .052$. Following this finding, an additional Pearson correlation coefficient was computed between K and magnitude of the P_D combined across go and no-go trials in an attempt to improve the signal-to-noise ratio. This test revealed a positive correlation (Figure 3.7C), $r(21) = .52$, $p = .012$. Results of this final set of tests is largely consistent with previous findings that P_D

magnitude predicts vWMC (Feldmann-Wüstefeld & Vogel, 2019; Gaspar et al., 2016). To help visualize the relationships in Figure 3.7, participants were sorted into two groups based on their K . Participants with a K larger than the median K were sorted to the high- K group and those with K smaller than the median K were sorted into the low- K group (see Figure 3.8).

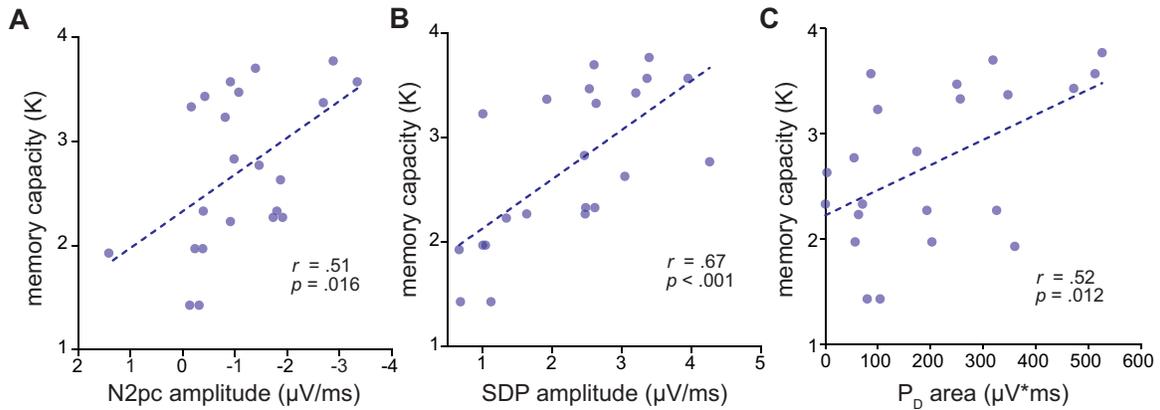


Figure 3.7 Scatter plots showing relationships between estimated visual working memory capacity (K) and magnitudes of the N2pc elicited by lower-field singletons on go trials (A), SDP elicited by all go-trial singletons (B), and P_D elicited by all upper-field singletons (C).

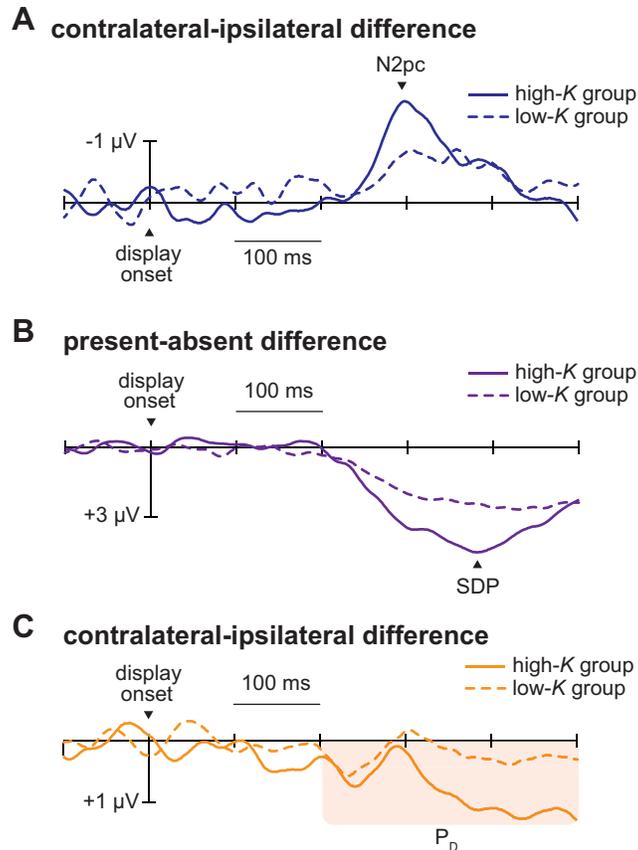


Figure 3.8 ERP visualizations of relationships between visual working memory capacity (K) and waveforms recorded over the lateral occipital scalp (PO7, PO8) illustrated in Figure 3.7. (A) Contralateral-ipsilateral difference waves elicited by lower-field singletons on go trials, separately for high- and low- K group ($N = 11$ per group). (B) Present-absent difference waves elicited by all singletons on go trials, separately for the high- and low- K group. (C) Contralateral-ipsilateral difference waves elicited by upper-field singletons combined across both go and no-go trials, separately for the high- and low- K group.

3.4. Discussion

Prior ERP studies of feature search mode have revealed that salience-driven attention capture can be prevented, but little was known about the automaticity of attention capture in singleton-detection tasks (i.e., when the target is underspecified). A novel go/no-go design was developed here to test predictions that could be made from different theoretical perspectives that differ in the (a) presumed automaticity of capture and in the (b) presumed means by which capture is prevented. Towards the more automatic end of the automaticity continuum (Figure 3.1), the salience-driven selection hypothesis proposes that observers invariably attend to visually salient objects because

stimulus-driven selection processes must be completed before processes informed by top-down knowledge can begin (e.g., to recover from capture; Theeuwes, 1991a, 1992, 2004, 2010). By this view, capture can be prevented only by restricting the size of the attentional window before search begins so that the salient object falls outside of the window (Belopolsky & Theeuwes, 2010; Belopolsky et al., 2007). Towards the other end of the continuum, top-down perspectives like the contingent capture hypothesis and the signal suppression hypothesis maintain that observers can ignore distractors by selectively up-weighting task-relevant features or down-weighting irrelevant features (Folk et al., 1994; Sawaki & Luck, 2010). To evaluate these theoretical perspectives, the present experiment focused on two ERP components as markers of attentional selection and suppression called the N2pc and the P_D, respectively. If salient-but-irrelevant singletons invariably capture attention, then these singletons should elicit the N2pc on no-go trials. Alternatively, if top-down processes can occur early to prevent salience-driven capture, then the singletons should not elicit the N2pc on no-go trials (and may even elicit the P_D if suppressed).

The present study revealed four important findings regarding the automaticity of salience-driven selection. First, singletons did not elicit the N2pc (nor the N1pc) on no-go trials. This finding suggests that observers did not spatially select (i.e., attend to) singletons on no-go trials, contrary to the first tenet of the salience-driven selection hypothesis that salient stimuli within the attentional window invariably capture attention. At the outset, it was assumed that the attentional window would remain wide enough to process all the items in the search array throughout the experiment because no item individuation was required to determine the color of the display. Although several recent findings are in line with this assumption (for discussion, see Chapter 4, Section 4.2), it could be questioned whether attention was narrowly focused at fixation at the start of each trial to determine the color of an individual item nearby. The absence of capture on no-go trials could then be ascribed to a restriction of the attentional window that precluded salience computations for the distant singleton. By this account, observers would also not be able to engage in parallel search for the singleton on go trials and thus would have to shift attention serially from item to item until the target was found (Belopolsky & Theeuwes, 2010). I tested this serial-search explanation more directly in a follow-up experiment (Supplementary Experiment 1; Appendix) that was similar to Experiment 2 but randomly varied the display set size (8 or 16 items) with equal

probability. If a serial-search strategy was used, RTs would be longer for 16-item displays than for 8-item displays (that is, a positive search slope would be found; e.g., Treisman & Gelade, 1980). Contrary to this prediction, RTs were numerically *shorter* for the larger set size but were statistically indistinguishable between the 8- and 16-item displays (643 ms vs. 636 ms, respectively), $t(11) = 1.26$, $p = .234$. The absence of a positive search function indicates that observers did not restrict the size of their attentional window and engage in a serial search, thereby buttressing the conclusion that the most salient item in the attentional window does not capture attention automatically.

Second, salient-but-irrelevant singletons appeared to elicit a P_D on no-go trials. The presence of a P_D indicates that observers managed to ignore the irrelevant singletons by actively suppressing them. This finding is broadly consistent with hypotheses toward the controlled end of the automaticity continuum and is specifically consistent with the signal-suppression hypothesis, which supposes that capture is always prevented by suppressing visual processing at the distractor location. However, this singleton-detection P_D is at odds with the notion that selection is entirely salience-driven in singleton detection mode (e.g., Bacon & Egeth, 1994). Interestingly, a P_D was also elicited by singletons on go trials. Such a target-elicited P_D is consistent the proposal that attentional processes are actively terminated following completion of perception (Sawaki et al., 2012).

