

What the Flip? What the P-N Flip Can Tell Us about Proactive Suppression

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Abstract

■ It has been debated whether salient distractors in visual search can be proactively suppressed to completely prevent attentional capture, as the occurrence of proactive suppression implies that the initial shift of attention is not entirely driven by physical salience. While the presence of a Pd component in the EEG (associated with suppression) without a preceding N2pc component (associated with selection) has been used as evidence for proactive suppression, the link between these ERPs and the underlying mechanisms is not always clear. This is exemplified in two recent articles that observed the same waveform pattern, where an early Pd-like component flipped to a N2pc-like component, but provided vastly different interpretations (Drisdelle, B. L., & Eimer, E. Pd components and distractor inhibition in visual search: New evidence for the signal suppression

hypothesis. *Psychophysiology*, 58, e13898, 2021; Kerzel, D., & Burra, N. Capture by context elements, not attentional suppression of distractors, explains the Pd with small search displays. *Journal of Cognitive Neuroscience*, 32, 1170–1183, 2020). Using RAGNAROC (Wyble et al., Understanding visual attention with RAGNAROC: A Reflexive Attention Gradient through Neural AttRactOr Competition. *Psychological Review*, 127, 1163–1198, 2020), a computational model of reflexive attention, we successfully simulated this ERP pattern with minimal changes to its existing architecture, providing a parsimonious and mechanistic explanation for this flip in the EEG that is unique from both of the previous interpretations. Our account supports the occurrence of proactive suppression and demonstrates the benefits of incorporating computational modeling into theory building. ■

INTRODUCTION

A major debate in the study of reflexive visual attention is whether or under what conditions attention would be captured by distractor items and such capture can be minimized or perhaps avoided entirely through suppression. Most impressively, it has been demonstrated that some cases of distractor suppression can occur so early that distractor-related attentional capture is completely prevented (see Luck, Gaspelin, Folk, Remington, & Theeuwes, 2021; Geng, 2014). This type of preventive suppression may occur as *proactive suppression*, in which attributes (feature or location) consistently associated with the distractor are inhibited *before the onset of the search display* (as suggested by the adjusted version of the signal suppression theory [SST]; Gaspelin & Luck, 2019).¹

The stimulus-driven selection account (Theeuwes, 1992, 2010), among others, suggests that the initial shift of attention after display or fixation onset is solely driven by bottom-up saliency signals in an automatic manner, such that attention is first attracted to the highest-salience location. Under this theory, attentional capture cannot be prevented, as a salient distractor can be suppressed reactively only after it has captured attention. On the other hand, some theories have argued for an early role of

top-down control that would allow for the initial attentional shift to deviate from the saliency signals and thus allow for the occurrence of proactive suppression. For example, the contingent-capture theory (Folk, Remington, & Johnston, 1992) suggests that salient distractors capture attention only when they are contingent with the task set. Furthermore, the SST (Gaspelin & Luck, 2019; Sawaki & Luck, 2010) directly suggests that the attraction signals (“attend-to-me signals”) from the salient distractors can be prevented by suppression mechanisms.

In their representative works on SST, Gaspelin, Leonard, and Luck (2015, 2017) found evidence for proactive featural suppression when the target and the salient distractor each has a consistent feature (we call it “fixed feature search” in this article). For example, in Experiments 2, 3, and 4 in Gaspelin et al. (2015), participants searched for a predefined shape target among heterogeneous shapes. In half of the trials, one of the distractors had a color different from the rest of the items. This distractor color was held constant across the experiment, and thus, the participants were able to learn the color association. No attentional capture effect was found, in that the presence of a color singleton did not slow RTs to the target. Furthermore, to measure the spatial distribution of attention, letter probes appeared briefly on the search items in about 30% of the trials, and participants were to report as many letters as they could. Critically, they observed the *probe suppression effect*, that is, the letter

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probe at the singleton location was reported less accurately than probes at nonsingleton distractor locations, such that the singleton's location was the least attended to among all items (see also Chang & Egeth, 2019, 2021). Importantly, the probe suppression effect was observed even for very briefly presented probes (100 msec) with zero display-to-probe delay (e.g., Experiment 4 in Gaspelin et al., 2015), making a rapid disengagement account (Theeuwes, 2010; Theeuwes, Atchley, & Kramer, 2000) improbable. This effect was found even with a highly salient distractor (a singleton color in a display of 20 items) with its standout saliency confirmed by an independently computed estimation (Stilwell, Egeth, & Gaspelin, 2022; Stilwell & Gaspelin, 2021).

In addition, with EEG data, the relative polarity between parietal-occipital scalp sites contralateral and ipsilateral to a visual item of interest (typical sites are PO7 and PO8) has been found to correlate with attention. Typically observed at around 200 msec from stimulus onset, a contralateral negativity, or the N2pc, correlates with attentional selection (Luck & Hillyard, 1994), whereas a contralateral positivity, or the Pd, correlates with attentional suppression (Hickey, Di Lollo, & McDonald, 2009). These two components have been adopted as tools to measure these attentional mechanisms with a particular emphasis on their temporal sequencing. For example, a Pd component toward the singleton distractor has been observed without a preceding N2pc, suggesting that the suppression process can occur proactively (Stilwell et al., 2022; Gaspelin & Luck, 2018a; Gaspar & McDonald, 2014; Jannati, Gaspar, & McDonald, 2013; Sawaki & Luck, 2010).

Although the N2pc and the Pd have played pivotal roles in the understanding of attentional suppression, we must keep in mind that there is no way to distinguish between attention of the item(s) on one side and suppression of the item(s) on the other side solely based on the EEG signals. This issue is exemplified in a recently observed ERP sequence (Drisdelle & Eimer, 2021; Kerzel & Burra, 2020). In detail, Kerzel and Burra (2020) suggested that at least some of the evidence for proactive featural suppression, especially those coming from small displays (but see Stilwell et al., 2022; Stilwell & Gaspelin, 2021), could be explained by a form of serial search when the items were heterogeneous (but see Gaspar & McDonald, 2014; Jannati et al., 2013). To investigate, Kerzel and Burra (2020) replicated the general experimental design used in Gaspelin et al. (2015) and analyzed EEG signals from lateral parietal-occipital sites. They observed an early Pd-like contralateral positivity (~185–235 msec, relative to the singleton distractor location), replicating Gaspelin and Luck (2018a). However, Kerzel and Burra (2020) also observed an N2pc-like contralateral negativity trailing the initial positivity (~265–315 msec), forming what we term here the P-N flip.² As it would not make sense for the attentional system to re-attend to a distractor that had already been suppressed, Kerzel and Burra (2020) proposed that the ERPs were in fact two successive N2pc components—the

first one reflecting attention toward the lateral nonsingleton distractor; the second one, attention toward the salient distractor. This might have occurred because of the use of a specific serial scanning strategy afforded by those specific task settings (small set size, heterogeneous displays), with three additional assumptions: (1) Participants tend to scan lateral items before vertical items; (2) when the salient distractor is one of the lateral items, they tend to scan the opposite-side distractor first because the consistent salient distractor color forms a “template for rejection” (see Arita, Carlisle, & Woodman, 2012)—leading to an initial attentional enhancement of the lateral nonsingleton distractor; and (3) they are unable to skip scanning the salient distractor after that, despite this template for rejection—leading to the subsequent attentional enhancement of the salient distractor. Note that Kerzel and Burra (2020) also emphasized that these interpretations were primarily speculative. However, if their interpretation is correct, it would mean that the presence of a consistent distractor feature may not prevent capture by singletons so much as delay it under some circumstances.

According to this serial search hypothesis, the P-N flip should disappear when there are no incentives for the participants to attend to the lateral positions. To test this idea, Drisdelle and Eimer (2021) included a condition in which the target never appeared laterally (the “focused midline” condition). Although participants were able to utilize this spatial regularity to their advantage, as they were substantially faster to respond to the target compared with the “unfocused” condition (where the target could appear at any of the four locations), the P-N flip was reliably observed in both conditions—meaning that a lateral-first serial search strategy cannot completely explain the P-N flip. Drisdelle and Eimer (2021) in turn proposed that the ERPs were two successive Pd components—the first one reflecting suppression of the singleton distractor, and the second one reflecting suppression of the lateral nonsingleton distractor. They further suggested that the suppression of the singleton distractor occurred earlier because of its superior salience. This is in line with the proposal of *active suppression* based on relative saliency signals (Sawaki & Luck, 2010; see also Footnote 1). However, this proposal is subject to challenges from studies that fail to observe successful preventive suppression of singleton distractors without a predictable feature value (e.g., Gaspelin & Luck, 2018b). This point will be further discussed in a later part of this article.

