

RAGNAROC, a model of reflexive visual attention

Understanding visual attention with RAGNAROC:
A Reflexive Attention Gradient through Neural AttRactOr Competition

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Abstract

A quintessential challenge for any perceptual system is the need to focus on task-relevant information without being blindsided by unexpected, yet important information. The human visual system incorporates several solutions to this challenge, one of which is a reflexive covert attention system that is rapidly responsive to both the physical salience and the task-relevance of new information. This paper presents a model that simulates behavioral and neural correlates of reflexive attention as the product of brief neural attractor states that are formed across the visual hierarchy ~~at the moment~~ when attention is engaged. Such attractors emerge from an attentional gradient distributed over a population of topographically organized neurons and serve to focus processing at one or more locations in the visual field, while inhibiting the processing of lower priority information. The model resolves key debates about the nature of reflexive attention, such as whether it is parallel or serial, and whether suppression effects are distributed in a spatial surround, or selectively at the location of distractors. Most importantly, the model develops a framework for understanding the neural mechanisms of visual attention as a spatiotopic decision process within a hierarchy and links them to observable correlates such as accuracy, reaction time, and the N2pc and P_D components of the EEG. This last contribution is the most crucial for repairing the disconnect that exists between our understanding of behavioral and neural correlates of attention.

1 Introduction

A quintessential challenge for any perceptual system is the need to focus on task-relevant information without being blindsided by unexpected information that is also important. For example, a driver must be able to stop in response to an unexpected obstacle even while searching intensely for a specific landmark. Understanding how perception meets this ubiquitous challenge is crucial for understanding how the brain balances the prioritization of sensory information according to its relevance.

This challenge is matched by a multitude of attentional systems operating across different senses and time scales. For example in vision there are overt and covert forms of [spatial](#) attention, and within covert attention, there is a further distinction between a rapid transient/reflexive form of [spatial](#) attention and a slower sustained/volitional form (Jonides 1981; Muller & Rabbit 1992; Hopfinger & Mangun 1998; Nakayama & Mackeben 1989). There are also non-spatial forms of attention that allow us to select among spatially overlapping visual inputs (Neisser & Becklen 1975). ~~As cognitive scientists we are tasked with understanding the mechanisms of these various attentional systems.~~ Decades of research have provided a multitude of data types that define the properties of visual attention, such as accuracy, reaction time and neural correlates such as Event Related Potentials (ERPs). These data have driven the development of many theories, but the great majority of them are linked to ~~a small number of~~ specific paradigms (e.g. a model of visual search, or a model of the attentional blink). Such models are a useful starting point, but their narrow focus makes it difficult to generalize across experimental paradigms, and also makes it easy to inadvertently overfit a theory to a specific kind of finding. Newell (1973) argued that instead of focusing on individual results as a way to attack or defend a theoretical edifice, we can use a collection of results most productively if we build a comprehensive model that addresses all of them. The approach used here is to build a model that is close to the algorithmic level of implementation (Marr 1982) and that maximizes the number of empirical constraints that can be applied (Love 2015) with a minimum of parameter adjustment.

The model described here, termed RAGNAROC, which is short for *Reflexive Attention Gradient through Neural AttRactOr Competition*, is intended as a theoretical framework for understanding how the visual system implements a reflexive form attention. The model addresses data in different forms (e.g. accuracy, reaction time and EEG), and from different paradigms. The outcome of this approach is to provide (1) a computational implementation of reflexive attention, (2) an intuition for how different forms of data (e.g. accuracy, reaction time and EEG) emerge from a common set of neural mechanisms and (3) suggested resolutions for

RAGNAROC, a model of reflexive visual attention

several ongoing debates in the literature by showing how one model is able to account for distinct patterns of data (e.g. simultaneous attention to two stimuli but also suppression of competing representations) that are often taken as support for mutually incompatible positions in an ongoing debate. For the reader who is more interested in the conclusions than the model methods, there is a section in the discussion that focuses on the lessons that have been learned through the construction of the model.

Scientific Philosophy of this account and intended audience :

This paper is written primarily with the perspective of the experimental scientist in mind for experimental psychologists. Equations will be kept to a minimum, except for the appendix, and figures will be used to explain the model's dynamics. Moreover, the development of RAGNAROC was driven almost entirely by data from visual cognition experiments, such that the neural mechanisms proposed here are the simplest possible solutions to explaining such data. ~~Thus, the paper his paper adopts~~ uses an ~~has a strongly an~~ *abductive* approach ~~to scientific discovery~~ in which the simplest explanation for a series of empirical phenomena is sought. RAGNAROC is our current best guess at ~~an abstraction of the mechanisms involved in reflexive attention, according to a list of empirical constraints.~~ We consider the problem to exist in the M-open class (Clarke, Clarke & Yu 2013), which is to say that it is practically intractable impossible to specify an exact specification of the biological system. ~~Therefore, model verification is impossible in the proper sense.~~ However Nevertheless, abstract neural models such as this one are nevertheless a powerful way to distill insights and predictions to guide future research, ~~and these are included in the general discussion.~~ The paper concludes with a set of lessons and predictions that should be of interest to anyone who studies visual cognition. ~~By publishing such predictions in advance of testing them, it is demonstrated that these predictions were generated a-priori.~~

1.1 Reflexive Attention The complexity of understanding attention

In ~~the broadest of~~ strokes, attention is perhaps best summarized as privileging certain representations at the expense of others and this prioritization takes many forms throughout the nervous system from internal control signals within the brain all the way down to ~~concentrated~~ hardwired receptor distributions in the fovea and fingertips. In terms of visual attention, a distinction is often drawn between *voluntary attention*, wherein volitional control mechanisms configure the spatial deployment of attention over an extended period of time and *reflexive*

RAGNAROC, a model of reflexive visual attention

attention, wherein the visual system reacts rapidly to stimulus onsets in order to attend them before the stimulus display changes or the eye moves (Jonides 1981; Muller & Rabbit 1992; Hopfinger & Mangun 1998; Nakayama & Mackeben 1989). The term *reflexive* invokes an analogy with muscle reflexes that are deployed rapidly in response to a stimulus, and without waiting for slower, deliberative processes.