Third, a $P2a$ emerged over the anterior scalp before the onset of the $N2pc$. This temporal sequence, together with the presumed functional significance of each ERP component, indicates that observers processed the relevancy of the displays before singleton selection took place. Importantly, this finding disconfirms the second tenet of the salience-driven selection hypothesis, namely that top-down control is possible only after salience-driven selection has occurred. This result is corroborated by the attenuated SDP and $N1$ on no-go trials, further suggesting that top-down processes can modulate early stages of visual-information processing to rapidly terminate search following evaluation of stimulus relevance.

Fourth, despite the high salience of the singleton, the go-trial $N2pc$ appeared relatively late in this study. A comparison of $N2pc$ latencies across Experiments 1 and 2 is not possible due to the different set sizes and colors, and so another follow-up

experiment (Supplementary Experiment 2; Appendix) was conducted to assess the N2pc latency. The same 16-item all-cyan and all-yellow displays were used, except participants were instructed to indicate the presence or absence of the singleton on all trials, regardless of item color (here termed the *all-go condition*; see Figure 3.9). Critically, N2pc onset latency (time at which the N2pc reached 25% of its peak amplitude) was delayed by 97-ms on the go trials of Experiment 2, relative to the all-go trials of the follow-up experiment (165 ms vs. 262 ms). This difference was found to be statistically significant $t(42) = 2.04, p = .048, d = 0.61$, using standard jackknife procedures (Miller et al., 1998). This delay indicates that, in the go/no-go task, observers first evaluated the global color of the display and then deployed attention to the singleton on go trials and that this evaluation took roughly 100 ms on average. Moreover, the delay is inconsistent with the salience-driven selection hypothesis, which supposes that relevance-driven processes cannot precede or modulate salience-driven selection within the attentional window.

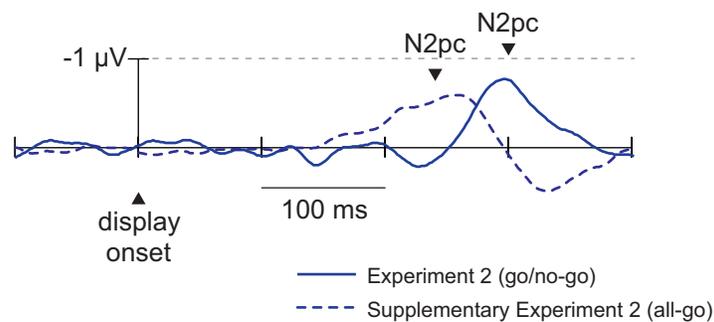


Figure 3.9 Comparison of grand-averaged contralateral-ipsilateral waveforms elicited by a target singleton between the present study (Experiment 2) and a follow-up experiment (Supplementary Experiment 2).

In addition to addressing questions relating to the automaticity of salience-driven selection, intercomponent analyses revealed that N2pc magnitude was positively correlated with SDP magnitude but not with N1 magnitude. Because the SDP has an earlier onset than the N2pc, it is tentatively concluded that the SDP is associated with the detection of the singleton itself, so that greater detection activity, especially early on, helps to facilitate subsequent orienting of attention to location of the singleton. Given that N1 magnitude positively correlated with N2pc magnitude in Experiment 1 but not in Experiment 2, it is concluded that the N1 is associated with analysis of features immediately relevant to the task at hand (here, discriminating between go and no-go display colors) and not with singleton detection per se. This interpretation is in line with

previous findings indicating that the N1 indexes a visual discrimination process within the attended region (Vogel & Luck, 2000).

Analysis of individual differences revealed that neural activity associated with singleton detection (SDP) and selection (N2pc) on go trials predicts vWMC. The relationship between measured N2pc amplitude and vWMC might explain, at least in part, the variance in N2pc magnitude seen across individuals in Chapter 2. This relationship is not always observable, however. For example, there was no such relationship in Gaspar et al.'s (2016) feature-search task. One possibility is that a relationship between N2pc and vWMC emerges only when the target-selection process requires more control and cannot be automated like it can in a search for a fixed-feature singleton that appears on every trial. The relationships of SDP and N2pc with vWMC might also suggest that low-capacity individuals have difficulty initiating singleton detection when search is not required on every trial or when switching from an initial global-color processing phase to a subsequent singleton-detection phase. This difficulty is not driven by one's ability to distinguish a go trial from a no-go trial because neural activity associated with go/no-go evaluation (P2a) and subsequent no-go inhibition (P3) did not predict vWMC. Despite this difficulty, there was no predictable RT difference between high- and low-capacity individuals. The lack of a behavioral difference may be explained by the simplicity of singleton detection or the presence of a compensatory mechanism among low-capacity individuals. Interestingly, whereas there was a difference in ability to initiate search on go trials between high- and low-capacity individuals, there was no difference in their ability to terminate search on no-go trials (as evidenced by the lack of relationship between vWMC and magnitude measured in the time interval of SDP and N2pc on no-go trials).

Chapter 4. General Discussion and Conclusions

The search for a visual object is often performed by holding a set of target features in mind and comparing objects in the visual field to this feature template until a match is found (a process called feature search). Sometimes, however, people must search for objects without foreknowledge of their features, rendering the feature-based search strategy impossible or at least ineffective. It has been found that the search for an object with underspecified features can be accomplished easily when it possesses at least one unique feature that makes it stand out from its surrounding, in which case, observers can search for a discontinuity in the visual field or otherwise let the most salient item in the visual field capture their attention (a process called singleton detection). While much is known about how feature search is accomplished, less is known about the processes involved in singleton detection. The present thesis investigated the role of attention in singleton detection, the automaticity of singleton detection, and the electrophysiological underpinnings of singleton detection.

4.1. Role of Attention in Singleton Detection

Over the past four decades, researchers have advanced numerous theories about the role of attention in visual perception (for a review, see Carrasco, 2011). Despite general agreement that attentional processes enable the conscious perception of specific objects in the visual environment, the role of attention in singleton detection has remained poorly understood. According to the *feature integration theory* (Treisman & Gelade, 1980), the presence of a specified feature can be detected preattentively by polling relevant feature maps directly without the involvement of attention to bind these features into an object. However, by this account, observers would have to simultaneously poll all potentially relevant feature maps to detect a singleton with underspecified features, rendering such a feature-based search strategy inefficient (but see Treisman, 1988). In such instances, observers might instead adopt a strategy to detect a discontinuity in the visual field (Bravo & Nakayama, 1992; Julesz, 1984; Julesz & Bergen, 1983; Pashler, 1988). According to Julesz and Bergen (1983), for example, conspicuous differences in local features can be detected rapidly without the involvement of attention; that is, singleton detection can be accomplished preattentively. But according to other theories, attention is required even for the simplest decisions

about visual input, such as whether the visual field contains a singleton (e.g., Theeuwes, 2010).

Using a singleton-detection task, Luck and Hillyard (1994) provided electrophysiological evidence for the view that singleton detection can be accomplished without involvement of spatial attention. In this study, observers searched for an orientation singleton (target) in displays containing eight vertical or horizontal lines. To discourage feature search and promote singleton detection, Luck and Hillyard swapped the orientation of the target with its surrounding nontargets, so that half the target-present trials showed a vertical line situated among seven horizontal lines and the other half showed a horizontal line situated among seven vertical lines. Luck and Hillyard reported that the singleton does not elicit the N2pc, nor any other notable electrophysiological activity associated with attention, under such conditions. This finding is consistent with the behavioral results from Bravo and Nakayama's (1992) singleton-detection task, whereby increases in set size has no effect on speed of detection (i.e., a flat search function; on the grounds that the involvement of capacity-limited attentive processes would yield a positive search function). However, a more recent study by Schubö et al. (2004) suggested that singletons might elicit the N2pc after all, at least in singleton-detection displays with more than six items.

By improving the statistical power of Luck and Hillyard's (1994b) singleton-detection task in Chapter 2, I showed that the singleton in a pure singleton-detection task does, in fact, elicit the N2pc. While the presence of N2pc in this experiment cannot demonstrate that attention is necessary for singleton detection, it does show that singleton detection involves attentional selection under normal circumstances (i.e., in the absence of a dual-task requirement or masking to prevent superfluous visual processes). The present results are consistent with proposals that attention must be deployed to the location of the singleton to detect its presence (e.g., Joseph et al., 1997; Theeuwes, 2010), but it is also possible that singleton detection precedes the selection process driving the N2pc and that selection of the singleton object is required not for detection but for subsequent stages of processing associated with object perception and storing or updating target information in visual working memory.