Motivated by this puzzle, we tried to simulate the P-N flip with RAGNAROC (Wyble et al., 2020). By modeling the dynamics of interacting neural populations, RAGNAROC provides a mechanistic description of the selection and suppression processes in covert reflexive attention, as well as how these underlying sources are linked to the associated ERPs (i.e., N2pc and Pd). Note that RAGNAROC was not designed with the explicit purpose to simulate the flip. It would therefore provide a parsimonious account if the simulation can be achieved with little to no alterations to the model.

With the model, we implemented a proactive form of distractor suppression that would be effective when the feature values of a distractor were consistent across trials. This was done by reducing the connection weights of features that are consistently and specifically associated with singleton distractors. With this change, RAGNAROC successfully simulates the flip using its existing circuitry (Figure 1). This provides a perspective on the underlying cause of the P-N flip that is unique from Kerzel and Burra (2020) and Drisdelle and Eimer (2021). We further explored the effect of target presence, set size, and the inclusion of probe trials on the simulation results in a fixed feature search, referencing relevant empirical evidence (Stilwell et al., 2022; Drisdelle & Eimer, 2021; Gaspelin & Luck, 2018a; Barras & Kerzel, 2016; Gaspelin et al., 2015). Simulation parameters are listed in Table A1.

Overall, our account supports the possibility of the occurrence of proactive featural suppression and shows *how* this would lead to the pattern of waveforms that have been observed. It also acts as an example to demonstrate some of the advantages in incorporating computational modeling into theory building. In the next section, we will introduce the model's architecture and illustrate the way in which these simulations were implemented.

MODEL MECHANISMS UNDERLYING THE P-N FLIP

Whereas the explanations from Kerzel and Burra as well as Drisdelle and Eimer focus on an iteration of attentional processes between the lateralized nonsingleton distractor and the salient distractor, our work with RAGNAROC proposes an important alternative in which the consistent singleton distractor has essentially no effect on attention because the visual attention system has learned to reduce its top-down relevance weighting to nearly at baseline. As

a result, both the P and N components are instead caused by the nonsingleton distractor on the other side.

To explain this, we will first provide a summary of the model, although readers are suggested to refer to Wyble et al. (2020) for a thorough introduction. Figure 2 shows RAGNAROC's macro-architecture as sheets of simulate neurons that correspond to stages of visual processing. Visual information presented to RAGNAROC passes through three layers of retinotopically arranged neurons in this order: early vision (EV), late vision (LV), and attention map (AM). The model assumes that physical saliences of stimuli are computed in the EV and affect the strength of signals projected to the feature-specific maps in LV. The next step from LV to AM incorporates top-down relevance weightings corresponding to the current goals of the observer. For each feature dimension, relevance weightings are independently computed and applied to its own retinotopic map. In addition, although feature-based relevance weightings are applied globally, the resulting attentional enhancement and attenuation can be spatially specific to the locations where those features are detected. Taking into account the interaction of the physical saliences and relevance weightings, the AM computes where attention will be deployed and where it will be suppressed. Importantly, the dynamics of the AM activations are translated into EEG recorded at posterior-occipital sites, with higher AM activations resulting in more negative EEG signals on the contralateral side. The mechanisms of RAGNAROC are supported by its ability to simulate behavioral and electrophysiological data from an array of empirical benchmarks (see Wyble et al., 2020).

The important aspect of RAGNAROC as regards the P-N flip is the competitive inhibitory circuits that implement a reactive form of inhibition that is proportional to stimulus strength. As signals first reach the AM, a brief competition across the entire AM occurs to determine which regions are to be attended to. When the competition is resolved,

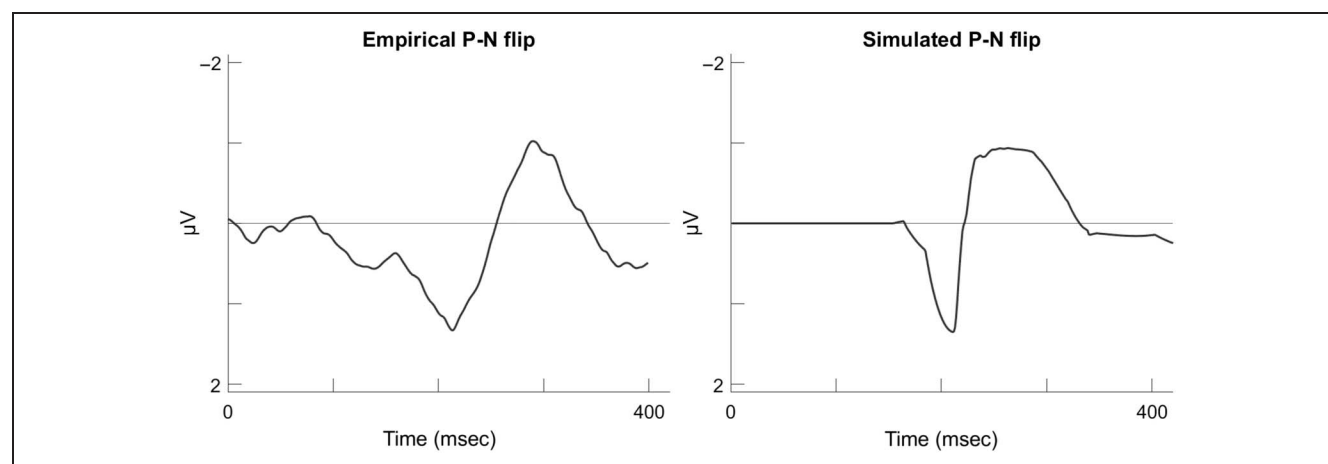


Figure 1. RAGNAROC's simulation of the P-N flip in fixed feature search. Both the empirical and simulated EEGs were generated from a target midline, singleton distractor lateral configuration with a set size of 4. Plotted are the difference waveforms between contralateral and ipsilateral EEG signals at occipital-parietal sites, pivoting on the singleton location. The empirical P-N flip in Kerzel and Burra's (2020) Experiment 2 (left) is simulated by RAGNAROC (right).

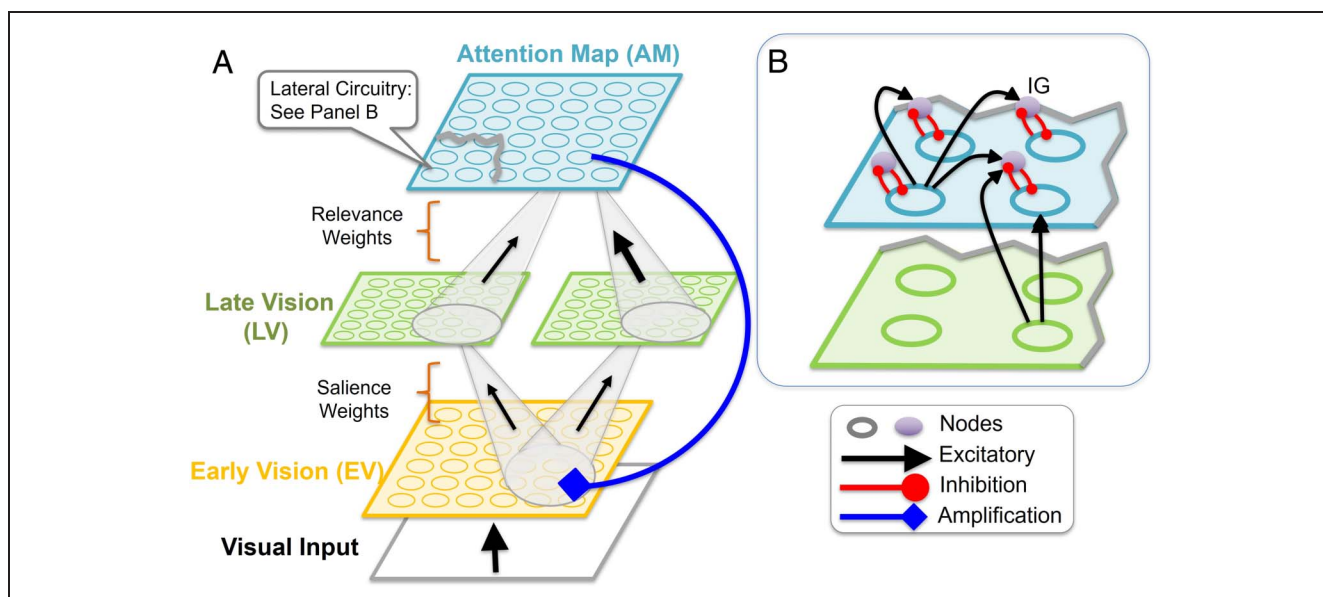


Figure 2. The macro-architecture of RAGNAROC adapted from Figure 4 in Wyble et al. (2020). Visual input passes through EV, LV, and finally the AM. The saliency signals are represented in connections from EV to LV. Then, top-down relevance weightings can vary to modulate signals from the feature-specific LV maps, indicated by the different thicknesses of the arrows from LV to AM. The down-weighting of the distractor-associated feature is the basis to implement proactive featural suppression. B shows how *reactive* suppression is implemented only for items with sufficient AM activation. Therefore, a proactively suppressed salient distractor receives little-to-no reactive suppression whereas the nonsingleton distractors that are not proactively suppressed receive stronger reactive suppression. These mechanisms combined allow RAGNAROC to successfully simulate the P-N flip.