This reflexive form of attention presumably plays a key role in selecting important information for further processing when the eyes are making saccades frequently. Moreover, it is known to be responsive to higher levels of cognitive control, such that ~~which means that stimuli are only available at any location on the retina for a brief period of time. It was originally suggested that this system is entirely automatic, and that subjects are unable to avoid attentional capture by singletons (i.e. stimuli that are physically dissimilar to other visible stimuli; Remington, Johnston, & Yantis 1992) but the attentional capture debate (Yantis 1996; Theeuwes 1991; Folk, Remington & Johnston, 1992; Woodman & Luck 1999; Egeth, Leonard & Leber 2011; Anderson, Laurent & Yantis 2011) has demonstrated that~~ goals, expectations and rewards moderate how strongly stimuli can trigger or capture attention. ~~Thus, when looking for a colored square, any uniquely colored stimulus has an enhanced influence on attention relative to a case in which someone is looking for a moving object or an object with a particular orientation. This task-based configuration is also responsive to categorical target signifiers such as letters among digits (Wyble, Potter, Bowman 2009; Nako, Wu & Eimer 2014), and superordinate concepts (e.g. "marine animal"; Wyble, Folk, Potter 2013). Likewise, neural data from the EEG reflect what are thought to be rapid attentional responses to task relevant colors (Eimer 1996); letters/words (Eimer 1996; Tan & Wyble 2015; Nako, Wu & Eimer 2014) and line drawings (Nako, Wu, Smith & Eimer 2014).~~

~~Reflexive attention is essentially a semi-autonomous decision-making system. Goals can influence what kinds of stimuli will be able to trigger attention, but the actual decision to deploy~~

~~attention is linked to the onset of a physical stimulus. Therefore, this system provides a tight coupling between bottom-up and top-down determinants of attentional control. Moreover, this form of covert attention is one of the earliest mechanisms involved in visual processing and presumably plays a key role in most aspects of daily vision, and should likewise manifest in a broad variety of tasks under the umbrella of visual cognition research.~~

What we do not yet understand is how such a rapid form of attention would function at the level of neural mechanisms. The earliest theories of such attentional effects described how attention was first engaged at a cued location, and would remain there until disengagement (Posner REF, CHLOE?)

Later theories elaborated the mechanisms proposing that attention ~~For example, attention has been theorized to involve~~ a combination of target enhancement (Eimer 1996), and suppression of distractors (Cepeda, Cave, & Bichot & Kim 1998, Gaspelin Leonard & Luck 2015). However, while it seems straightforward to postulate such attentional effects, ~~building simulations of attention that are specified at the level of neural networks reveals that~~ these operations are non-trivial to implement in a visual system that is distributed across cortical regions. In such a system, it is not immediately obvious how neural representations could be tagged as belonging to a target or distractor. One question that arises is how does the visual system rapidly determine which neurons are currently representing distractors in order that they can be suppressed? Furthermore, how does the brain implement such a coordinated ~~modulatory~~ attentional process across ~~this visual system's~~ network of interconnected maps without requiring an exhaustively large number of intra-cortical connections? Limitations on white matter density mean that it is not feasible for all neurons to communicate directly with all other neurons, which makes seemingly straightforward decision-making approaches such as *winner-take-all* (i.e. the strongest representation suppresses all others) ~~difficult to implement in practice~~ impractical.

An additional complication arises when we consider that the attentional system cannot afford to implement a crisp categorical distinction between targets and distractors. No matter how strongly a person is engaged on a task, there must always be a possibility for task-irrelevant information to trigger attention so that the system remains responsive to unexpected dangers. ~~This requirement explains why attentional capture is such a robust phenomenon. Participants can be told to ignore certain kinds of stimuli and yet those stimuli, when presented with sufficient~~

~~saliency¹, consistently produce capture costs (Theeuwes 1991).~~ Thus, it must be the case that all stimuli, whether designated as targets or distractors by the experimental paradigm, are evaluated to some degree. One might be tempted to argue that inattention blindness experiments (Rock, Linnett, Grant & Mack 1992; Neisser & Becklen 1975; Simons, & Chabris 1999) demonstrate effective suppression of unexpected information. However, many subjects do notice the unexpected stimulus in such experiments. Moreover, the proportion of participants who noticed, for example, the black gorilla in Simons & Chabris (1999), was influenced by the attentional set of the observer. ~~Those monitoring the players in black shirts noticed the black gorilla more often than those monitoring the players in white shirts. Thus it must be the case that specific visual features related to the task irrelevant gorilla are evaluated.~~

The goal of this paper is to ~~better understand the architecture and neural mechanisms for implementing reflexive attention in a distributed visual system using computational modeling. This model will~~ describe neural mechanisms that make reflexive decisions about where to deploy visual attention, and implement the consequences of those decisions (i.e. the enhancement and suppression of processing)~~as an integrated system. This model will be constrained by neurocomputationally formalized approach provides the luxury of using both behavioral and EEG data as constraints on model development. Thereby,~~ a diverse set of constraints ~~will be brought into contact with the theory,~~ including neural plausibility ~~at the architectural level,~~ behavioral accuracy, and reaction time measures of attentional influences on behavior, and also the N2pc and P_D EEG components which are commonly associated with stimulus-evoked visual attention ~~deployment. Furthermore, because the model is a neural simulation that simulates EEG components, it provides an account of the underlying cause of those potentials in terms of neural mechanisms.~~

Model scope. This model is not to be taken as a complete model of visual attention, which would be beyond the scope of any single paper. RAGNAROC does not address, for example, how attentional control affects eye movements (Rao, Zelinsky Hayhoe, & Ballard 2002; Zelinsky 2008) or slower forms of covert attention that are more firmly under volitional control and can

¹~~In this work, to remain consistent with terminology in the attentional capture literature, the term saliency will refer to physical features (e.g. color, shape) that stand out from neighboring stimuli because of their dissimilarity. Saliency can also be used in a broader sense to refer to information that has importance for any reason, including task relevance (see Bowman & Wyble 2007).~~

be maintained for a prolonged duration (e.g. multiple object tracking Pyslyshyn & Storm 1988). The model includes a mechanism for the enhancement of information processing, but this is intended only as a proxy for more comprehensive explanations that would interface more directly with single-unit data (e.g. Reynolds & Heeger 2009; Beuth & Hamker 2015). Another variety of attentional mechanisms not addressed here are those that track object features rather than spatial locations (e.g. Neisser & Becklen 1975; Blaser, Pylyshyn & Holcombe 2000). In terms of anatomy, we describe the reflexive attentional system in terms of a hierarchy of multiple maps that is inspired by work on the macaque posterior cortex and reinforced by the fact that the lateralized EEG components associated with attention discussed here are also primarily posterior in origin. However it is likely that a combination of frontal and subcortical areas are involved in these processes, and it is not our intent to suggest that reflexive attention is exclusively mediated by posterior areas. [Moreover, the model is focused on attention effects at approximately the time scale of one fixation, and thus is not directly applicable to tasks that require multiple cycles of attentional engagement.](#)