4.2. Automaticity of Singleton Detection

The results of Experiment 2 (Chapter 3) have important implications for the debate surrounding the automaticity of attention capture by salient-but-irrelevant singletons. According to the salience-driven selection hypothesis (Theeuwes, 1991a, 1992, 2010), the initial shift of focal attention invariably goes to the most salient singleton within the attentional window (Tenet 1). After that stimulus is attended, the visual system is able to evaluate whether it is relevant to the task at hand. In other words, this hypothesis proposes that goal-driven processes cannot begin until after purely bottom-up selection processes are completed (Tenet 2). Four key findings from Chapter 3 would seem to argue against the core tenets of the salience-driven selection hypothesis. The first two findings were that the orientation singleton—which was the most salient stimulus in the display—did not elicit the N2pc and instead elicited the P_D on no-go trials. Such findings indicate that the stimulus was suppressed proactively to prevent salience-driven distraction. The third finding was that top-down processes reflected by the P2a began prior to the onset of the N2pc, showing that processes informed by top-down knowledge can, in fact, take place prior to bottom-up selection processes. The fourth finding was that the N2pc was delayed on go trials compared to the N2pc elicited in an all-go condition (Supplementary Experiment 2; Appendix), indicating that observers can postpone salience-driven selection to process other relevant aspects of the display. Together, these findings demonstrate that early top-down processes can delay salience-driven processes or override them entirely to prevent capture by salient singletons.

In light of this conclusion, one may ask *how* observers managed to prevent capture by singletons on no-go trials of Experiment 2. One possibility that stems from proponents of the salience-driven selection hypothesis is that observers adopted a strategy to restrict their attentional focus around the fixation cross in order to carefully inspect the color of a nearby item. This explanation is consistent with the results of prior distractor-interference studies that manipulated the size of the attentional focus (the so-called attentional window) prior to the appearance of the search display (Belopolsky & Theeuwes, 2010; Belopolsky et al., 2007). For example, using a go/no-go paradigm, Belopolsky and Theeuwes (2010) reported that a salient distractor did not interfere with search for a less-salient target when observers had to identify a letter presented at fixation before commencing (or aborting) search. According to these investigators,

reducing the size of the attentional window helps observers to ignore salient stimuli because salience computation takes place only within the attentional window and thus salience of singletons outside of the window is essentially unknown. By this account, observers would have started each trial of Experiment 2 with a narrow attentional window and would then have to engage in a serial search for the singleton on go trials (because the salience of the singleton would not have been computed).

There are three considerations that argue against this serial-search explanation. First, there was no incentive for participants to restrict the size of their attentional window because every item in the display was the same color (i.e., there was no need to individuate any particular item). Second, prior N2pc studies have demonstrated that item individuation does not occur when the task does not require it. For example, when observers view displays containing one, two, or three red color singletons (targets), the N2pc grows in amplitude with each increase in the number of targets when the task is to enumerate the targets but not when the task is to detect the presence of at least one target item (Mazza & Caramazza, 2011). The amplitude growth indicates that observers individuated each target in the enumeration task, and the lack of amplitude growth in the detection task indicates that red items were treated as a whole rather than as separate objects. Third, based on the observed timing and amplitude of the N2pc, one can conclude that attention was oriented rapidly, and likely directly, to the singleton once the trial was determined to be a go trial. A serial search for the singleton would lead to a smaller, more sustained contralateral negativity or no N2pc at all (Figure 12.5; Luck, 2012, p. 339; Dowdall et al., 2012; see also Christie et al., 2015)

In addition to these considerations, the results of Supplementary Experiment 1 (Appendix) help to disconfirm the serial-search explanation (Section 3.4). This experiment presented displays identical to those used in Experiment 2 except that half the displays contained 8 items instead of 16. The rationale was that if observers adopted a serial-search strategy by narrowing their attentional window prior to their search, then they should be faster at finding the singleton on go trials in 8-item displays than in 16-item displays (resulting in a positive search function; see, e.g., Treisman & Gelade, 1980). Critically, participants were no faster at detecting a singleton among 8 items than among 16 items (in fact, numerically, RTs were shorter for 16-item displays than for 8-item displays; 636 ms vs. 643 ms, respectively). Given that search remained efficient on

go trials, there is simply no evidence that attention was narrowly focused at the outset of each trial.

With the attentional window presumably remaining wide throughout Experiment 2, another possibility is that observers suppressed the salient-but-irrelevant singleton prior to the deployment of attention (as proposed by the signal suppression hypothesis; Sawaki & Luck, 2010). Such suppression was predicted to give rise to a singleton-elicited P_D on no-go trials. In line with this prediction, the results showed that the singleton elicited a P_D on no-go trials, with no earlier N2pc preceding the P_D . This pattern of results is important for at least four reasons. First, it shows that observers can exhibit genuine top-down control over salience-driven capture not only by restricting the spatial focus of attention so that the salience of the singleton is unknown (Belopolsky & Theeuwes, 2010; Belopolsky et al., 2007), but also by deciding to process a global feature of the display that does not require object individuation. Second, it shows that salience-driven capture can be prevented not only in feature-search tasks that may inadvertently lower the salience of the singleton (as has been claimed by Wang and Theeuwes, 2020) but also in tasks that involve singleton detection. Third, it shows that suppression can prevent capture proactively, not just reactively to recover from capture once it occurs (Theeuwes, 2010). Fourth, it confirms that capture can be prevented by suppressing salient-but-irrelevant items, not just by upweighting target features.

4.3. Electrophysiological Underpinnings of Singleton Detection

Noninvasive recordings of brain potentials have enabled researchers to study covert attentional processes even in the absence of an overt behavioral response. For over two decades, researchers have tracked the deployment of visual attention using the N2pc component to inform theories of visual attention. This ERP component is found when observers search for a singleton based on a defining feature (i.e., in feature search mode), but a debate remains as to whether an N2pc can be elicited when search cannot be guided by a specific feature but only by a target's uniqueness (i.e., in singleton detection mode). Luck and Hillyard (1994b) proposed that the N2pc is associated with the resolution of neural ambiguity by way of a spatial-filtering process that attenuates neural responses to irrelevant (and presumably unattended) items in the vicinity of the attended object (see also Luck et al., 1997). By this proposal, it was predicted that the

N2pc should be absent when observers search for an oddball (i.e., singleton) rather than a specific feature, on the grounds that filtering would presumably interfere with the process of comparing the singleton with its surrounding items during singleton detection (Luck, 2012; Luck & Hillyard, 1994b). Consistent with this prediction, Luck and Hillyard failed to find an N2pc when the orientation of a target singleton and nontargets were swapped randomly across trials to discourage search for an item with a specific orientation. No other ERP component was associated with singleton detection in that seminal experiment. By contrast, the present thesis experiments show that singleton detection is associated with ERP components including the N1pc, the N2pc, the SDP, and the P_D. Furthermore, my results show how these electrophysiological processes vary predictably across healthy young adults. In the following sections, I discuss each of the electrophysiological correlates of singleton detection.

4.3.1. The N1pc

The N1pc is a lateralized negativity observed in the time range of the N1. Because of its distribution over the posterior scalp, the N1pc has been hypothesized to reflect some form of early visual processing, including the reflexive orienting of attention to unilateral stimuli (Wascher & Beste, 2010a, 2010b) and the stimulus-driven selection of a salient stimulus during the initial sweep of visual processing (Verleger et al., 2012). Across the two thesis experiments, it was found that the N1pc is sometimes associated with singleton detection: Results of Chapter 2 showed that the N1pc was present on fast-response trials but absent on slow-response trials, indicating that the N1pc facilitates singleton detection. This conclusion is consistent with the finding that a large N1pc predicts a large N2pc across individuals. This facilitatory process, however, is unaffected by the priming of pop-out across consecutive trials because there was no difference in the timing or magnitude of N1pc between repeat- and change-orientation trials. This finding thus suggests that priming of pop-out influences visual processing at a later stage (starting in the time range of the N2pc, as seen in Experiment 1). Interestingly, the go/no-go singleton-detection task in Chapter 3 failed to elicit an N1pc despite the increased singleton salience, indicating that the N1pc is a stimulus-driven process that can be inhibited in favor of the ongoing task at hand (i.e., global processing of display color in Experiment 2).

4.3.2. The N2pc

As previously mentioned, the N2pc has been largely hypothesized to reflect a spatial-filtering process that suppresses the flow of visual information arising from items in the vicinity of the attended object, and the absent N2pc in Luck and Hillyard's (1994b) singleton-detection task is one of the main reasons the N2pc has been assumed to reflect this filtering process. The results of my thesis experiments (Experiments 1, 2, and Supplementary Experiment 2) disconfirm this view by showing the presence of a sizable N2pc in similar singleton-detection tasks that presumably minimizes spatial filtering. Results of Experiment 1 (Chapter 2) show that this singleton-detection-mode N2pc resembles the N2pc found in other studies: namely, it is maximal at electrodes PO7/8 (Luck, 2012), larger for lower-field targets (Luck et al., 1997), earlier on repeat-orientation trials (Christie et al., 2015; Eimer et al., 2010), and earlier on fast-response trials (McDonald et al., 2013). Following Luck and Hillyard's (1994b) rationale for their seminal singleton-detection study, it is proposed that the N2pc does not therefore reflect a spatial-filtering process that suppresses information from unattended items but instead reflects a selection process that acts on the attended item (or group of items) itself. This selection process may be associated with (a) the localization of to-be-attended objects prior to the deployment of attention (Tan & Wyble, 2015), (b) the enhancement of task-relevant features following the deployment of attention (Eimer, 1996), or (c) object individuation (Mazza & Caramazza, 2011). Because the N2pc occurs in both feature search and singleton detection, it can be concluded that the component is not associated with a template-matching process (as previously proposed in Section 1.3.3).