the “losers” (i.e., areas with weaker activation) will be suppressed in proportion to the input they receive from the LV, that is, a more activated item will be more deeply inhibited if it loses the competition for attention. This mechanism is informed by behavioral tests showing that locations containing distractors are more inhibited than blank regions (Cepeda, Cave, Bichot, & Kim, 1998). In RAGNAROC, this same inhibitory circuit is also thought to be the source of selective inhibition of salient distractors without a consistent feature value (Burra & Kerzel, 2013; McDonald, Green, Jannati, & Di Lollo, 2013; Kiss, Grubert, Petersen, & Eimer, 2012). We also note here that this reactive inhibitory circuit is spatially graded: Locations closer to the winning stimulus will be more strongly suppressed. This point will be revisited when the effect of set size on the EEG is considered in a later section.

Now, consider a case of fixed feature search, where a color singleton distractor is always red and the target never appears in red. In RAGNAROC, proactive suppression of this consistent distractor feature can be implemented by reducing the feature-specific relevance weighting from the LV to the AM. In turn, the ability of a location containing that feature to recruit attention can be greatly reduced, even if it contains a highly salient item. Thus, the input to the AM driven by a consistent singleton distractor can be weaker than input driven by nonsingleton distractors that are not proactively suppressed. The mechanisms in the model dictates that a location with a weaker AM input will translate into a more positive EEG signal at the contralateral electrode, and thus, in a contralateral subtraction,

results in a positivity. This simulates the first component in the P-N flip.

The dynamics of stimuli activations from the EV to the AM in the case of proactive suppression is further illustrated in Figure 3. Importantly, this implementation of proactive suppression cannot suppress an item below baseline on the AM. Instead, the AM activation will be at approximately baseline. Note that it is unlikely to be exactly at baseline because the singleton item still possesses other visual features, such as shape, which may not have been proactively suppressed. Regardless, as the AM input at the singleton location is extremely weak, the AM dynamics will develop as if the distractor was absent. Thus, proactive featural suppression can be better described as a strong “ignoring” of the item through feature down-weighting. However, the salient distractor is “suppressed” in the sense that this feature value’s weight is selectively inhibited.

Given that the proactively inhibited singleton distractor produces an extremely small AM signal, how does it then appear to elicit a subsequent N component that can be interpreted as attention toward itself (Kerzel & Burra, 2020)? To this point, RAGNAROC provides a subtle and interesting alternative to understand the P-N flip using the characteristic of *proportional inhibition* in its reactive suppression mechanism (visualized in Figure 4). As the AM input at the singleton distractor location is weaker than that at the nonsingleton distractor location, reactive inhibition from the target is weaker for the singleton location. Thus, as reactive inhibition progresses, the nonsingleton

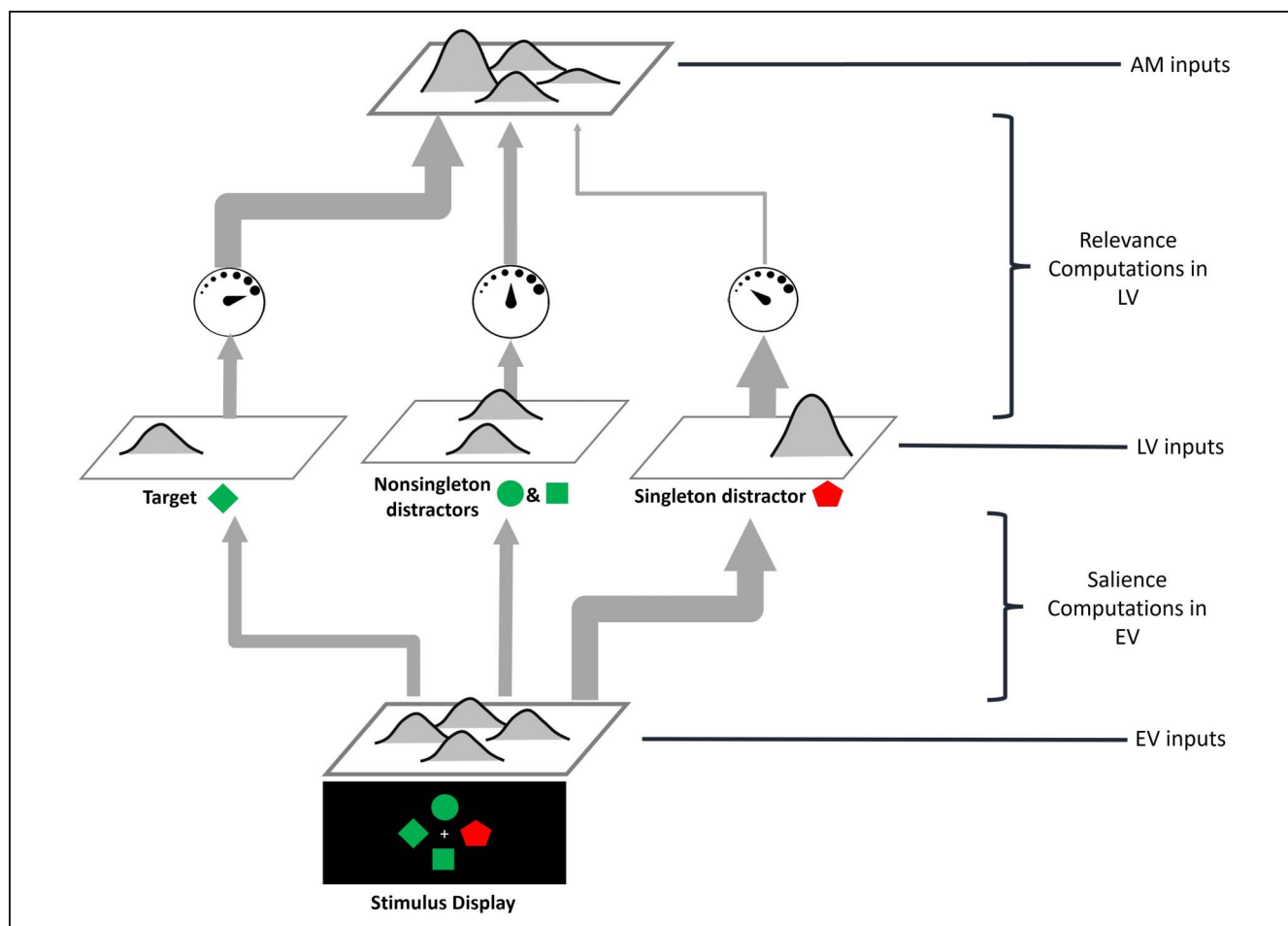


Figure 3. The implementation of proactive suppression in RAGNAROC. In this example, participants always searched for a green diamond and one of the distractors always appeared in red, allowing it to be proactively suppressed. The singleton distractor is the most salient, thus producing the strongest LV input as shown by the thickness of the arrows from EV to LV. However, the neural activities are then modulated by task relevance weights before entering the AM. The relevance weights are indicated by the dials in the top half of the figure. The diamond shape is associated with the target and is therefore “dialed up.” The color red, on the other hand, is associated with the singleton distractor and is therefore “dialed down,” indicating proactive suppression of this input. As a result, in the AM, the target became the most activated, followed by the nonsingleton distractors whose corresponding signals were unmodulated. The singleton distractor location ends up with the weakest AM signals. When the same target is placed at the horizontal midline, the mechanisms illustrated in this figure contribute to the EEG dynamics in the period where the P component in the flip can be observed (see blue boxes in Figure 4).

distractor locations get suppressed more and eventually to the point where they are less activated than the singleton distractor location. This results in the singleton location AM activities being relatively stronger. The mechanisms in the model dictates that a location with a stronger AM activity will translate into a more negative EEG waveform at the contralateral electrode, and thus, we see a relative negativity after contralateral subtraction. This simulates the second component of the flip (see the green boxes in Figure 4).