1.2 Behavioral evidence for covert attentional control mechanisms in vision

1.2.1 Reflexive Attention

Reflexive attention is likely to play a role in many visual tasks, and its [likely](#) effects can be observed in paradigms that produce attentional cueing (Posner 1980; see Chen & Wyble 2018) attentional capture (Theeuwes 1991, Folk, Remington & Johnston 1992; Yantis 1996) and the [early lags of the](#) attentional blink (Shapiro, Raymond & Arnell 1992; Chun & Potter 1995) (Figure 1). In these paradigms, the effect of attention varies according to the nature of the stimuli and the required response. For example, [in cueing paradigms](#) a [visual](#) cue increases the accuracy and decreases reaction times for a subsequent target at the [same-cued](#) location, while having the opposite effect for targets at uncued locations. In attentional capture paradigms, a highly salient distractor causes slower and/or less accurate report of a target presented at a different location and enhanced report of a target at the same location as the salient singleton (Folk, et al. 1992). In attentional blink paradigms, when two targets (T1 and T2) are presented sequentially at a Stimulus Onset Asynchrony (SOA) of about 100ms or less, the second target is easy to see but only when the two targets are presented at the same location (Visser Bischof & DiLollo 1999; Wyble & Swan 2015).

1.2.2 Semi-Autonomous attentional control

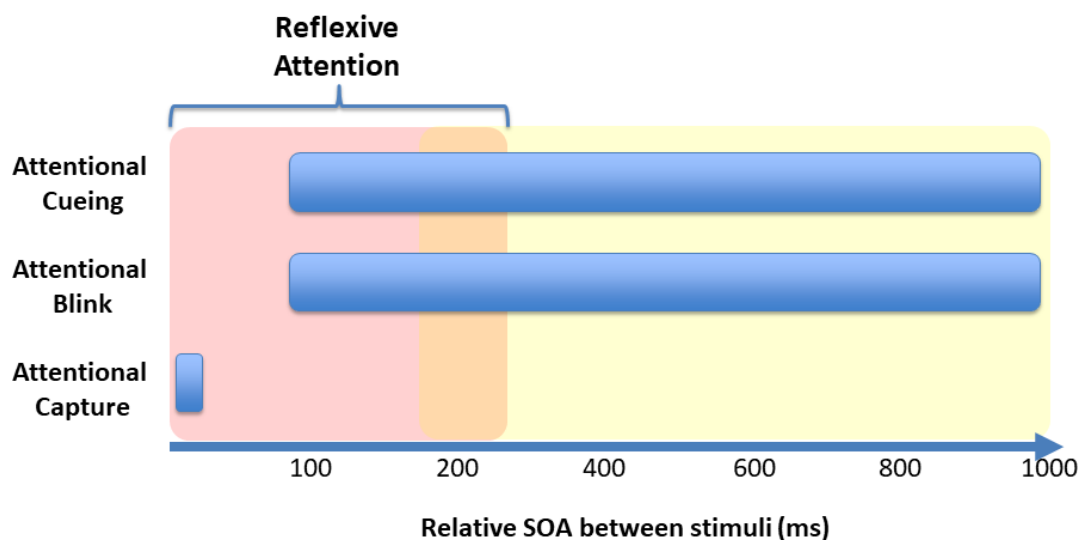


Figure 1. Paradigms that measure attentional effects often present two simultaneous or sequential stimuli and measure the influence of one on the other (e.g. a cue followed by a target, or a T1 followed by a T2). The blue bars indicate the inter-stimulus temporal separations that are most typically studied for three common paradigms. The red portion on the left is the temporal interval over which we consider reflexive attention to play a dominant role in the effect of one stimulus on the other. Other attentional effects that involve more volitional forms of processing are dominant at inter-stimulus longer asynchronies.

During normal visual function, the eyes-brief duration of eye movements requires a move rapidly and abruptly from one location to another which means that information is only available at a given location in the visual field for a few hundred milliseconds. Therefore it seems crucial that some form of attentional control is able to that makes rapid decisions without waiting for confirmation from slower, volitional forms of cognitive control. In this view, reflexive attention is a solution to the demands of the saccadic visual system in that it provides a semi-autonomous decision-making process for selecting information from prioritized locations in the visual field. Reflexive attention is *semi-autonomous* in the sense that the decision process obeys a configuring attentional set that modifies how readily different stimulus attributes will trigger attention. Such attention is strongly driven by salient singletons ² (Remington, Johnston, &

² There is an ongoing debate concerning the ability of top-down goal settings to mediate attentional capture (Awh, Belopolsky & Theeuwes 2012; Failing & Theeuwes 2018), with positions ranging from attention being entirely driven by Top-down factors, to the opposite extreme in which the first stage of attention is entirely driven by physical characteristics of stimuli.

Yantis 1992 REF) but the likelihood of a stimulus to capture attention is also strongly affected by the similarity between a stimulus and the current goals of the subject (Folk, Remington & Johnston, 1992; Woodman & Luck 1999 REF CHECK; Egeth, Leonard & Leber 2011 REF CHECK, and to some degree the amount of reward a stimulus has received (Anderson, Laurent & Yantis 2011)³

This task-based configuration is even responsive to categorical target signifiers such as letters among digits (Wyble, Potter, Bowman 2009; Nako, Wu & Eimer 2014), and superordinate concepts (e.g. "marine animal"; Wyble, Folk, Potter 2013). Likewise, neural data from the EEG reflect what are thought to be rapid attentional responses to task relevant colors (Eimer 1996); letters/words (Eimer 1996; Tan & Wyble 2015; Nako, Wu & Eimer 2014) and line drawings (Nako, Wu, Smith & Eimer 2014). Therefore, this system provides a tight coupling between bottom-up (i.e. attention as driven by physical characteristics of the stimulus) and top-down (i.e. attention as driven by expectations, goals and rapid learning) determinants of attentional control. This task-defined specificity coupled with the rapidity of reflexive attention provides a potent way for attention to select task-relevant information even when stimuli are changing rapidly (e.g. Potter 1976; Schneider & Shiffrin 1977).