As seen in the thesis experiments, the N2pc elicited by singletons in the present singleton-detection paradigm is later and smaller than that typically elicited by singletons in feature-search paradigms. Specifically, the N2pc in the present study appears approximately 250 ms after the onset of the search array and is smaller than $-1 \mu\text{V}$. By contrast, the N2pc elicited by target singletons in Luck and Hillyard's (1994b, Experiment 1) feature-search task appeared 50 ms earlier and was at least twice the magnitude. One possibility for this disparity is that feature-search paradigms enable an attentional set for a specific feature, and when combined with a history of selecting the same feature across every trial, may boost the neural sensitivity to the target and thus enhancing its perceived salience. Consistent with this explanation, the N2pc elicited by

salient targets appear earlier and larger than the N2pc elicited by less-salient targets (e.g., see figure 5 of Gaspar & McDonald, 2014).

Another possibility is that the N2pc typically observed in feature-search tasks reflects two underlying mechanisms, one being a nonspatial feature-selection mechanism that enhances all task-relevant features in the visual field, and another being a subsequent object-individuation mechanism, whereby features at a location are integrated in such a way as to enable the perception of these separate features as one unitary object in space. This two-stage process was evidenced by results showing that nontarget objects possessing only one of two task-relevant features elicited an N2pc simultaneous to that elicited by the target, but the nontarget-elicited N2pc was smaller than that elicited by the target (Eimer & Grubert, 2014; Kiss, Grubert, & Eimer, 2013; see also Bichot et al., 2005; Hopf et al., 2004). This finding suggests that the task-relevant feature of the nontarget triggered the nonspatial feature-selection mechanism but, because the nontarget did not possess both task-relevant features, was insufficient to trigger the subsequent object-individuation mechanism. Therefore, since the singleton-detection task in Chapter 2 discourages the search for a particular feature, the early, feature-selection portion of the N2pc would not be elicited, resulting in the appearance of a smaller and later N2pc. And although the singleton-detection task in Experiment 2 (Chapter 3) permitted an attentional set for a specific color, the target singleton still elicited a smaller and later N2pc because the color of the surrounding nontargets would also trigger the feature-selection mechanism, so that the activity observed as the N2pc would only reflect the object-individuation mechanism triggered by the target. This two-stage selection mechanism is consistent with various theories of visual search (Cave, 1999; Treisman & Gelade, 1980; Treisman & Sato, 1990; Wolfe, 1994), whereby feature-based attention first provides a map of probable target locations that then guides spatial attention to those locations for detailed perceptual analysis.

4.3.3. The SDP

The SDP, which was discovered in Experiment 1, is a sustained positivity that starts approximately 200 ms over the bilateral posterior scalp following the presentation of a target singleton and roughly 30 ms prior to the N2pc. The SDP is isolated by subtracting ERPs elicited by singleton-absent trials from those of singleton-present trials (i.e., the present-absent difference wave). The magnitude of the SDP was found to be

positively correlated with N2pc magnitude across individuals within each experiment. And in Experiment 1, an earlier-onsetting SDP was associated with faster manual responses. Interestingly, the go/no-go singleton-detection task in Chapter 3 revealed that the process underlying the SDP can be greatly attenuated when the global color of the display indicates that detection is not required (i.e., on no-go trials). Taken together, I propose that the SDP reflects the detection of a singleton, or perhaps any salient individuated stimulus, and that such processes can be terminated when item individuation is unnecessary or suppressed.

Surprisingly, the attenuated SDP evident on no-go trials did not vary as a function of vWMC, suggesting that low-capacity individuals were no more likely to inadvertently detect the singleton on no-go trials than high-capacity individuals. Upon initial consideration, this finding appears to run counter to those showing that high-capacity individuals tend to have better inhibitory control. For example, Gaspar et al. (2016) found that low-capacity individuals have greater difficulty suppressing salient-but-irrelevant singletons compared to high-capacity individuals (as revealed by a positive correlation between memory capacity and magnitude of P_D). However, the two findings are not at odds if one assumes that low-capacity individuals have a specific inhibitory-control deficit that takes place during object individuation, that the deficits are revealed in tasks that require more control (that more control is required to ignore one of two singletons in the same display), or that no inhibition was required to terminate singleton detection after the initial global-color processing stage revealed search was unnecessary.

Although low-capacity individuals did not appear to have an inhibitory control deficit on no-go trials in Experiment 2, they did appear to differ from their high-capacity counterparts on go trials. Specifically, on go trials, both the SDP and the N2pc were smaller for low-capacity individuals than for high-capacity individuals. This difference may indicate that low-capacity individuals have difficulty initiating singleton detection when search is not required on every trial or when switching from an initial global-color processing phase to a subsequent singleton-detection phase. Regardless, it is clear that this difference was not due to a reduced ability to distinguish a go trial from a no-go trial among low-capacity individuals because amplitudes of the P2a and no-go P3 were found to not correlate with vWMC.

4.3.4. The P_D

The P_D is a positivity elicited by a visually suppressed item over the contralateral occipital scalp. At its discovery, the P_D was thought to reflect the active suppression of an irrelevant item in the visual field (Hickey et al., 2009). More recently, this suppression mechanism was also observed for attended objects, and it was hypothesized that a common suppression mechanism was involved in both preventing and terminating the allocation of attention (Sawaki et al., 2012). Experiment 2 (Chapter 3) provided evidence for both a target-elicited P_D (on go trials) and a distractor-elicited P_D (on no-go trials). And although no statistical test was performed in Experiment 1 (Chapter 2) for a target-elicited P_D, a P_D-like positivity could also be seen in Figure 2.4B (for upper-field targets). The present study provided further evidence that the target- and distractor-elicited P_D share a common suppression mechanism by positively correlating magnitudes of the two components across individuals. Importantly, whereas previous evidence for the P_D had been found exclusively in feature-search studies, the present study provided the first evidence for suppression in singleton detection. Similar to the P_D found in previous feature-search studies, this singleton-detection P_D was marginally larger for upper-field singletons on no-go trials (Hickey et al., 2009) and larger among individuals with high vWMC (Gaspar et al., 2016). The singleton-detection P_D therefore contradicts the notion that selection is entirely salience-driven in singleton detection mode.

References

- Arcizet, F., Mirpour, K., & Bisley, J. W. (2011). A pure salience response in posterior parietal cortex. *Cerebral Cortex*, *21*(11), 2498-2506.
- Arnott, S. R., & Alain, C. (2002). Stepping out of the spotlight: MMN attenuation as a function of distance from the attended location. *NeuroReport*, *13*(17), 2209-2212.
- Astikainen, P., Ruusuvirta, T., Wikgren, J., & Korhonen, T. (2004). The human brain processes visual changes that are not cued by attended auditory stimulation. *Neuroscience Letters*, *268*(2), 231-234.
- Bacon, W. F., & Egeth, H. E. (1994). Overriding stimulus-driven attentional capture. *Perception & Psychophysics*, *55*(5), 485-496.
- Belopolsky, A. V., & Theeuwes, J. (2010). No capture outside the attentional window. *Vision Research*, *50*, 2543-2550.
- Belopolsky, A. V., Zwaan, L., & Theeuwes, J. (2007). The size of an attentional window modulates attentional capture by color singletons. *Psychonomic Bulletin & Review*, *14*(5), 934-938.
- Bergen, J. R., & Julesz, B. (1983). Parallel versus serial processing in rapid pattern discrimination. *Nature*, *303*, 696-698.
- Bichot, N. P., Rossi, A. F., & Desimone, R. (2005). Parallel and serial neural mechanisms for visual search in macaque area V4. *Science*, *308*, 529-534.
- Bichot, N. P., & Schall, J. D. (1999). Effects of similarity and history on neural mechanisms of visual selection. *Nature Neuroscience*, *2*, 549-554.
- Bisley, J. M., & Goldberg, M. E. (2010). Attention, intention, and priority in the parietal lobe. *Annual Review of Neuroscience*, *33*, 1-21.
- Bokura, H., Yamaguchi, S., & Kobayashi, S. (2001). Electrophysiological correlates for response inhibition in a go/nogo task. *Clinical Neurophysiology*, *112*(12), 2224-2232.
- Bravo, M. J., & Nakayama, K. (1992). The role of attention in different visual-search tasks. *Perception & Psychophysics*, *51*(5), 465-472.
- Bruin, K. J., Wijers, A. A., & van Staveren, A. S. J. (2001). Response priming in a go/nogo task: Do we have to explain the go/nogo N2 effect in terms of response activation instead of inhibition? *Clinical Neurophysiology*, *112*(9), 1660-1671.
- Bundesen, C. (1990). A theory of visual attention. *Psychological Review*, *97*(4), 523-547.