Interim Discussion

In brief, RAGNAROC explains the P-N flip as a result of a unique interaction between proactive and reactive suppression. At the LV layer, the singleton color is proactively down-weighted, resulting in a relatively weaker AM input at the singleton location (P component). Then, reactive

suppression works to inhibit all distractors, but the nonsingleton distractors are inhibited more strongly than the singleton, because the proactively suppressed singletons produce a weaker initial priority signal. The weaker reactive inhibition results in a relatively stronger AM signal at the singleton location (N component), which follows the earlier P component.

The P-N flip alone is not sufficient to support the entirety of this account because enhancement of the target color at the LV could also explain the P component, because the nonsingleton distractors had the same color as the target. However, we believe that both proactive suppression and enhancement are involved because of convergent behavioral evidence of suppression even when the nonsingleton distractors were in a different color (Chang & Egeth, 2019, 2021). Still, future studies will be required to see if the P-N flip can be observed when the nonsingleton distractors do not share the target’s color.

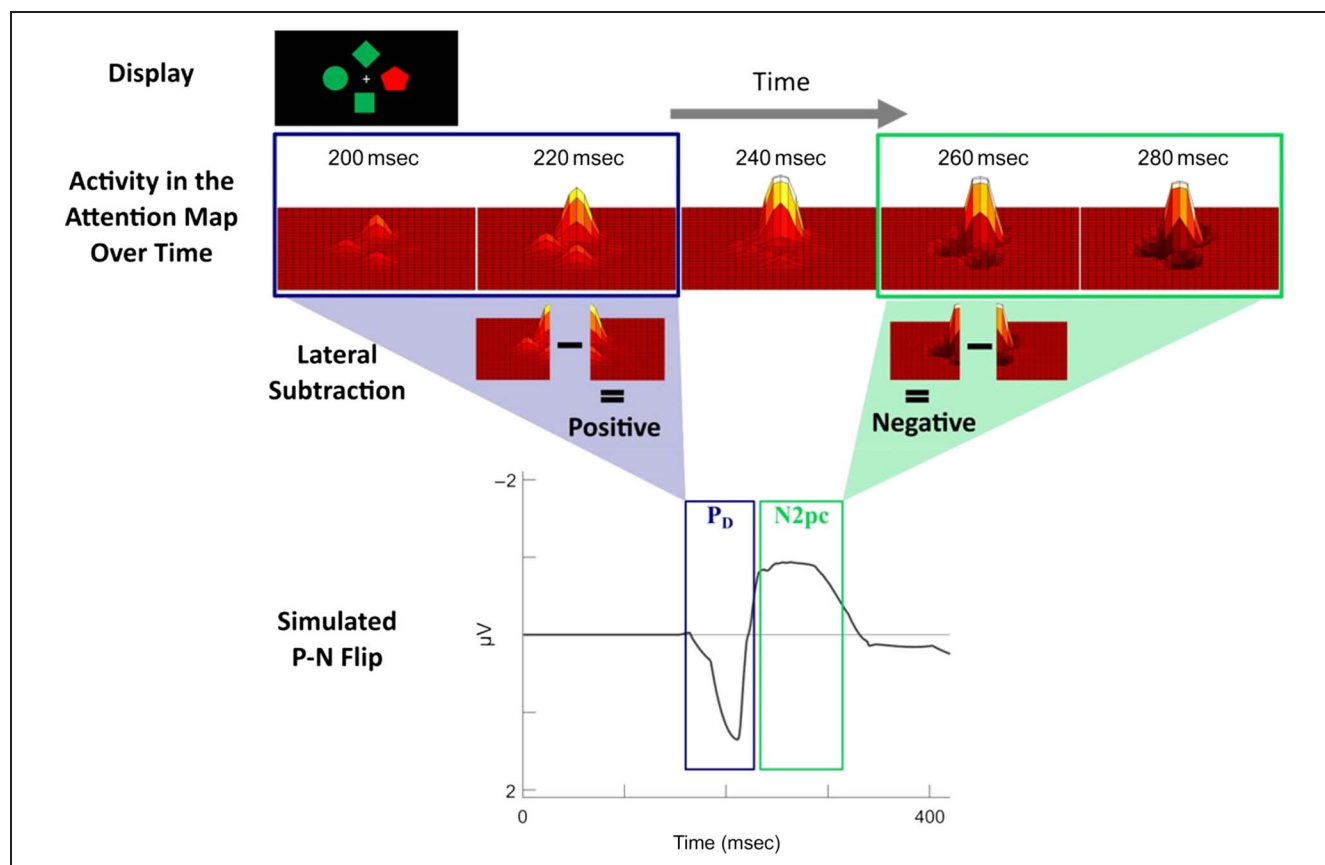


Figure 4. Attentional dynamics that underlie RAGNAROC's simulation of the P-N flip. In this example, participants always searched for a green diamond and one of the distractors always appeared in red, allowing it to be proactively suppressed. Top: Relevant dynamics in the AM at the critical timepoints for the flip (200–280 msec after array onset). A positive deflection on the map indicates enhancement of attention for items at the deflection location. The blue box indicates the P component: The lateral nonsingleton distractor (NS) had a weak but unsuppressed activation, whereas the singleton (S) had a near-baseline activation because of feature down-weighting. Technically, the weaker activation at the singleton location translates to a relative positivity at its contralateral electrode, resulting in a positivity after contralateral subtraction. As the polarity of this resultant component will always be the same as the result of directly subtracting the AM activities of the singleton side from that of the nonsingleton side, the process of contralateral subtraction is visualized as subtraction between AM activities from the two sides for ease of visualization. The green box indicates the N component: Unselected items are suppressed proportional to their activation strengths. As a result, the more-activated NSs got suppressed more than the less-activated S, resulting in a contralateral negativity. Bottom: A simulated ERP is generated from the simulated AM activity by just averaging the total synaptic activity for each side of the AM and subtracting one side from the other.

A limitation in our approach is that RAGNAROC does not consider the possibility of latency differences for different feature dimensions when signals are sent from different feature maps in the LV to the AM. In its current instantiation, the LV weights were assigned considering both color- and shape-based task relevance, but in reality, it is possible that relevance weights from the more discriminable feature starts influencing attention earlier (Smid, Jakob, & Heinze, 1997). In the currently simulated search display, color is likely more discriminable than shape because there are two colors but four shapes. If color weights are sent to the AM earlier than the shape weights, the target might start out being equally activated as the nonsingleton distractors (only color weights considered) before quickly garnering the highest priority (both color and shape weights considered), triggering reactive suppression. The lack of this latency difference in the current simulations may also explain why the simulated N component has a slightly earlier onset than the empirical

one (see Figure 1). However, the general explanation of the P-N flip is not affected, because none of the distractors (singleton or nonsingleton) had a predictable shape (other than being “not the target shape”). Thus, shape-based relevance weightings should mainly up-weight the target shape, and if the nontarget shapes are suppressed, the singleton and nonsingleton distractors will be suppressed with similar strength. In other words, when the target is presented on the midline, shape-based weightings should have no direct influence on the amplitudes of the lateral ERPs.

Another point of clarification regards why the AM reactively suppresses distractor locations below the baseline activity level, given that the target already has the strongest AM activation at 200 msec (see Figure 4). The mechanism for reactive suppression to suppress items below baseline in RAGNAROC is based on multiple theoretical and empirical considerations. First, the reactive suppression mechanism is theoretically driven by the idea that attention

must localize the target before engaging (Posner, Inhoff, Friedrich, & Cohen, 1987). The model was thus designed to single-out the target location as precisely as possible, and the reactive suppression mechanism also serves the purpose of implementing surround inhibition at the target location (Wyble et al., 2020). The subbaseline suppression is also driven by empirical observations that distractor locations are more inhibited compared with a blank location using a probe display (Cepeda et al., 1998). Finally, suppression below baseline is typical in the real neural systems that inspired the activation dynamics of this model. Suppressed neurons often have firing rates that are lower than their own baseline as excitatory and inhibitory inputs to these neurons are not directly coupled (O'Reilly & Munakata, 2000). In other words, there is no natural mechanism for a neuron to exactly balance out the amount of excitation and inhibition it receives, so that suppressing activation reliably would involve overshooting the baseline.