Despite the fact that reflexive attention is receptive to attentional signals,

However the actual decision to deploy attention is made directly in response to stimulus onset.
The partial autonomy of this system is evident in the phenomenon of attentional capture,
wherein the attention system makes inappropriate and sometimes detrimental decisions about
where to deploy attention when faced with highly distracting information in which attention can
be deployed to stimuli that appear in locations of the visual field that are known to always be
task-irrelevant-(Remington, Johnston & Yantis 1992; Theeuwes 1992; Wyble, Folk & Potter 2013; Folk, Leber & Egeth 2002). These studies show that certain kinds of salient stimuli that
appear in locations of the visual field that are known to always be task irrelevant by the
experimental subject can nevertheless trigger the deployment of attention. Similarly, salient

³ There is an ongoing debate concerning the ability of top-down goal settings to mediate attentional capture (Awh, Belopolsky & Theeuwes 2012; Failing & Theeuwes 2018), with positions ranging from attention being entirely driven by Top-down factors, to the opposite extreme in which the first stage of attention is entirely driven by physical characteristics of stimuli.

~~distractors that are expected and known to be irrelevant to the task will continue to distract attentional control mechanisms over many repeated trials (Remington, Johnston & Yantis 1992; Theeuwes 1992).~~ If reflexive attention were not semi-autonomous, top down control signals would be able to ensure that stimuli presented in locations known to be irrelevant, ~~or stimulus forms that are themselves known to be task irrelevant would never be able to trigger attention.~~ Note that there are some cases in which top down control settings seem to eliminate salience-based capture (Bacon & Egeth 1994).

Another indication of automaticity comes from Krose & Julesz (1989) who demonstrated that cueing effects were localized to the specific location of a cue in a ring of stimuli, even when subjects were informed that the location of the target would typically be opposite to the location of the cue on the ring (see also Jonides 1981). Thus, expectation induced by both task instructions and experience with the task were unable to eliminate the immediate, reflexive deployment of attention to the specific location of cues at Cue-Target SOAs up to 260ms⁴. A finding in electrophysiology by Ansorge, Kiss, Worschech & Eimer (2011) showed that spatial cues which are never in the target's position will nevertheless generate an N2pc component, with an amplitude that is weighted by top-down feature settings.

A further line of evidence for automaticity is found in a series of experiments in which the cue (a pair of lines) was much larger than the target, and the subject could, in principle, learn how the cue's properties (e.g. color or shape) determined which part of the cue indicated the likely location of the target (Kristjansson & Nakayama 2003; Kristjansson, Mackeben & Nakayama 2001). It was found that subjects could learn simple relationships, such as that part of a cue (e.g. its left or right half) was more likely to cue a target's location if that relationship remained consistent across trials.

Another limitation on reflexive attention is that its temporal window is limited in duration, even when it would be advantageous for attention to remain engaged for a longer time period. A good example of this is the transient attention demonstration of Nakayama & Mackeben, (1989) in which, a cue appeared, and stayed on the screen to indicate the location of the target. Even though this cue stayed on the screen and was perfectly predictive of the target location, targets that occurred in the 200ms window after cue onset were reported more accurately than targets

⁴ CTSOAs were only evaluated in the range of 100-260ms.

appearing at later time points. This effect was replicated by Wilschut, Theeuwes & Olivers (2011) though with a smaller magnitude. This transient effect is not merely an alerting effect since it is spatially selective (Müller & Rabbitt 1989).

~~Therefore, reflexive attention seems to be locked to the onset of a stimulus, being triggered at a the stimulus' spatial and temporal coordinates. However, one aspect of attention that is amenable to control is what kinds of stimuli can trigger it. Remington, Folk & Johnston (1992) showed that attentional capture effects are moderated by the type of target, such that when subjects are trying to discriminate targets according to their color, distracting stimuli of the target's color are able to cause capture, while stimuli possessing other unique attributes (e.g. motion) have a weaker and sometimes non-existent ability to capture attention⁵. The functional advantage of attention being directed by top-down factors is clear, since it allows goals to direct attentional deployment to information that is more likely to be useful. This task-defined specificity coupled with the rapidity of reflexive attention provides a potent way for attention to select task-relevant information even when stimuli are changing rapidly (e.g. Potter 1976; Schneider & Shiffrin 1977).~~

1.2.3 Processing Enhancement at a cued or target location

Several independent lines of research suggest that deploying reflexive attention enhances the processing of targets in the same corresponding location. For example, spatial cueing paradigms find that relative to an uncued condition, a cue will reduce the reaction time to respond to a probe at that location (Eriksen & Yeh 1985) or increase the accuracy of responding to a masked target at that location within about 100ms (Nakayama & Mackeben 1989; Cheal, Lyon & Gottlob 1994; Wyble, Bowman, Potter 2009). ~~These effects typically onset very soon after a cue (i.e. within about 80ms). This rapid deployment of attention can be contrasted with a slower time course of attention when the cue indicates the to-be-attended location through a symbolic form such as an arrow (Cheal & Lyon 1991; Müller & Rabbit 1989).~~ The key defining characteristic of the rapid onset of attentional enhancement seems to be that the cue and target appear at the same location, which dovetails with the semi-autonomous nature of reflexive attention. Another

⁵-There is an ongoing debate concerning the ability of top-down goal settings to mediate attentional capture (Awh, Belopolsky & Theeuwes 2012; Failing & Theeuwes 2018), with positions ranging from attention being entirely driven by Top-down factors, to the opposite extreme in which the first stage of attention is entirely driven by physical characteristics of stimuli.

case of reflexive attention occurs when two targets are presented in close succession. If they are at the same location and at an SOA of ~100ms, the second target report is enhanced.

~~While most studies use cues to trigger the deployment of attention,~~ Wyble Bowman & Potter (2009) ~~tested the hypothesis that targets trigger attention, given that the presumed role of reflexive attention is to rapidly enhance target processing. In a design that presented two sequential targets among distractors in a continuously changing array, it was found that report of a second target was more accurate, when it occurred immediately after a preceding target, and in the same spatial position.~~ This spatially localized enhancement of processing is also consistent with the finding that lag-1 sparing effects in the attentional blink are strongly linked to spatial congruence between T1 and T2 (Visser Bischof & DiLollo 1999).