- Buzsáki, G., Anastassiou, C. A., & Koch, C. (2012). The origin of extracellular fields and currents – EEG, ECoG, LFP and spikes. *Nature Reviews Neuroscience*, *13*, 407-420.
- Callahan-Flintoft, C., Chen, H., & Wyble, B. (2018). A hierarchical model of visual processing simulates neural mechanisms underlying reflexive attention. *Journal of Experimental Psychology: General*, *147*(9), 1273-1294.
- Carrasco, M. (2011). Visual attention: The past 25 years. *Vision Research*, *51*, 1484-1525.
- Cave, K. R. (1999). The FeatureGate model of visual selection. *Psychological Research*, *62*(2-3), 182-194.
- Chelazzi, L., Duncan, J., Miller, E. K., & Desimone, R. (1998). Responses of neurons in inferior temporal cortex during memory-guided visual search. *Journal of Neurophysiology*, *80*(6), 2918-2940.
- Chelazzi, L., Miller, E. K., Duncan, J., & Desimone, R. (1993). A neural basis for visual search in inferior temporal cortex. *Nature*, *363*, 345-347.
- Christie, G. J., Livingstone, A. C., & McDonald, J. J. (2015). Searching for inefficiency in visual search. *Journal of Cognitive Neuroscience*, *27*(1), 46-56.
- Christie, G. J., Spalek, T. M., & McDonald, J. J. (2018). Saliency drives overt selection of two equally relevant visual targets. *Attention, Perception, & Psychophysics*, *80*(6), 1342-1349.
- Comerchero, M. D., & Polich, J. (1998). P3a, perceptual distinctiveness, and stimulus modality. *Cognitive Brain Research*, *7*(1), 41-48.
- Comerchero, M. D., & Polich, J. (1999). P3a and P3b from typical auditory and visual stimuli. *Clinical Neurophysiology*, *110*(1), 24-30.
- Constantinidis, C., & Steinmetz, M. A. (2005). Posterior parietal cortex automatically encodes the location of salient stimuli. *Journal of Neuroscience*, *25*(1), 233-238.
- Cosman, J. D., Lowe, K. A., Zinke, W., Woodman, G. F., & Schall, J. D. (2018). Prefrontal control of visual distraction. *Current Biology*, *28*, 414-420.
- Courchesne, E., Hillyard, S. A., & Galambos, R. (1975). Stimulus novelty, task relevance and the visual evoked potential in man. *Electroencephalography and Clinical Neurophysiology*, *39*(2), 131-143.
- Courchesne, E., Kilman, B. A., Galambos, R., & Lincoln, A. J. (1984). Autism: Processing of novel auditory information assessed by event-related brain potentials. *Electroencephalography and Clinical Neurophysiology/Evoked Potentials Section*, *59*(3), 238-248.

- Cowan, N. (2001). The magical number 4 in short-term memory: A reconsideration of mental storage capacity. *Behavioral and Brain Sciences*, 24, 87-185.
- Cycowicz, Y. M., & Friedman, D. (1998). Effect of sound familiarity on the event-related potentials elicited by novel environmental sounds. *Brain and Cognition*, 36(1), 30-51.
- Czigler, I., Balázs, L., & Pató, L. G. (2004). Visual change detection: Event-related potentials are dependent on stimulus location in humans. *Neuroscience Letters*, 364(3), 149-153.
- Desimone, R., & Duncan, J. (1995). Neural mechanisms of selective visual attention. *Annual Review of Neuroscience*, 18, 193-222.
- Donkers, F. C. L., & van Boxtel, G. J. M. (2004). The N2 in go/no-go tasks reflects conflict monitoring not response inhibition. *Brain and Cognition*, 56(2), 165-176.
- Dowdall, J. R., Luczak, A., & Tata, M. S. (2012). Temporal variability of the N2pc during efficient and inefficient visual search. *Neuropsychologia*, 50, 2442-2453.
- Downing, P. E., & Treisman, A. M. (1997). The line-motion illusion: Attention or impletion? *Journal of Experimental Psychology: Human Perception and Performance*, 23(3), 768-779.
- Duncan, J. (1985). Visual search and visual attention. In M. I. Posner & O. S. M. Marin (Eds.), *Attention and performance XI: Attention and neuropsychology* (pp. 85-106). Hillsdale, NJ: Lawrence Erlbaum Associates, Inc.
- Duncan, J., & Humphreys, G. W. (1989). Visual search and stimulus similarity. *Psychological Review*, 96(3), 433-458.
- Egeth, H. E., & Dagenbach, D. (1991). Parallel versus serial processing in visual search: Further evidence from subadditive effects of visual quality. *Journal of Experimental Psychology: Human Perception and Performance*, 17(2), 551-560.
- Egeth, H. E., Leonard, C. J., & Palomares, M. (2008). The role of attention in subitizing: Is the magical number 1? *Visual Cognition*, 16(4), 463-473.
- Eimer, M. (1993). Effects of attention and stimulus probability on ERPs in a go/nogo task. *Biological Psychology*, 35, 123-138.
- Eimer, M. (1996). The N2pc component as an indicator of attentional selectivity. *Electroencephalography and Clinical Neurophysiology*, 99(3), 225-234.
- Eimer, M., & Grubert (2014). The gradual emergence of spatially selective target processing in visual search: From feature-specific to object-based attentional control. *Journal of Experimental Psychology: Human Perception and Performance*, 40(5), 1819-1831.

- Eimer, M., & Kiss, M. (2008). Top-down search strategies determine attentional capture in visual search: Behavioral and electrophysiological evidence. *Attention, Perception, & Psychophysics*, 72(4), 951-962.
- Eimer, M., Kiss, M., & Cheung, T. (2010). Priming of pop-out modulates attentional target selection in visual search: Behavioural and electrophysiological evidence. *Vision Research*, 50(14), 1353-1361.
- Escera, C., Alho, K., Winkler, I., & Näätänen, R. (1998). Neural mechanisms of involuntary attention to acoustic novelty and change. *Journal of Cognitive Neuroscience*, 10(5), 590-604.
- Escera, C., Yago, E., Corral, M. J., Corbera, S., & Nuñez, M. I. (2003). Attention capture by auditory significant stimuli: Semantic analysis follows attention switching. *European Journal of Neuroscience*, 18(8), 2408-2412.
- Ester, E. F., Drew, T., Klee, D., Vogel, E. K., & Awh, E. (2012). Neural measures reveal a fixed item limit in subitizing. *Journal of Neuroscience*, 32(21), 7169-7177.
- Fallgatter, A. J., Bartsch, A. J., & Herrmann, M. J. (2002). Electrophysiological measurements of anterior cingulate function. *Journal of Neural Transmission*, 109, 977-988.
- Feldmann-Wüstefeld, T., & Vogel, E. K. (2019). Neural evidence for the contribution of active suppression during working memory filtering. *Cerebral Cortex*, 29, 529-543.
- Folk, C. L., & Remington, R. W. (1998). Selectivity in distraction by irrelevant featural singletons: Evidence for two forms of attentional capture. *Journal of Experimental Psychology: Human Perception and Performance*, 24, 847-858.
- Folk, C. L., & Remington, R. W. (2006). Top-down modulation of preattentive processing: Testing the recovery account of contingent capture. *Visual Cognition*, 14:4-8, 445-465.
- Folk, C. L., & Remington, R. W. (2010). A critical evaluation of the disengagement hypothesis. *Acta Psychologica*, 135(2), 103-105.
- Folk, C. L., Remington, R. W., & Johnston, J. C. (1992). Involuntary covert orienting is contingent on attentional control settings. *Journal of Experimental Psychology: Human Perception and Performance*, 18(4), 1030-1044.
- Folk, C. L., Remington, R. W., & Wright, J. H. (1994). The structure of attentional control: Contingent attentional capture by apparent motion, abrupt onset, and color. *Journal of Experimental Psychology: Human Perception and Performance*, 20(2), 317-329.