In the model, the ability to suppress the level of attention below baseline also separates reactive suppression from proactive suppression. This in turn allows for a critical empirical test between proactive and reactive suppression that we will illustrate below.

Predicted Empirical Distinction of Proactive and Reactive Suppression

In RAGNAROC, proactive and reactive suppression have distinct mechanisms with different effects on behavior and EEG. The most critical difference is how attention is allocated within the AM. Proactive suppression prevents attention toward the distractor by effectively ignoring the distractor. Therefore, it does not suppress the corresponding AM signal below baseline. On the other hand, reactive suppression can produce inhibitory wells (Figure 4A, 260–280 msec). Thus, we predict that a proactively suppressed location will never be activated less than an empty location whereas a reactively suppressed location will possibly be.

The test could be as follows: A salient color singleton with a predictable color is sometimes presented in a visual search task. When the target is presented on the midline and the salient distractor is lateral, we predict an EEG pattern resembling the P-N flip if a nonsingleton distractor occupies the location contralateral to the salient distractor. In contrast, no observable ERPs will be produced if the contralateral side is empty. Again, this is because when the salient singleton has a consistent feature, both the P and N components of the P-N flip are caused by the nonsingleton distractor. It should be noted here that a few studies have inspected the EEG waveforms with respect to a consistent-color distractor positioned contralateral to an empty space, but a Pd was observed (Hilimire, Hickey, & Corballis, 2012; Hickey et al., 2009). However, this Pd occurred slightly later (onset at ~220 msec) than the P component in the P-N flip (~185 msec in Kerzel &

Burra, 2020; ~110 msec in Drisdelle & Eimer, 2021) and was sometimes preceded by a N2pc; a distractor-present RT cost was also observed in some cases (Hilimire et al., 2012). These observations suggest that participants may not have employed proactive suppression, despite it having a consistent color. One speculation is that proactive suppression is only employed when a search task is sufficiently difficult, as proactive suppression is absent in studies that used a highly distinctive target–distractor pair (a shape vs. a line), required a simple discrimination task based on the target's outline, and employed a minimalistic search display with only one or two items. However, these factors influencing task difficulty are not taken into account by RAGNAROC. Further research (in both empirical and modeling terms) would be required to determine how task requirements influence suppression processes.

The predicted waveform is different for a salient distractor that is reactively suppressed, for example, when it does not have a consistent feature value.³ Given the same target-midline, distractor-lateral configuration, an N-P flip is predicted, no matter whether the contralateral side consists of a nonsingleton distractor or an empty space. However, the amplitudes of both components would be smaller when the nonsingleton distractor is present, compared with when it is absent, as that item has an initial above-baseline activation and will then be reactively inhibited, discounting the activation difference between itself and the salient distractor in both the initial activation and the reactive suppression stages.

EXTENSIONS OF THE P-N FLIP SIMULATION

Effect of Target Presence

Whether the search target is present critically affects the competition for attention in the AM. In the example we used to illustrate the P-N flip, the target is assumed to be the “winner” of this competition, and it exerts proportional inhibition toward the nonsingleton distractors (stronger) and the singleton distractor (weaker). However, if the target is absent, the nonsingleton distractors may win the competition, or no winner is determined and the AM activations gradually return to baseline. In either case, we will not expect the “flip” because AM signals will not be stronger on the singleton side. Thus, we suggest that target presence selectively influences the N component (see Figure 5A). This is consistent with the data in Drisdelle and Eimer (2021).

Effect of Set Size

The effect of set size on the P-N flip can be complicated and counterintuitive because multiple parameters covary as set size changes. For example, as set size increases, the singleton is thought to be further “singled out,” resulting in a higher salience (Stilwell et al., 2022; Stilwell & Gaspelin, 2021; Wang & Theeuwes, 2020). In addition,

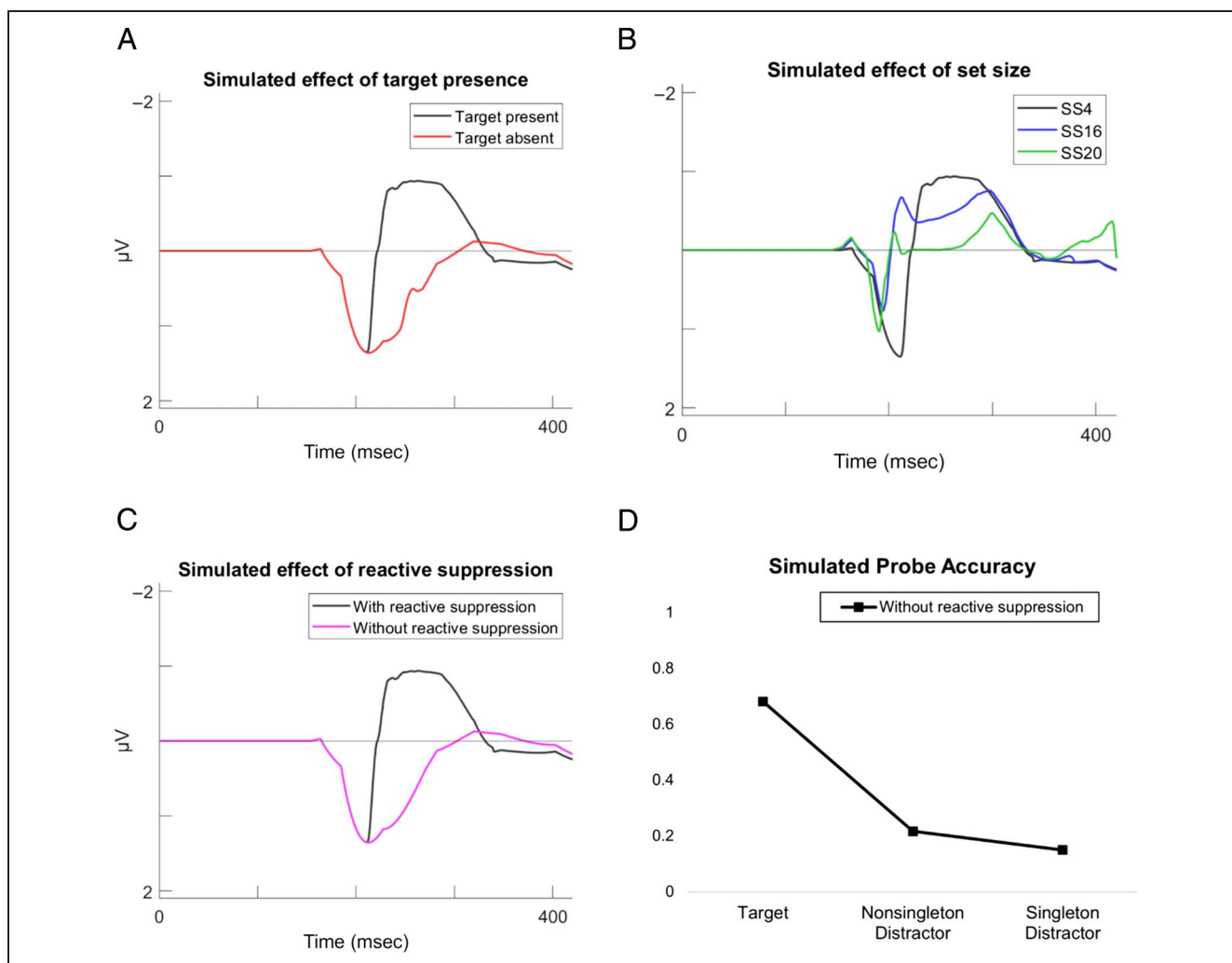


Figure 5. Extending the P-N flip simulation onto other related effects. (A) Absence of search targets selectively reduces the N component in the simulation, consistent with Drisdelle and Eimer (2021). (B) Increasing the set size changes a number of parameters, including target salience, singleton salience, and inter-item distance. The simulated pattern suggests that the P-N flip is preserved at set size 16, whereas the N component is selectively reduced at set size 20. This mimics the pattern observed in Stilwell et al. (2022). (C–D) Simulations performed with reactive suppression disabled in RAGNAROC to implement the decrease of spatial selectivity when probe trials are included. (C) The N component is selectively reduced, consistent with the visual inspection of Experiment 1 in Gaspelin and Luck (2018a). (D) The probe suppression effect observed in Experiment 2 in Gaspelin et al. (2015) can still be successfully simulated when reactive suppression is disabled.

increasing the set size often comes with a cost to the display heterogeneity, as shapes are often reused among the distractors (Stilwell et al., 2022; Stilwell & Gaspelin, 2021; Wang & Theeuwes, 2020; Barras & Kerzel, 2016). This makes the target shape more unique and increases the salience of the target. Furthermore, having more items on the screen often means that they are closer together. As noted earlier, reactive suppression in RAGNAROC depends on the graded lateral connections among the AM neurons: Locations closer to the winner will be more strongly suppressed. Therefore, the crowdedness of the stimuli also plays a role in the simulated EEG.