1.2.4 Visual attention suppresses the processing of information at the location of distractors

Because distractors are, by definition, not explicitly reported or responded to, it has been more difficult to understand how they are affected by attention. One source of information has been to record directly from neurons within the visual system and there are indications in neurophysiology that representations elicited by distractors are suppressed. In single-unit data from monkeys, neurons responsive to a distractor exhibit a sharp reduction in firing rate after about 100 ms when presented alongside a target in the visual field (Chelazzi, Miller, Duncan & Desimone 1993). This finding has been taken as evidence that targets and distractors engage in a competition that is biased towards the target (Desimone & Duncan 1995).

In human behavior, evidence of distractor inhibition in response to a target takes two forms. First, information is suppressed in the surrounding vicinity of a target, as demonstrated ~~by methods that ask when~~ subjects ~~to report two targets presented in rapid sequence or simultaneously~~ T and these methods reveal an effect termed Localized Attentional Interference (LAI), ~~such that. For example, Mounts (2000) varied the separation of two sequential targets and that the second target is~~ was most accurately reported when ~~it was~~ in the same position as the first target, ~~and much less~~ least accurately reported in the area surrounding the first target (~3 degrees) ~~and more accurate again at farther separations (Mounts (2000)). Note that this paradigm does not measure~~ This is not a direct form of distractor suppression, since the effect is actually observed on a target. directly but it does indicate that processing is suppressed in a region of the visual field near the target. Bahcall & Kowler (1999) presented a similar finding in which two

RAGNAROC, a model of reflexive visual attention

~~simultaneous~~ targets were presented ~~at various separations-simultaneously, and their spatial proximity was varied. They found that accuracy of reporting both targets was higher when they were presented farther apart.~~ Cutzu & Tsotsos (2003) ~~also~~ reported a similar finding ~~using a cue and a single target in which a cue induced a spatial inhibitory surround that was measured with target report accuracy.~~ Hickey & Theeuwes (2011) showed that the effect of a distractor that captures attention is greater when spatially proximal to a target, which also implicates a proximity based form of inhibition, centered at the location of a highly-salient distractor.

In addition to ~~spatial~~ inhibition in the ~~surrounding~~ vicinity of ~~a~~ targets, suppression is also ~~focused-centered~~ at the spatial location of distractors. Cepeda, Cave, Bichot & Kim (1998) found that when distractors were presented concurrently with a to-be-reported target, a subsequent probe would be reported more slowly at the location of that distractor, compared to a previously blank location. The implication is that the distractors in the display were suppressed and this suppression carried forward in time to impede~~d~~ the processing of probes presented at the same location. Similarly, Gaspelin, et al. (2015) found that probe letters in a spatial array following or coincident with a search display were harder to report if there had previously been a salient distractor at the location of that letter (although it is crucial to note that this only occurred when participants knew which specific feature to look for; this point will be discussed later).

Thus ~~there seems to be~~~~there are~~ two ~~different kinds~~~~lines~~ of evidence for ~~active~~~~distractor~~ inhibition, one ~~which is spatially~~-locked to the region surrounding a target, and the other ~~centered~~ ~~which occurs~~ at the location of distractors. The model presented below will attempt to reconcile these two forms of evidence.

1.3 Electrophysiological correlates of visual attention

~~An important complement to the behavioral evidence of reflexive attention are studies~~ ~~One of the most influential experimental approaches in the study of visuospatial attention that~~ uses Event Related Potential (ERPs) extracted from the EEG, ~~and likewise Event Related Fields (ERFs) from the MEG.~~ ERPs ~~and ERFs~~ provide a measure ~~of neural activity~~ that is precisely timed to underlying neural events ~~and thus provides crucial information about the relative timing of attentional processes, and therefore can be linked to distinct levels of processing.~~

1.3.1 ERPs reflecting the current location of spatial attention

RAGNAROC, a model of reflexive visual attention

When spatial attention has been directed to a specific location prior to the onset of a stimulus, the ERPs evoked by that stimulus will differ according to whether it is inside or outside of the attended location. For example, components elicited by the onset of a visual stimulus ~~early components~~ such as the N1/P1 complex, ~~elicited by the onset of a visual stimulus~~, are larger in amplitude for a stimulus that appears in an attended location (Mangun 1995; Hillyard & Anllo-Vento 1998) and presumably reflects increased neural activity evoked by stimuli at those locations. Likewise, increased amplitude of the Steady State Visual Evoked Potential (SSVEP) for a flickering stimulus has served as a robust indicator of the location of attention and can last multiple seconds (Müller & Hillyard 2000). These effects indicate that ongoing spatial attention affects the processing of stimuli at the earliest levels of cortical processing. Moreover, they are also useful for demonstrating when shifts of attention have occurred, as in

~~These early components can indicate short term changes in the attentional state evoked by an immediately preceding stimulus. For example, in the case of Hopf, Boehler, Luck, Tsotsos, Heinze & Schoenfeld (2006), who demonstrated a neural correlate of the spatial distribution of surround suppression evoked by an attended stimulus (Mounts 2000). probe stimuli were presented 250 milliseconds after a target display, and the amplitude of the magnetic impulse induced by the probe in MEG mapped the spatial distribution of attention evoked by the target. The probe evoked a larger response when presented at the same location as the target, the lowest response when presented just next to the target and a more moderate response at more distal locations. Thus, the ERPs provide a measure of the spatial distribution of attention effects that resembles the behavioral measure of the spatial profile of attention described by Mounts (2000).~~

1.3.2 ERPs indicating a change in the spatial distribution of attention

Another class of EEG component is thought to indicate the neural mechanisms involved in the initiation ~~deployment~~ of attention. ~~Unlike the N1/P1 and SSVEP, which indicate the influence of ongoing attentional states on the processing of new stimuli, this second class of ERPs indicate the active deployment of attention in response to the onset of new stimuli, a subset of which are to be attended and the others are to be ignored.~~ These potentials, termed the N2pc and the P_D, occur later in time than the modulations of the N1/P1, which is consistent with the idea that they reflect changes in attention evoked by new stimuli.