- Friedman, D., Cycowicz, Y. M., & Gaeta, H. (2001). The novelty P3: An event-related brain potential (ERP) sign of the brain's evaluation of novelty. *Neuroscience & Biobehavioral Reviews*, 25(4), 355-373.
- Friedman, D., & Simpson, G. V. (1994). ERP amplitude and scalp distribution to target and novel events: Effects of temporal order in young, middle-aged and older adults. *Cognitive Brain Research*, 2(1), 49-63.
- Fukuda, K., & Vogel, E. K. (2009). Human variation in overriding attentional capture. *Journal of Neuroscience*, 29(27), 8726-8733.
- Fukuda, K., & Vogel, E. K., (2011). Individual differences in recovery time from attentional capture. *Psychological Science*, 22(3), 361-368.
- Garrido, M. I., Kilner, J. M., Stephen, K. E., & Friston, K. J. (2009). The mismatch negativity: A review of underlying mechanisms. *Clinical Neurophysiology*, 120(3), 453-463.
- Gaspar, J. M., Christie, G. J., Prime, D. J., Jolicœur, P., & McDonald, J. J. (2016). Inability to suppress salient distractors predicts low visual working memory capacity. *Proceedings of the National Academy of Sciences*, 113(13), 3693-3698.
- Gaspar, J. M., & McDonald, J. J. (2014). Suppression of salient objects prevents distraction in visual search. *Journal of Neuroscience*, 34(16), 5658-5666.
- Gaspelin, N., Leonard, C. J., & Luck, S. J. (2015). Direct evidence for active suppression of salient-but-irrelevant sensory inputs. *Psychological Science*, 26(11), 1740-1750.
- Gaspelin, N., Leonard, C. J., & Luck, S. J. (2017). Suppression of overt attentional capture by salient-but-irrelevant color singletons. *Attention, Perception, & Psychophysics*, 79(1), 45-62.
- Gaspelin, N., & Luck, S. J. (2018a). Combined electrophysiological and behavioral evidence for the suppression of salient distractors. *Journal of Cognitive Neuroscience*, 30(9), 1265-1280.
- Gaspelin, N., & Luck, S. J. (2018b). Distinguishing among potential mechanisms of singleton suppression. *Journal of Experimental Psychology: Human Perception and Performance*, 44(4), 626-644.
- Gaspelin, N., & Luck, S. J. (2018c). The role of inhibition in avoiding distraction by salient stimuli. *Trends in Cognitive Sciences*, 22(1), 79-92.
- Giard, M. H., Perrin, F., Pernier, J., & Bouchet, P. (1990). Brain generators implicated in the processing of auditory stimulus deviance: A topographic event-related potential study. *Psychophysiology*, 27(6), 627-640.

- Goldstein, A., Spencer, K. M., & Donchin, E. (2002). The influence of stimulus deviance and novelty on the P300 and novelty P3. *Psychophysiology*, 39(6), 781-790.
- Green, J. J., Conder, J. A., McDonald, J. J. (2008). Lateralized frontal activity elicited by attention-directing visual and auditory cues. *Psychophysiology*, 45, 579-587.
- Hasher, L., & Zacks, R. T. (1979). Automatic and effortful processes in memory. *Journal of Experimental Psychology: General*, 108, 356-388.
- Hickey, C., Di Lollo, V., & McDonald, J. J. (2009). Electrophysiological indices of target and distractor processing in visual search. *Journal of Cognitive Neuroscience*, 21(4), 760-775.
- Hickey, C., McDonald, J. J., & Theeuwes, J. (2006). Electrophysiological evidence of the capture of visual attention. *Journal of Cognitive Neuroscience*, 18(4), 604-613.
- Hopf, J. M., Boelmans, K., Schoenfeld, M. A., Luck, S. J., & Heinze, H. J. (2004). Attention to features precedes attention to locations in visual search: Evidence from electromagnetic brain responses in humans. *Journal of Neuroscience*, 24(8), 1822-1832.
- Ipata, A. E., Gee, A. L., Gottlieb, J., Bisley, J. W., & Goldberg, M. E. (2006). LIP responses to a popout stimulus are reduced if it is overtly ignored. *Nature Neuroscience*, 9(8), 1071-1076.
- Itti, L., & Koch, C. (2000). A saliency-based search mechanism for overt and covert shifts of visual attention. *Vision Research*, 40(10-12), 1489-1506.
- Itti, L., & Koch, C. (2001). Computational modelling of visual attention. *Nature Reviews Neuroscience*, 2, 194-203.
- Jääskeläinen, I. P., Ahveninen, J., Bonmassar, G., Dale, A. M., Ilmoniemi, R. J., Levänen, S., ... Belliveau, J. W. (2004). Human posterior auditory cortex gates novel sounds to consciousness. *Proceedings of the National Academy of Sciences*, 101(17), 6809-6814.
- James, W. (1890). *The principles of psychology*. New York, NY: Henry Holt and Co.
- Jannati, A., Gaspar, J. M., McDonald, J. J. (2013). Tracking target and distractor processing in fixed-feature visual search: Evidence from human electrophysiology. *Journal of Experimental Psychology: Human Perception and Performance*, 39(6), 1713-1730.
- Jeon, Y. W., & Polich, J. (2001). P3a from a passive visual stimulus task. *Clinical Neurophysiology*, 112(12), 2202-2208.
- Joseph, J. S., Chun, M. M., & Nakayama, K. (1997). Attentional requirements in a 'preattentive' feature search task. *Nature*, 387, 805-807.

- Julesz, B. (1984). A brief outline of the texton theory of human vision. *Trends in Neurosciences*, 7(2), 41-45.
- Julesz, B., & Bergen, J. R. (1983). Textons, the fundamental elements in preattentive vision and perception of textures. *The Bell System Technical Journal*, 62(6), 1619-1645.
- Julesz, B. (1986). Texton gradients: The texton theory revisited. *Biological Cybernetics*, 54, 245-251.
- Kahneman, D., & Chajczyk (1983). Tests of the automaticity of reading: Dilution of Stroop effects by color-irrelevant stimuli. *Journal of Experimental Psychology: Human Perception and Performance*, 9(4), 497-509.
- Kahneman, D., Treisman, A., & Burkell, J. (1983). The cost of visual filtering. *Journal of Experimental Psychology: Human Perception and Performance*, 9(4), 510-522.
- Kahneman, D., Treisman, A., & Gibbs, B. J. (1992). The reviewing of object files: Object-specific integration of information. *Cognitive Psychology*, 24, 175-219.
- Kane, N. M., Curry, S. H., Butler, S. R., & Cummins, B. H. (1993). Electrophysiological indicator of awakening from coma. *The Lancet*, 341(8846), 668.
- Katayama, J. I., & Polich, J. (1998). Stimulus context determines P3a and P3b. *Psychophysiology*, 35(1), 23-33.
- Kiss, M., Grubert, A., & Eimer, M. (2013). Top-down task sets for combined features: behavioral and electrophysiological evidence for two stages in attentional object selection. *Attention, Perception, & Psychophysics*, 75, 216-228.
- Knight, R. T. (1984). Decreased response to novel stimuli after prefrontal lesions in man. *Electroencephalography and Clinical Neurophysiology/Evoked Potentials Section*, 59(1), 9-20.
- Kok, A. (1986). Effects of degradation of visual stimuli on components of the event-related potential (ERP) in go/nogo reaction tasks. *Biological Psychology*, 23(1), 21-38.
- Kwak, H. W., Dagenbach, D., & Egeth, H. (1991). Further evidence for a time-independent shift of the focus of attention. *Perception & Psychophysics*, 49(5), 473-480.
- Lange, J. J., Wigers, A. A., Mulder, L. J. M., & Mulder, G. (1998). Color selection and location selection in ERPs: Differences, similarities and neural specificity. *Biological Psychology*, 48, 153-182.
- Leber, A. B., & Egeth, H. E. (2006). It's under control: Top-down search strategies can override attentional capture. *Psychonomic Bulletin & Review*, 13(1), 132-138.

- Logan, G. D. (1978). Attention in character-classification tasks: Evidence for the automaticity of component stages. *Journal of Experimental Psychology: General*, 107, 32-63.
- Luck, S. J. (2012). Electrophysiological correlates of the focusing of attention within complex visual scenes: N2pc and related ERP components. In S. J. Luck, & E. S. Kappenman (Eds.), *The Oxford handbook of event-related potential components* (pp. 329-360). Oxford, UK: Oxford University Press.
- Luck, S. J., & Ford, M. A. (1998). On the role of selective attention in visual perception. *Proceedings of the National Academy of Sciences*, 95, 825-830.
- Luck, S. J., Girelli, M., McDermott, M. T., & Ford, M. A. (1997). Bridging the gap between monkey neurophysiology and human perception: An ambiguity resolution theory of visual selective attention. *Cognitive Psychology*, 33, 64-87.
- Luck, S. J., & Hillyard, S. A. (1990). Electrophysiological evidence for parallel and serial processing during visual search. *Perception & Psychophysics*, 48(6), 603-617.
- Luck, S. J., & Hillyard, S. A. (1994a). Electrophysiological correlates of feature analysis during visual search. *Psychophysiology*, 31, 291-308.
- Luck, S. J., & Hillyard, S. A. (1994b). Spatial filtering during visual search: Evidence from human electrophysiology. *Journal of Experimental Psychology: Human Perception and Performance*, 20(5), 1000-1014.
- Luck, S. J., & Gold, J. M. (2008). The construct of attention in schizophrenia. *Biological Psychiatry*, 61(1), 34-39.
- Luck, S. J., & Vogel, E. K. (1997). The capacity of visual working memory for features and conjunctions. *Nature*, 390, 279-281.
- Maljkovic, V., & Nakayama, K. (1994). Priming of pop-out: I. Role of features. *Memory & Cognition*, 22(6), 657-672.
- Marini, F., Chelazzi, L., & Maravita, A. (2013). The costly filtering of potential distraction: Evidence for a supramodal mechanism. *Journal of Experimental Psychology: General*, 142(3), 906-922.
- May, P., Tiitinen, H., Ilmoniemi, R. J., Nyman, G., Taylor, J. G., & Näätänen, R. (1999). Frequency change detection in human auditory cortex. *Journal of Computational Neuroscience*, 6, 99-120.
- Mazza, V., & Caramazza, A. (2011). Temporal brain dynamics of multiple object processing: The flexibility of individuation. *PLoS one*, 6(2), e17453.
- Mazza, V., Pagano, S., & Caramazza, A. (2013). Multiple object individuation and exact enumeration. *Journal of Cognitive Neuroscience*, 25(5), 697-705.