Implementing these parameter changes, we in fact successfully simulated the EEG at set size 16 and 20 reported in Stilwell et al. (2022). At set size 16, the flip is observed, consistent with their Experiment 1. At set size 20, the P component is preserved whereas the N component is

disproportionately reduced or even eliminated, consistent with their Experiment 2 (see Figure 5B).⁴

Effect of Including Probe Trials

In terms of letter probe reports (e.g., Gaspelin et al., 2015), the timing of the P-N flip predicts that only probes presented rapidly after the search array would be suppressed, in contrast to probes presented at a longer latency. However, probe suppression was still observed for probes appearing with a 200-msec delay to the onset of the search items (Gaspelin & Luck, 2018a; Gaspelin et al., 2015).⁵

To account for this inconsistency, it may be important to note that the presence of the letter probe task may itself affect the mechanisms of attentional selection. In fact, it has been suggested that the inclusion of probe trials influences the way attention is distributed by encouraging the

spreading of attention to more item locations, which will in turn influence the EEG (Drisdelle & Eimer, 2021; Kerzel & Burra, 2020). When discussing the findings from Gaspelin and Luck (2018a), Kerzel and Burra (2020) also observed that the inclusion of probe trials in Gaspelin and Luck's Experiment 1 seems to have selectively eliminated the N component.

In RAGNAROC, a plausible way to simulate the reduction of spatial selectivity of attention is to reduce the connective strengths in the lateral circuits on the AM that mediate reactive suppression. With this assumption, we repeated the simulation of the P-N flip using a version of RAGNAROC where the reactive suppression mechanism is completely disabled. This modification resulted in the selective elimination of the N component (Figure 5C), which is consistent with Kerzel and Burra's observation. Moreover, this version of the model can still simulate the behavioral probe suppression effect (Figure 5D). Still, although preliminary evidence for the selective influence of probe trials on the N component exists, further studies would be needed to directly assess the influence of the probe trial paradigm or other manipulations of the spread of attention on the EEG in this type of search task.

RELATIONSHIPS WITH EXISTING OBSERVATIONS AND THEORIES

One-to-many Mapping from ERPs to Neural Sources

Our account emphasizes that proactive and reactive suppression have distinct mechanisms, which is consistent with the viewpoint of Geng (2014). However, despite having distinct mechanisms and underlying neural sources, RAGNAROC predicts both forms of suppression to result in a positivity for the suppressed item, although at different time points. For a proactively suppressed item, the positivity is caused by the AM bump elicited by the contralateral nonsingleton item, whereas for a reactively suppressed item, the positivity is caused by a stronger suppression of the salient item from the selected item. These simulations are inconsistent with theories that propose a common mechanism for two suppression processes based on them both yielding a Pd (Sawaki, Geng, & Luck, 2012), or a seemingly definitive mapping between attention and N2pc, or suppression and Pd (Chelazzi, Marini, Pascucci, & Turatto, 2019; Gaspelin & Luck, 2018c; Noonan, Crittenden, Jensen, & Stokes, 2018). We suggest instead that the polarity of an ERP alone is not sufficient to drive a strong inference about the underlying causes, especially when the latency differs.

Salience May Be Unnecessary for Proactive Featural Suppression

Our formulation of proactive featural suppression is essentially an implementation of the down-weighting of

a specific feature value. This is largely consistent with the position of the adjusted SST (Gaspelin and Luck in Luck et al., 2021; Gaspelin & Luck, 2019). However, the role of the physical salience of the to-be-suppressed item is often maintained in the adjusted SST, such that an implicit assumption seems to be that the proactively suppressed item must have been a salient distractor to begin with. However, in RAGNAROC, any distractor items can be proactively suppressed if they possess a predictable feature that does not overlap with the target feature. A recent study by Lien, Ruthruff, and Hauck (2022) found empirical evidence that distractor saliency is not essential for feature-based suppression to occur. Nonsingleton distractors were introduced in their "triplet" condition, where three items (including the target) consistently shared a color and another three items consistently shared another (distractor) color. As the number of items in the target color and the distractor color were the same, the distractor items were not salient. However, these nonsingleton distractors imposed no cost to search RT and demonstrated a probe suppression effect, indicating that their activations were below that of the distractors sharing the target color.

Although we agree with Lien et al. (2022) that saliency is not essential for suppression, in RAGNAROC, singleton distractors do elicit saliency signals (or "attend-to-me signals") that can lead to attentional capture if not quickly suppressed (Hickey, McDonald, & Theeuwes, 2006; Theeuwes, 1992, 2004; Theeuwes & Burger, 1998). In addition, the idea that saliency is not necessary for suppression does not mean that saliency plays no role in suppression. For example, we speculated earlier in this article that proactive suppression may only be implemented when a task is sufficiently difficult, making it beneficial to suppress a distractor. In addition, some level of distinguishability is likely required for this distractor-associated feature to be recognized, learned, and suppressed.

Still, this viewpoint that dissociates proactive featural suppression from physical salience has theoretical implications on the understanding of *active* and *proactive suppression*. To elaborate, Drisdelle and Eimer (2021) interpreted the P-N flip as two acts of suppression. They suggested that the first suppression (toward the salient distractor) occurred earlier because of this distractor's "attend-to-me signal" driven by its higher relative saliency (see also Sawaki & Luck, 2010). This salience-based suppression mechanism can occur only after the relative physical saliences are computed and thus cannot occur "proactively" (before the stimuli appear). However, as saliency signals are available before the signals are sent to the AM, a successful salience-based suppression may also prevent any attention toward the suppressed item, such that it should not be considered an instance of "reactive" mechanisms. Consistent with the original SST (Sawaki & Luck, 2010), we think that this salience-based suppression mechanism should be termed "active" and be distinguished from both proactive and reactive

suppression. Whether active saliency suppression actually takes place is a topic for future research.

Proactive Featural Suppression as a Form of Template for Rejection

This proactive suppression mechanism can be viewed as a subclass of the idea of templates for rejection (Carlisle & Nitka, 2019; Arita et al., 2012). Arita et al. (2012) reported that precueing a nonsingleton task-irrelevant color sped up visual search, even when the precued color varied randomly from trial to trial. With a different search task, Cunningham and Egeth (2016) also observed a distractor color precueing benefit for search items with heterogeneous colors (i.e., the cued color was not salient), but only in the latter half of the experiment when the precued color was consistent throughout. Conceivably, under different circumstances, a template for rejection may be updated based on trial-to-trial cueing (Arita et al., 2012), require repeated use of the same cue (Cunningham & Egeth, 2016), or require repeated exposure to a consistent association between a feature value and the distractor (which is the condition simulated in the current article).

Conclusion

In this article, we described a new account for the P-N flip in fixed feature search (Drisdelle & Eimer, 2021; Kerzel & Burra, 2020) through a combination of proactive featural suppression and reactive suppression implemented with RAGNAROC. We suggest that as the consistent feature of the singleton distractor is proactively suppressed, the

singleton distractor is essentially ignored by the attentional system. Thus, the P-N flip is driven by attentional dynamics corresponding to the contralateral nonsingleton distractor, which is first activated and then reactively suppressed. We proposed empirical tests to evaluate this prediction and explored whether the P-N flip simulation is able to account for the empirical effects of target presence, set size, and the inclusion of probe trials on the EEG pattern. In general, we observe a good qualitative compatibility between the data and simulations across these different manipulations.

It should be noted that this article does not contain a complete mechanistic taxonomy of all possible suppression mechanisms. For example, the mechanism of proactive spatial suppression (e.g., Wang, van Driel, Ort, & Theeuwes, 2019) was not described. Providing a complete mechanistic taxonomy is not our intention. Instead, we use the unintuitive P-N flip to demonstrate how computational modeling can aid the interpretation of empirical data. All empirical data suffer from the reverse inference problem. In the case of N2pc and Pd, which are measured through a lateralized subtraction, the polarity of N and P can be equally caused by a positivity on one side or a negative on the other. A straightforward interpretation of contralateral negativity as attention and contralateral positivity as suppression is thus challenging. The modeling approach allows for formalized theorization of the suppression mechanisms in play and simulations of the ways they manifest, which can be helpful in resolving apparent conflicts between observations and theories, theory choosing, and generating new empirical predictions.