RAGNAROC, a model of reflexive visual attention

The N2pc component:

The N2pc is a brief negativity elicited by a laterally presented target stimulus. The evoked potential is small in amplitude and occurs on posterior areas of the scalp contralateral to the target, approximately 200-300ms after the onset of the target, and is typically less than 100ms in duration. The original theories proposed by the seminal publications on the N2pc suggested that it reflects either the suppression of distractors (Luck & Hillyard, 1994) or the enhancement of the target (Eimer, 1996). The N2pc has also been referred to as a Posterior Contralateral Negativity or PCN (Töllner, Rangelov & Müller 2012).

Newer findings have provided different perspectives. For example, it has been suggested that the N2pc reflects the process of individuating the target from surrounding stimuli, as its amplitude increases with the number of presented targets, but only when target numerosity is task relevant (Pagano & Mazza 2012). Also, Hickey, Di Lollo, & McDonald, (2009) suggested that when a target is paired with a contralateral distractor, the N2pc to the target is composed of two dissociable components: a negativity evoked by the target (the N_t) and a positivity evoked by the distractor (the P_D). Since the N2pc is measured as a difference wave between target-contralateral and target-ipsilateral sides of the scalp, the P_D would be measured as a negativity relative to the target, thus contributing to the N2pc amplitude. The N_t and P_D components were isolated by presenting the distractor or the target, respectively, in the middle of the display, which eliminates their contributions to the ERP and reveals the neural signature evoked by the other stimulus.

Another perspective on ~~what processes are indicated by~~ the N2pc stems from a finding in which two sequential targets are presented at either the same or different locations on the screen (Tan Wyble 2015). In the same-location condition, subjects could easily see the second target, however it elicited no additional N2pc beyond the N2pc evoked by the first target. In contrast, when the second target was on the opposite side of the display, a strong second N2pc was evoked by that second target. In terms of behavior, subjects were ~~actually~~ better at reporting the same-location target, which did not evoke an N2pc, compared to the different-location target which did evoke an N2pc. ~~From this work, the~~ We ~~concluded~~ sion is that the N2pc indicates only the process of initial localization of a to-be-attended stimulus of a target, rather than enhancement or suppression. This explains the missing-N2pc in the same-location result, since the second target inherits the attention deployed by the first target, and no additional N2pc is evoked. Moreover, this missing-N2pc phenomenon is only true when T1 and T2 are presented closely in time. At longer temporal separations (e.g. 600 ms), the T2 elicits a second N2pc, even

RAGNAROC, a model of reflexive visual attention

if subjects have a clear expectation that the target will occur in that location (Callahan-Flintoft & Wyble 2018). This finding is crucial because it underscores that reflexive attention is driven by a stimulus, and cannot be maintained for an extended period of time without stimuli to keep attention engaged.

With these various theories in contention, it is clear that little consensus as to the underlying cause of the N2pc exists. Moreover, a crucial complexity of the N2pc literature is that distractors evoke an N2pc in certain cases (Hickey McDonald & Theeuwes 2006; Burra & Kerzel 2013; Kiss, Grubert, Petersen, & Eimer, 2012; McDonald, Green, Jannati, & Di Lollo, 2012; Liesefeld, Liesefeld, Töllner, & Müller 2017). Such findings highlight the complexity of attentional mechanisms and the difficulty of ascribing unitary functions to neural correlates.

The P_D Component:

Another ERP related to attentional control is the P_D-component, a positivity evoked in posterior scalp regions that are contralateral to a distractor (Hickey, McDonald & Theeuwes 2009). ~~For example, a target presented in the middle of a display with a flanking distractor on the right or left has been found to elicit a positivity on the posterior scalp contralateral to the distractor.~~ The fact that distractors selectively elicit a P_D is additional evidence that inhibition is selectively deployed at the location of distractors ~~and. This finding dovetails with behavioral evidence that distractors are selectively inhibited and~~ reinforces the idea that attention has mechanisms for both enhancing and suppressing information in a spatially ~~specific-selective~~ format.

However, ~~the situation becomes more complex when search difficulty is varied.~~ When target search is made extremely easy by re-using the same target-defining feature on each trial and using many repeated trials, salient distractors can be ignored entirely, without producing a P_D, or an observable behavioral cost (Barras & Kerzel 2016) suggesting that ~~there-in some cases distractors can be simply ignored rather than suppressed is no need to suppress distractors when selection is made extremely easy.~~ In other cases salient distractors elicit a P_D in the EEG and a minimal cost on the speed of finding the target (Burra & Kerzel 2013) with a concomitant suppression of the distractor's location as measured by behavioral probes (Gaspelin, Leonard & Luck 2015; Gaspelin & Luck 2018). These results suggest that sometimes the distractor has the potential to interfere, and is inhibited to reduce its influence. Finally, if the search task is made sufficiently difficult by varying the target's defining feature from trial to trial, then the distractor evokes an N2pc, while also eliciting a strong behavioral capture cost (Burra & Kerzel 2013)

suggesting that in such cases there was a consistent failure to inhibit the distractor. This distractor-induced N2pc also supports the suggestion that distractors have an inherent salience which must be inhibited (Sawaki & Luck 2010).

~~In broad strokes,~~ These findings can be summarized as follows. When search is made extremely easy by using many trials and highly prescriptive visual targets, the visual system learns to exclude some kinds of distracting information ~~without even requiring attention~~ without spatial attention. When the task becomes more difficult, distractors are suppressed by spatial inhibition mechanisms, eliciting a P_D but no behavioral cost on target response. With a further increase in difficulty by using unpredictable singleton targets, distractors are not as effectively suppressed, ~~such allowing them to that they~~ produce an N2pc and a sizeable behavioral capture effect. Such findings complicate the straightforward attribution of the P_D as a correlate of distractor suppression but also underscore the importance of building integrative theories that combine behavioral and neural forms of evidence. As we will argue below, these divergent findings can be explained as a range of outcomes that arise from the competition for attention between putative targets and distractors in a spatially topographic attentional priority map.

2. Computational architectures for distractor suppression

Moving to a discussion of how reflexive attentional control might be implemented, we begin by considering several architectures that could support the ability to selectively enhance and suppress in response to a target.