- Mazza, V., Turatto, M., & Caramazza, A. (2009a). An electrophysiological assessment of distractor suppression in visual search tasks. *Psychophysiology*, *46*, 771-775.
- Mazza, V., Turatto, M., & Caramazza, A. (2009b). Attention selection, distractor suppression and N2pc. *Cortex*, *45*, 879-890.
- McDonald, J. J., Green, J. J., Jannati, A., & Di Lollo, V. (2013). On the electrophysiological evidence for the capture of visual attention. *Journal of Experimental Psychology: Human Perception and Performance*, *39*(3), 849-860.
- Miller, J., Patterson, T., & Ulrich, R. (1998). Jackknife-based method for measuring LRP onset latency differences. *Psychophysiology*, *35*(1), 99-115.
- Moher, J., Ashinoff, B. K., & Egeth, H. E. (2013). Detection is unaffected by the deployment of focal attention. *Frontiers in Psychology*, *4*, 284.
- Motter, B. C. (1994). Neural correlates of attentive selection for color or luminance in extrastriate visual area V4. *Journal of Neuroscience*, *14*(4), 2178-2189.
- Müller, B. W., Achenbach, C., Oades, R. D., Bender S., & Schall, U. (2002). Modulation of mismatch negativity by stimulus deviance and modality of attention. *NeuroReport*, *13*(10), 1317-1320.
- Näätänen, R. (1982). Processing negativity: An evoked-potential reflection of selective attention. *Psychological Bulletin*, *92*(3), 605-640.
- Näätänen, R., & Alho, K. (1995). Mismatch negativity-a unique measure of sensory processing in audition. *International Journal of Neuroscience*, *80*(1-4), 317-337.
- Neisser, U. (1967). *Cognitive psychology*. East Norwalk, CT: Appleton-Century-Crofts.
- Opitz, B., Rinne, T., Mecklinger, A., von Cramon, D. Y., & Schröger, E. (2002). Differential contribution of frontal and temporal cortices to auditory change detection: fMRI and ERP results. *Neuroimage*, *15*(1), 167-174.
- Pagano, S., & Mazza, V. (2012). Individuation of multiple targets during visual enumeration: New insights from electrophysiology. *Neuropsychologia*, *50*, 754-761.
- Pashler, H. (1988a). Cross-dimensional interaction and texture segregation. *Perception & Psychophysics*, *41*, 191-201.
- Pashler, H. (1988b). Familiarity and visual change detection. *Perception and Psychophysics*, *44*, 369-378.
- Perrin, F., Pernier, J., Bertrand, O., & Echallier, J. F. (1989). Spherical splines for scalp potential and current density mapping. *Electroencephalography and Clinical Neurophysiology*, *72*(2), 184-187.

- Phipson, B., & Smyth, G. K. (2010). Permutation P-values should never be zero: calculating exact P-values when permutations are randomly drawn. *Statistical Applications in Genetics and Molecular Biology*, 9(1).
- Piazza, M., Fumarola, A., Chinello, A., & Melcher, D. (2011). Subitizing reflects visuo-spatial object individuation capacity. *Cognition*, 121, 147-153.
- Posner, M. I. (1980). Orienting of attention. *Quarterly Journal of Experimental Psychology*, 32(1), 3-25.
- Potts, G. F. (2004). An ERP index of task relevance evaluation of visual stimuli. *Brain and Cognition*, 56, 5-13.
- Potts, G. F., Liotti, M., Tucker, D. M., & Posner, M. I. (1996). Frontal and inferior temporal cortical activity in visual target detection: Evidence from high spatially sampled event-related potentials. *Brain Topography*, 9, 3-14.
- Potts, G. F., & Tucker, D. M. (2001). Frontal evaluation and posterior representation in target detection. *Cognitive Brain Research*, 11, 147-156.
- Proulx, M. J., & Serences, J. T. (2006). Searching for an oddball: Neural correlates of singleton detection mode in parietal cortex. *Journal of Neuroscience*, 26(49), 12631-12632.
- Pylyshyn, Z. (1989). The role of location indexes in spatial perception: A sketch of the FINST spatial-index model. *Cognition*, 32(1), 65-97.
- Raymond, J. E., Shapiro, K. L., & Arnell, K. M. (1992). Temporary suppression of visual processing in an RSVP task: An attentional blink? *Journal of Experimental Psychology: Human Perception and Performance*, 18(3), 849-860.
- Regan, J. E. (1981). Automaticity and learning: Effects of familiarity on naming letters. *Journal of Experimental Psychology: Human Perception and Performance*, 7, 180-195.
- Roberts, L. E., Rau, H., Lutzenberger, W., & Birbaumer, N. (1994). Mapping P300 waves onto inhibition: Go/no-go discrimination. *Electroencephalography and Clinical Neurophysiology*, 92, 44-55.
- Robison, M. K., Miller, A. L., & Unsworth, N. (2018). Individual differences in working memory capacity and filtering. *Journal of Experimental Psychology: Human Perception and Performance*, 44(7), 1038-1053.
- Robison, M. K., & Unsworth, N. (2017). Working memory capacity and mind-wandering during low-demand cognitive tasks. *Consciousness and Cognition*, 52, 47-54.

- Saarinen, J., Paavilainen, P., Schröger, E., Tervaniemi, M., & Näätänen, R. (1992). Representation of abstract attributes of auditory stimuli in the human brain. *NeuroReport*, 3(12), 1149-1151.
- Saalin, J., Kaartinen, J., & Lyytinen, H. (1994). Is the appearance of mismatch negativity during stage 2 sleep related to the elicitation of K-complex? *Electroencephalography and Clinical Neurophysiology*, 91(2), 140-148.
- Sams, M., Paavilainen, P., Alho, K., Näätänen, R. (1985). Auditory frequency discrimination and event-related potentials. *Electroencephalography and Clinical Neurophysiology/Evoked Potentials Section*, 62(6), 437-448.
- Sawaki, R., Geng, J. J., & Luck, S. J. (2012). A common neural mechanism for preventing and terminating the allocation of attention. *Journal of Neuroscience*, 32(31), 10725-10736.
- Sawaki, R., & Luck, S. J. (2010). Capture versus suppression of attention by salient singletons: Electrophysiological evidence for an automatic attend-to-me signal. *Attention, Perception, & Psychophysics*, 72(6), 1455-1470.
- Serences, J. T., & Yantis, S. (2006). Spatially selective representations of voluntary and stimulus-driven attentional priority in human occipital, parietal, and frontal cortex. *Cerebral Cortex*, 17(2), 284-293.
- Schröger, E. (1993). Event-related potentials to auditory stimuli following transient shifts of spatial attention in a go/nogo task. *Biological Psychology*, 36, 183-207.
- Schubö, A., & Müller, H. J. (2009). Selecting and ignoring salient objects within and across dimensions in visual search. *Brain Research*, 1283, 84-101.
- Schubö, A., Schröger, E., & Meinecke, C. (2004). Texture segmentation and visual search for pop-out targets: An ERP study. *Cognitive Brain Research*, 21(3), 317-334.
- Simons, R. F., Graham, F. K., Miles, M. A., & Chen, X. (2001). On the relationship of P3a and the novelty-P3. *Biological Psychology*, 56(3), 207-218.
- Simson, R., Vaughan Jr, J. G., & Ritter, W. (1977). The scalp topography of potentials in auditory and visual discrimination tasks. *Electroencephalography and Clinical Neurophysiology*, 42, 528-535.
- Shiffrin, R. M., & Schneider, W. (1977). Controlled and automatic human information processing: II. Perceptual learning, automatic attending, and a general theory. *Psychological Review*, 84(2), 127-190.
- Shipstead, Z., Harrison, T. L., & Engle, R. W. (2016). Working memory capacity and fluid intelligence: Maintenance and disengagement. *Perspective on Psychological Science*, 11(6), 771-799.