APPENDIX

Table A1. Parameters Used in Simulations

<i>Simulation</i>	<i>Tar_BU</i>	<i>NS_BU</i>	<i>S_BU</i>	<i>Tar_TD</i>	<i>NS_TD</i>	<i>S_TD</i>	<i>AMtoIG_excite</i>
P-N flip	.1	.1	.15	.4	.15	.01	.4
Target absence (Figure 5A, red line)	NA	.1	.15	NA	.15	.01	.4
SS16 (Figure 5B, blue line)	.17	.1	.22	.4	.15	.01	.4
SS20 (Figure 5B, green line)	.19	.1	.24	.4	.15	.01	.4
Reactive suppression (Figure 5C, magenta line)	.1	.1	.15	.4	.15	.01	0
Probe accuracy (Figure 5D)	.1	.1	.15	.4	.15	.01	0

In these simulations, items are positioned with an eccentricity of four units from the display center, except for the simulations for SS16 and SS20, which had items in the inner ring positioned with an eccentricity of four units and items in the outer ring positioned with an eccentricity of eight units. Tar = target; NS = nonsingleton distractor; S = singleton distractor; BU = bottom-up weight; TD = top-down weight; AMtoIG_excite = parameter for reactive suppression; reactive suppression is disabled when AMtoIG_excite equals zero.

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Data Availability Statement

All materials used for the simulations are available on the Open Science Framework: <https://osf.io/vdpmw/>.

Author Contributions

Joyce Tam: Conceptualization; Formal analysis; Investigation; Methodology; Project administration; Visualization; Writing—Original draft; Writing—Review & editing. Chloe Callahan-Flintoft: Conceptualization; Formal analysis; Investigation; Methodology; Visualization; Writing—Review & editing. Brad Wyble: Conceptualization; Formal analysis; Funding acquisition; Investigation; Methodology; Supervision; Visualization; Writing—Review & editing.

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Diversity in Citation Practices

Retrospective analysis of the citations in every article published in this journal from 2010 to 2021 reveals a persistent pattern of gender imbalance: Although the proportions of authorship teams (categorized by estimated gender identification of first author/last author) publishing in the *Journal of Cognitive Neuroscience (JoCN)* during this period were $M(\text{an})/M = .407$, $W(\text{oman})/M = .32$, $M/W = .115$, and $W/W = .159$, the comparable proportions for the articles that these authorship teams cited were $M/M = .549$, $W/M = .257$, $M/W = .109$, and $W/W = .085$ (Postle and Fulvio, *JoCN*, 34:1, pp. 1–3). Consequently, *JoCN* encourages all authors to consider gender balance explicitly when selecting which articles to cite and gives them the opportunity to report their article's gender citation balance.

Notes

1. Preventive suppression may also manifest as active suppression, where suppression is said to operate on early saliency signals but only after display onset (Sawaki & Luck, 2010). We note here that this type of salience-based active suppression is sometimes discussed as a mechanism of “proactive” suppression (Drisdelle & Eimer, 2021; Luck et al., 2021; Gaspelin & Luck, 2019). However, our view is that a suppression process should be classified as “proactive” only if the inhibition process occurs before display onset. Therefore, proactive featural suppression relies on foreknowledge of the to-be-suppressed stimulus' feature(s), and in other words, the to-be-suppressed stimulus must possess some learnable consistent features. Suppression that

can potentially prevent attention to the salient distractor without learnable distractor attributes (Sawaki & Luck, 2010) may also exist, but it requires a different mechanism than proactive suppression, as it is logically impossible for saliency signals to become available before display onset. This point will be further discussed in a later part of the article.

2. As noted by Kerzel and Burra (2020), this P-N flip also seemed to have occurred in Gaspelin and Luck's (2018a) Experiment 3. The ERP waveform is visually inspectable from Figure 9 in Gaspelin and Luck (2018a). However, the second ERP component was not analyzed or discussed in Gaspelin and Luck (2018a).

3. Note that a salient distractor without a consistent feature value may sometimes capture attention fully. For example, a Pd that indicates reactive suppression was not observable on trials with slow RTs (Gaspar & McDonald, 2014), or for individuals with low visual working memory capacity (Gaspar, Christie, Prime, Jolicoeur, & McDonald, 2016). The discussion here focuses on the scenarios in which the salient distractor is successfully suppressed via reactive suppression.

4. We chose not to simulate the EEG at set size 8 reported by Barras and Kerzel (2016): In their experiments, the target is always a circle among heterogeneous distractors that are either a triangle, a square, or a diamond. The circle target may thus be highly salient as the curvilinear singleton. In fact, Stilwell and Gaspelin (2021) reported saliency model estimations on a similar display used in their Experiment 4 and found the circle to be even more salient than the color singleton distractor. Having a high-salient search target can greatly impact the search strategy, as it may allow for the use of singleton search mode and may even negate the necessity of engaging in proactive featural suppression. As we wish to focus on EEG from a fixed feature search task, the EEG reported by Barras and Kerzel (2016) is not simulated in this article.

5. Note that a probe array that appears with a 200-msec offset probably captures the attentional dynamics at a slightly later timepoint.

REFERENCES

- Arita, J. T., Carlisle, N. B., & Woodman, G. F. (2012). Templates for rejection: Configuring attention to ignore task-irrelevant features. *Journal of Experimental Psychology: Human Perception and Performance*, 38, 580–584. <https://doi.org/10.1037/a0027885>, PubMed: 22468723
- Barras, C., & Kerzel, D. (2016). Active suppression of salient-but-irrelevant stimuli does not underlie resistance to visual interference. *Biological Psychology*, 121, 74–83. <https://doi.org/10.1016/j.biopsycho.2016.10.004>, PubMed: 27756581
- Burra, N., & Kerzel, D. (2013). Attentional capture during visual search is attenuated by target predictability: Evidence from the N2pc, Pd, and topographic segmentation. *Psychophysiology*, 50, 422–430. <https://doi.org/10.1111/psyp.12019>, PubMed: 23418888
- Carlisle, N. B., & Nitka, A. W. (2019). Location-based explanations do not account for active attentional suppression. *Visual Cognition*, 27, 305–316. <https://doi.org/10.1080/13506285.2018.1553222>
- Cepeda, N. J., Cave, K. R., Bichot, N. P., & Kim, M. S. (1998). Spatial selection via feature-driven inhibition of distractor locations. *Perception & Psychophysics*, 60, 727–746. <https://doi.org/10.3758/BF03206059>, PubMed: 9682600
- Chang, S., & Egeth, H. E. (2019). Enhancement and suppression flexibly guide attention. *Psychological Science*, 30, 1724–1732. <https://doi.org/10.1177/0956797619878813>, PubMed: 31693453
- Chang, S., & Egeth, H. E. (2021). Can salient stimuli really be suppressed? *Attention, Perception, & Psychophysics*, 83, 260–269. <https://doi.org/10.3758/s13414-020-02207-8>, PubMed: 33241528