2.1 Assumptions

This discussion is predicated on several assumptions that are implicit in existing models of attention. An anatomical assumption is that the visual system is hierarchically organized, beginning with low level feature extraction in cortical area V1 that projects to various cortical areas specialized for more specific kinds of information, such as color, and various forms (Van Essen & Maunsell 1983, Kravitz, Saleem, Baker, Ungerleider, & Mishkin, M. 2013; Konkle & Caramazza 2013). These higher-level representations are assumed to maintain the spatial topography of V1 albeit with larger receptive fields (DiCarlo & Maunsell 2003; Silver, Ress & Heeger 2005). This hierarchy places some important constraints on how different kinds of information flow through the model. Another crucial assumption is that *there is no indicator that definitively determines which stimuli should be attended*. Instead, the attentional system perceives stimuli with varying combinations of intrinsic salience and task relevance. It then

RAGNAROC, a model of reflexive visual attention

decides which stimuli to attend according to the broader goals of the organism, which may sometimes transcend the specific task imposed by the experimenter (i.e. if there was an earthquake, the subject would presumably notice). In other words, the notional distinction between targets and distractors as imposed by any specific task is not the ultimate designation of stimulus priority as far as the visual system is concerned. The system must decide what will be attended and what will be suppressed on each trial and this decision is not pre-ordained by other a higher level cognitive systems, except perhaps in cases where the visual search is highly prescriptive and repeated many times (Theeuwes 2012; Burra & Kerzel 2013)

A final crucial assumption is that there are no a-priori labels as to which neurons are processing to-be-attended vs to-be-ignored stimuli. When a decision has been made to attend to a stimulus, there must exist an efficient means to rapidly distribute the consequence of that decision across a diverse set of cortical areas. For example, a given neuron in early visual cortex may be firing in response to a stimulus that downstream areas of the visual system have determined should be attended, but how is credit assigned back to that neuron?

Given these assumptions, a candidate model of reflexive attention must include mechanisms for making rapid decisions about where to attend, and also mechanisms that rapidly implement that decision by routing information between different portions of the visual system.

2.2 Four potential architectures:

It is helpful to understand the advantages and drawbacks of various architectures by which attentional decisions are could be communicated to other maps in a hierarchically organized visual system. To this end, this section outlines four possibilities concerning how attentional enhancement and suppression effects would interact between different processing areas.

2.2.1 Local Attentional Control:

The simplest method of reflexive attention can be implemented is at the local circuit level. In such a model, stimuli are processed separately within different maps (Figure 2a).

Representations of each stimulus compete within these cortical areas, and one or more winners of that local competition would be attended, according to internal mechanisms within that area. While simple, this architecture has difficulty explaining how stimuli of different kinds can affect one another. For example, attentional capture by a color singleton affects processing of a shape singleton target (e.g. Theeuwes 1991) which requires that. To explain such data requires an

RAGNAROC, a model of reflexive visual attention

~~attentional architecture in which~~ decision consequences can propagate between maps selective for different kinds of information.

2.2.2 Peer to Peer attentional control:

~~The simplest architecture that allows attentional effects to propagate involves connections between cortical areas (Figure 2b illustrates a model in which). A~~ any map that resolves a competition between stimuli projects ~~signals to enhancement and suppression to the~~ other maps ~~by using intracortical pathways that take advantage of exploiting~~ the spatiotopic correspondence between feature maps, ~~thus so as to ensure~~ that the correct locations are excited or inhibited across maps.

The disadvantage of this architecture is that it requires an enormous number of intracortical projections. Each feature map within the visual system must send projections to every other map so that targets in one map can enhance or suppress representations in all other maps. Thus, the number of intra-areal connections grows as $M \cdot N^2$, where M is the number of neurons within each cortical area and N is the number of areas. However it has been estimated that only about 30% of the total proportion of possible intra-areal connections exists within the macaque visual system (Felleman & Van Essen 1991) which argues against strong peer-to-peer ~~connectivity~~ attentional control.

2.2.3 Feedback Attentional Control:

The third architecture is more efficient in terms of intracortical projection (Figure 2c) because it exploits the hierarchical nature of the visual system. Once a stimulus has won a local competition in any map, it projects a combination of enhancement and inhibition back down to the earliest levels of processing in the visual hierarchy (i.e. perhaps V1 or even LGN). These effects then propagate forward to the descendent visual processing areas.

This approach requires fewer inter-areal connections than the peer-to-peer model, growing linearly with the number of feature maps. The selective tuning model of Tsotsos (2011) et al provides a thorough formalization of such a system.

The disadvantage of this approach is that resolving a competition between two stimuli represented in distinct feature maps would require multiple iterations of feedforward and feedback processing through the hierarchy since the higher level maps do not directly communicate with one another. Furthermore the suppressed information is cut off at the earliest level, which precludes it from analysis by higher levels of the visual system. This makes it difficult for deeper levels of meaning to be computed from stimuli that are not attended.

2.2.4 Inhibition at a superordinate map:

The final architecture that we consider, and the one that is used in RAGNAROC, confines the competition to a single cortical area: an attention map that is hierarchically superordinate to all of the spatiotopic maps that comprise the ventral visual system (Figure 2d)⁶. The attention map