- Smith, J. L., Smith, E. A., Provost, A. L., & Heathcote, A. (2010). Sequence effects support the conflict theory of N2 and P3 in the go/nogo task. *International Journal of Psychophysiology*, 75(3), 217-226.
- Sperling, G. (1960). The information available in brief visual presentations. *Psychological Monographs: General and Applied*, 74(11), 1-29.
- Störmer, V. S., McDonald, J. J., & Hillyard, S. A. (2019). Involuntary orienting of attention to sight or sound relies on similar neural biasing mechanisms in early visual processing. *Neuropsychologia*, 132.
- Stroop, J. R. (1935). Studies of interference in serial verbal reactions. *Journal of Experimental Psychology*, 18(6), 643-662.
- Tan, M. & Wyble, B. (2015). Understanding how visual attention locks on to a location: Toward a computational model of the N2pc component. *Psychophysiology*, 52, 199-213.
- Tervaniemi, M., Maury, S., & Näätänen, R. (1994). Neural representations of abstract stimulus features in the human brain as reflected by the mismatch negativity. *Neuroreport*, 5(7), 844-846.
- Theeuwes, J. (1991a). Cross-dimensional perceptual selectivity. *Perception & Psychophysics*, 50(2), 184-193.
- Theeuwes, J. (1991b). Exogenous and endogenous control of attention: The effect of visual onsets and offsets. *Perception & Psychophysics*, 49(1), 83-90.
- Theeuwes, J. (1992). Perceptual selectivity for color and form. *Perception & Psychophysics*, 51(6), 599-606.
- Theeuwes, J. (2004). Top-down search strategies cannot override attentional capture. *Psychonomic Bulletin & Review*, 11(1), 65-70.
- Theeuwes, J. (2010). Top-down and bottom-up control of visual selection. *Acta Psychologica*, 135, 77-99.
- Theeuwes, J., Atchley, P., & Kramer, F. (2000). On the time course of top-down and bottom-up control of visual attention. *Attention and Performance*, 18, 104-124.
- Treisman, A. M. (1988). Features and objects: The fourteenth Bartlett memorial lecture. *The Quarterly Journal of Experimental Psychology*, 40A(2), 201-236.
- Treisman, A. M., & Gelade, G. (1980). A feature-integration theory of attention. *Cognitive Psychology*, 12(1), 97-136.
- Treisman, A. M., & Sato, S. (1990). Conjunction search revisited. *Journal of Experimental Psychology: Human Perception and Performance*, 16(3), 459-478.

- Unsworth, N., & Robison, M. K. (2016). The influence of lapses of attention on working memory capacity. *Memory & Cognition*, 44(2), 188-196.
- Verleger, R., vel Grajewska, B. Ź., & Jaśkowski, P. (2012). Time-course of hemispheric preference for processing contralateral relevant shapes: P1pc, N1pc, N2pc, N3pc. *Advances in Cognitive Psychology*, 8(1), 19-28.
- Vogel, E. K., & Luck, S. J. (2000). The visual N1 component as an index of a discrimination process. *Psychophysiology*, 37, 190-203.
- Vogel, E. K., & Machizawa, M. G. (2004). Neural activity predicts individual differences in visual working memory capacity. *Nature*, 428, 748-751.
- Vogel, E. K., McCollough, A. W., & Machizawa, M. G. (2005). Neural measures reveal individual differences in controlling access to working memory. *Nature*, 438, 500-503.
- Wang, B., & Theeuwes, Y. (2020). Saliency determines attentional orienting in visual selection. *Journal of Experimental Psychology: Human Perception and Performance*, 46(10), 1051-1057.
- Wascher, E., & Beste, C. (2010a). Spatial representations as an emergent feature of perceptual processing. *Journal of Psychophysiology*, 24(3), 161-172.
- Wascher, E., & Beste, C. (2010b). Tuning perceptual competition. *Journal of Neurophysiology*, 103(2), 1057-1065.
- Wijers, A. A., Lange, J. J., Mulder, G., & Mulder, L. J. M. (1997). An ERP study of visual spatial attention and letter target detection for isoluminant and nonisoluminant stimuli. *Psychophysiology*, 34, 553-565.
- Wolfe, J. M. (1994). Guided search 2.0 a revised model of visual search. *Psychonomic Bulletin & Review*, 1(2), 202-238.
- Wolfe, J. M. (2007). *Guided search 4.0: Current progress with a model of visual search*. In W. D. Gray (Ed.), *Series on cognitive models and architectures. Integrated models of cognitive systems* (p. 99-119). Oxford University Press.
- Wolfe, J. M., Friedman-Hill, S. R., Stewart, M. I., & O'Connell, K. M. (1992). The role of categorization in visual search for orientation. *Journal of Experimental Psychology: Human Perception and Performance*, 18(1), 34-49.
- Woodman, G. F., & Luck, S. J. (1999). Electrophysiological measurement of rapid shifts of attention during visual search. *Nature*, 400, 867-869.
- Woodman, G. F., & Luck, S. J. (2003). Serial deployment of attention during visual search. *Journal of Experimental Psychology: Human Perception and Performance*, 29(1), 121-138.

- Woods, D. L., Knight, R. T., & Scabini, D. (1993). Anatomical substrates of auditory selective attention: Behavioral and electrophysiological effects of posterior association cortex lesions. *Cognitive Brain Research*, 1(4), 227-240.
- Wykowska, A., & Schubö, A. (2011). Irrelevant singletons in visual search do not capture attention but can produce nonspatial filtering costs. *Journal of Cognitive Neuroscience*, 23(3), 645-660.
- Yantis, S., & Egeth, H. E. (1999). On the distinction between visual salience and stimulus-driven attentional capture. *Journal of Experimental Psychology: Human Perception and Performance*, 25(3), 661-676.
- Yantis, S., & Jonides, J. (1990). Abrupt visual onsets and selective attention: Voluntary versus automatic allocation. *Journal of Experimental Psychology: Human Perception and Performance*, 16(1), 121-134.

Appendix

Supplementary Experiment 1

Method

Participants

Participant recruitment and screening procedures were identical to those in Experiment 2 (Chapter 3). Data from 12 (9 females; all right-handed; mean age: 21.6 years) of 14 participants were used in the final analysis. Data from the remaining two participants were discarded due to excessive ocular artifacts.

Apparatus, Stimuli, and Procedure

Apparatus, stimuli, and procedure used were identical to those of the go/no-go singleton-detection task in Experiment 2 (Chapter 3) except (a) half the stimulus arrays contained 8 lines instead of 16 and (b) the entire experiment comprised of 18 blocks of 40 trials for a total of 720 trials.

Behavior

Analysis of median RTs was similar to those in Experiment 2 (Chapter 3), but with set size as an additional factor. A difference in speed of target-present responses between 8- and 16-item displays was assessed using a two-tailed, paired-sample *t* test.

Electrophysiology

No EEG signals were recorded, but vertical and horizontal EOG activity were recorded to detect ocular artifacts (eye movements and blinks). Vertical eye movements and eye blinks were tracked using a pair of electrodes placed above and below the left eye. EOG recording methods were identical to those in Experiment 2 (Chapter 3).

Result

Responses to targets on 8-item displays were no faster than to targets on 16-item displays (643 ms vs. 636 ms, respectively), $t(11) = 1.26$, $p = .234$.

Supplementary Experiment 2

Method

Participants

Participant recruitment and screening procedures were identical to those in Experiment 2 (Chapter 3). Data from 22 (13 females; 19 right-handed; mean age: 19 years) of 24 participants were used in the final analysis. Data from the remaining two participants were discarded due to excessive ocular artifacts.

Apparatus, Stimuli, and Procedure

Apparatus, stimuli, and procedure used were identical to those of the go/no-go singleton-detection task in Experiment 2 (Chapter 3) except (a) all participants responded to both cyan and yellow stimulus displays (i.e., all-go condition) and (b) the entire experiment comprised of 20 blocks of 40 trials for a total of 800 trials.

Electrophysiology

The recording and preprocessing of electrophysiological signals were identical to those in Experiment 2 (Chapter 3). Onset latency of the N2pc was measured as the first time point at which the N2pc reached 25% of its peak amplitude within a 150-ms window 150 ms after target onset, using the standard jackknife approach (Miller et al., 1998). A difference in onset latency between N2pc elicited in this experiment and in Experiment 2 (Chapter 3) was assessed using a two-tailed, two-sample t test.

Result

Onset latency of the N2pc in this experiment was shorter than that of the N2pc in Experiment 2 (Chapter 3; 165 ms vs. 262, respectively), $t(42) = 2.04$, $p = .048$, $d = 0.61$.