- Chelazzi, L., Marini, F., Pascucci, D., & Turatto, M. (2019). Getting rid of visual distractors: The why, when, how, and where. *Current Opinion in Psychology*, 29, 135–147. <https://doi.org/10.1016/j.copsyc.2019.02.004>, PubMed: 30856512
- Cunningham, C. A., & Egeth, H. E. (2016). Taming the white bear: Initial costs and eventual benefits of distractor inhibition. *Psychological Science*, 27, 476–485. <https://doi.org/10.1177/0956797615626564>, PubMed: 26893292
- Drisdelle, B. L., & Eimer, M. (2021). P_D components and distractor inhibition in visual search: New evidence for the signal suppression hypothesis. *Psychophysiology*, 58, e13898. <https://doi.org/10.1111/psyp.13878>, PubMed: 34110022
- 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, 1030–1044. <https://doi.org/10.1037/0096-1523.18.4.1030>, PubMed: 1431742
- Gaspar, J. M., Christie, G. J., Prime, D. J., Jolicoeur, P., & McDonald, J. J. (2016). Inability to suppress salient distractors predicts low visual working memory capacity. *Proceedings of the National Academy of Sciences, U.S.A.*, 113, 3693–3698. <https://doi.org/10.1073/pnas.1523471113>, PubMed: 26903654
- Gaspar, J. M., & McDonald, J. J. (2014). Suppression of salient objects prevents distraction in visual search. *Journal of Neuroscience*, 34, 5658–5666. <https://doi.org/10.1523/JNEUROSCI.4161-13.2014>, PubMed: 24741056
- Gaspelin, N., Leonard, C. J., & Luck, S. J. (2015). Direct evidence for active suppression of salient-but-irrelevant sensory inputs. *Psychological Science*, 26, 1740–1750. <https://doi.org/10.1177/0956797615597913>, PubMed: 26420441
- Gaspelin, N., Leonard, C. J., & Luck, S. J. (2017). Suppression of overt attentional capture by salient-but-irrelevant color singletons. *Attention, Perception, & Psychophysics*, 79, 45–62. <https://doi.org/10.3758/s13414-016-1209-1>, PubMed: 27804032
- Gaspelin, N., & Luck, S. J. (2018a). Combined electrophysiological and behavioral evidence for the suppression of salient distractors. *Journal of Cognitive Neuroscience*, 30, 1265–1280. https://doi.org/10.1162/jocn_a_01279, PubMed: 29762104
- Gaspelin, N., & Luck, S. J. (2018b). Distinguishing among potential mechanisms of singleton suppression. *Journal of Experimental Psychology: Human Perception and Performance*, 44, 626–644. <https://doi.org/10.1037/xhp0000484>, PubMed: 29035072
- Gaspelin, N., & Luck, S. J. (2018c). The role of inhibition in avoiding distraction by salient stimuli. *Trends in Cognitive Sciences*, 22, 79–92. <https://doi.org/10.1016/j.tics.2017.11.001>, PubMed: 29191511
- Gaspelin, N., & Luck, S. J. (2019). Inhibition as a potential resolution to the attentional capture debate. *Current Opinion in Psychology*, 29, 12–18. <https://doi.org/10.1016/j.copsyc.2018.10.013>, PubMed: 30415087
- Geng, J. J. (2014). Attentional mechanisms of distractor suppression. *Current Directions in Psychological Science*, 23, 147–153. <https://doi.org/10.1177/0963721414525780>
- Hickey, C., Di Lollo, V., & McDonald, J. J. (2009). Electrophysiological indices of target and distractor processing in visual search. *Journal of Cognitive Neuroscience*, 21, 760–775. <https://doi.org/10.1162/jocn.2009.21039>, PubMed: 18564048
- Hickey, C., McDonald, J. J., & Theeuwes, J. (2006). Electrophysiological evidence of the capture of visual attention. *Journal of Cognitive Neuroscience*, 18, 604–613. <https://doi.org/10.1162/jocn.2006.18.4.604>, PubMed: 16768363
- Hilimire, M. R., Hickey, C., & Corballis, P. M. (2012). Target resolution in visual search involves the direct suppression of distractors: Evidence from electrophysiology. *Psychophysiology*, 49, 504–509. <https://doi.org/10.1111/j.1469-8986.2011.01326.x>, PubMed: 22176697
- 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, 1713–1730. <https://doi.org/10.1037/a0032251>, PubMed: 23527999
- Kerzel, D., & Burra, N. (2020). Capture by context elements, not attentional suppression of distractors, explains the P_D with small search displays. *Journal of Cognitive Neuroscience*, 32, 1170–1183. https://doi.org/10.1162/jocn_a_01535, PubMed: 31967520
- Kiss, M., Grubert, A., Petersen, A., & Eimer, M. (2012). Attentional capture by salient distractors during visual search is determined by temporal task demands. *Journal of Cognitive Neuroscience*, 24, 749–759. https://doi.org/10.1162/jocn_a_00127, PubMed: 21861683
- Lien, M.-C., Ruthruff, E., & Hauck, C. (2022). On preventing attention capture: Is singleton suppression actually singleton suppression? *Psychological Research*, 86, 1958–1971. <https://doi.org/10.1007/s00426-021-01599-y>, PubMed: 34561719
- Luck, S. J., Gaspelin, N., Folk, C. L., Remington, R. W., & Theeuwes, J. (2021). Progress toward resolving the attentional capture debate. *Visual Cognition*, 29, 1–21. <https://doi.org/10.1080/13506285.2020.1848949>, PubMed: 33574729
- Luck, S. J., & Hillyard, S. A. (1994). Electrophysiological correlates of feature analysis during visual search. *Psychophysiology*, 31, 291–308. <https://doi.org/10.1111/j.1469-8986.1994.tb02218.x>, PubMed: 8008793
- 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, 849–860. <https://doi.org/10.1037/a0030510>, PubMed: 23163789
- Noonan, M. A. P., Crittenden, B. M., Jensen, O., & Stokes, M. G. (2018). Selective inhibition of distracting input. *Behavioural Brain Research*, 355, 36–47. <https://doi.org/10.1016/j.bbr.2017.10.010>, PubMed: 29042157
- O'Reilly, R. C., & Munakata, Y. (2000). *Computational explorations in cognitive neuroscience: Understanding the mind by simulating the brain*. Cambridge, MA: MIT Press. <https://doi.org/10.7551/mitpress/2014.001.0001>
- Posner, M. I., Inhoff, A. W., Friedrich, F. J., & Cohen, A. (1987). Isolating attentional systems: A cognitive-anatomical analysis. *Psychobiology*, 15, 107–121. <https://doi.org/10.3758/BF03333099>
- 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, 10725–10736. <https://doi.org/10.1523/JNEUROSCI.1864-12.2012>, PubMed: 22855820
- 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, 1455–1470. <https://doi.org/10.3758/APP.72.6.1455>, PubMed: 20675793
- Smid, H. G. O. M., Jakob, A., & Heinze, H. J. (1997). The organization of multidimensional selection on the basis of color and shape: An event-related brain potential study. *Perception & Psychophysics*, 59, 693–713. <https://doi.org/10.3758/BF03206016>, PubMed: 9259637
- Stilwell, B. T., Egeth, H., & Gaspelin, N. (2022). Electrophysiological evidence for the suppression of highly salient distractors. *Journal of Cognitive Neuroscience*, 34, 787–805. https://doi.org/10.1162/jocn_a_01827, PubMed: 35104346
- Stilwell, B. T., & Gaspelin, N. (2021). Attentional suppression of highly salient color singletons. *Journal of Experimental Psychology: Human Perception and Performance*, 47,

- 1313–1328. <https://doi.org/10.1037/xhp0000948>, PubMed: 34766817
- Theeuwes, J. (1992). Perceptual selectivity for color and form. *Perception & Psychophysics*, *51*, 599–606. <https://doi.org/10.3758/BF03211656>, PubMed: 1620571
- Theeuwes, J. (2004). Top-down search strategies cannot override attentional capture. *Psychonomic Bulletin & Review*, *11*, 65–70. <https://doi.org/10.3758/BF03206462>, PubMed: 15116988
- Theeuwes, J. (2010). Top-down and bottom-up control of visual selection. *Acta Psychologica*, *135*, 77–99. <https://doi.org/10.1016/j.actpsy.2010.02.006>, PubMed: 20507828
- Theeuwes, J., Atchley, P., & Kramer, A. F. (2000). On the time course of top-down and bottom-up control of visual attention. In S. M. J. Driver (Ed.), *Attention & performance* (Vol. 18, pp. 105–125). Cambridge, MA: MIT Press.
- Theeuwes, J., & Burger, R. (1998). Attentional control during visual search: The effect of irrelevant singletons. *Journal of Experimental Psychology: Human Perception and Performance*, *24*, 1342–1353. <https://doi.org/10.1037/0096-1523.24.5.1342>, PubMed: 9778827
- Wang, B., & Theeuwes, J. (2020). Salience determines Attentional orienting in visual selection. *Journal of Experimental Psychology: Human Perception and Performance*, *46*, 1051–1057. <https://doi.org/10.1037/xhp0000796>, PubMed: 32757594
- Wang, B., van Driel, J., Ort, E., & Theeuwes, J. (2019). Anticipatory distractor suppression elicited by statistical regularities in visual search. *Journal of Cognitive Neuroscience*, *31*, 1535–1548. https://doi.org/10.1162/jocn_a_01433, PubMed: 31180265
- Wyble, B., Callahan-Flintoft, C., Chen, H., Marinov, T., Sarkar, A., & Bowman, H. (2020). Understanding visual attention with RAGNAROC: A reflexive attention gradient through neural AttRactOr competition. *Psychological Review*, *127*, 1163–1198. <https://doi.org/10.1037/rev0000245>, PubMed: 32772529