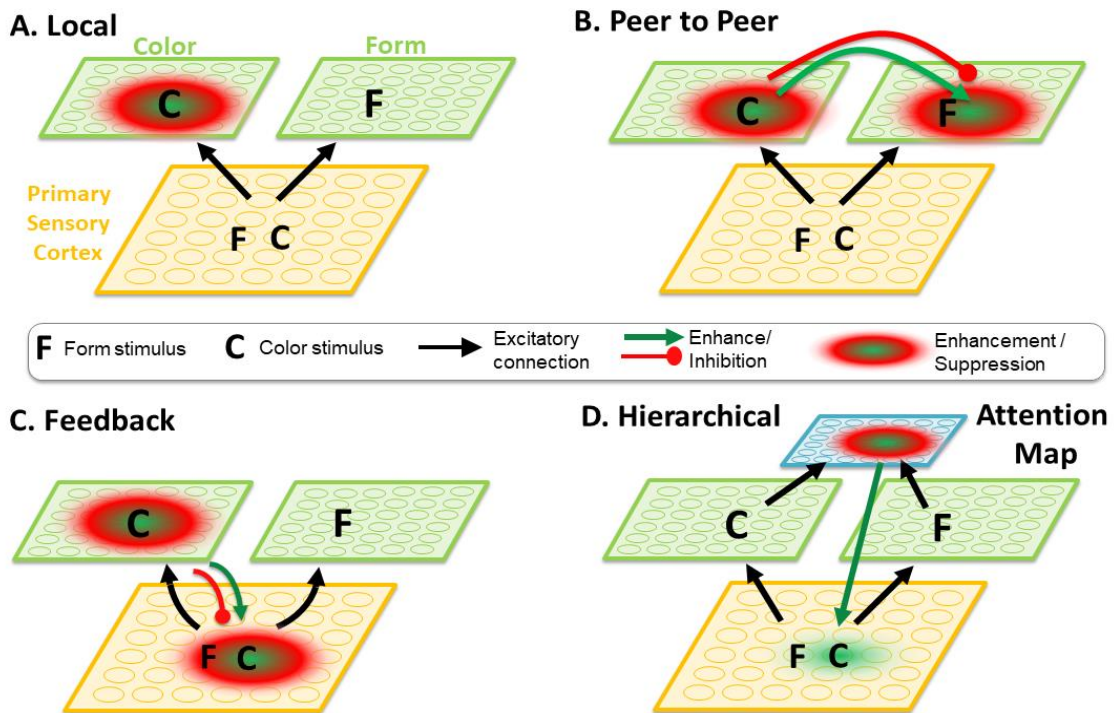


Figure 2. Illustration of four architectures for mediating the competition between two stimuli for which the most salient attributes are processed in different maps (e.g. color singleton vs a form singleton). The illustrations indicate how attentional enhancement and suppression effects elicited by a highly salient color singleton can propagate between areas.

⁶ For simplicity we assume that there is only a single cortical area that computes attentional priority, although the functionality would be essentially similar if there is a small family of interconnected cortical areas that mediate attention. .

RAGNAROC, a model of reflexive visual attention

provides a compact method to make rapid decisions about where to deploy attention in the visual field, since it accumulates information about the priority of different stimuli from many subordinate topographic maps into a single brain region.

Once a spatial region within the attention map has been sufficiently activated by input from subordinate maps, those neurons enhance the processing of information at the corresponding region of the earliest processing level, and that enhancement then carries forward through the ventral hierarchy. ~~In this framework, inhibition of distracting information is accomplished by inhibiting regions of the attention map rather than neurons within the subordinate maps.~~

~~An important distinction of this architecture relative to the others is that~~ there is no direct suppression of information in the subordinate layers. Instead, suppression is achieved indirectly by reducing the availability of attention at particular locations in the visual field. Thus, attention is represented as a gradient field of activation levels distributed across the spatial extent of the visual field (LaBerge & Brown 1989, Cheal Lyon & Gottlob 1994). Changes in these activation levels provides a convenient way to throttle the processing of information through all of the feature maps that are descended from the early visual area with a relative minimum of intracortical projections. This approach mitigates the disadvantages of the preceding architectures as follows. Attentional decisions can be made rapidly even between stimuli with distinct representations, since the competition occurs within a single map. Also, suppressing attentional priority, rather than representations in the subordinate layers, preserves the information at the earliest levels of processing, which allows a stimulus in an unattended region the chance to make contact with deeper levels of processing should it be required (i.e. no information is lost).

3. RAGNAROC specification

3.1 Inspiration from existing models

There is a substantial literature on computational models of attention that collectively addresses a broad set of mechanisms and processes. The RAGNAROC model is informed by many of these models, theories and ideas. Starting from the very earliest cueing paradigms was the theory that attention is briefly engaged at a given location (Posner REF) which briefly

precludes it from being deployed elsewhere. RAGNAROC implements a brief “lock-on” attractor state when attention is deployed, and this implementation is similar to the engagement of attention as originally proposed.

Another ~~One~~ of the ~~most~~ formative models for our approach is the Theory of Visual Attention (TVA; Bundesen 1990; Bundesen, Habekost, & Kyllingsbæk, 2011), which provides a mathematical formulation for how goals adjust the pertinence of certain kinds of information (i.e. when one is looking for red digits, the pertinence of red is upweighted to increase the rate at which stimuli with that color are processed). This pertinence weighting applies across the entire visual field, which explains how stimuli are able to capture attention when they match top-down settings despite being located in a to-be-ignored location of the visual field. TVA also formalizes the understanding of stimulus-driven attention as a decision making process. In terms of implementing a hierarchical architecture for attention, the Koch & Ulfman (1985) and Itti, Koch & Niebur (1998) models of salience were crucial for establishing the utility of a shared salience map, which accumulates information from subordinate layers of processing and allows them to compete on an even footing in a compact neural field. Li (2002) helped to establish the idea of salience being a product primarily of anatomically early levels of processing. Zehetleitner, Koch, Goschy & Müller (2013) elaborated the circuitry of competition at the top of this hierarchy, to provide an illustration of how attention ~~operations~~ decisions can be considered a race between competing selection operations.

In terms of implementing selection,

~~Whereas a salience map is an output of what amounts to a feed forward process,~~ the Selective Tuning (ST) model of Tsotsos (1995) illustrates how recurrent ~~excitatory~~ signals, propagating backwards through the visual hierarchy could implement the selection process at the earliest levels of the hierarchy. ~~However, a~~ Another class of models has been even more influential in that highlight ~~ings~~ the importance of recurrence in iteratively shaping the spatial profile of attention. One of the clearest examples of this process is SAIM (Heinke & Humphreys 2003; cite more recent one REF) in which a pool of selection neurons interacts with incoming information to create a spatially localized selection and routing of information to a different group of neurons that represent the focus of attention. In SAIM, the selection process is an emergent property of the shared topographic connectivity between the selection system and the

retinal input. Moreover, a series of top-down connections provides an additional form of resonance that selects for coherent objects that match the visual search template. This idea is also present in adaptive resonance models by Grossberg and colleagues, and in particular the attentional shroud model of (Fazl, Grossberg & Mingolla 2009), which describes a process to delineate the boundaries for the purpose of learning.

~~-suggests a metaphor of shrouds that drape across to be attended regions of the visual field (Fazl, Grossberg, & Mingolla 2009).~~

The idea of reflexive attention, as a brief burst of enhancement to increase the processing at a particular moment in time was simulated in the STST (Bowman & Wyble 2007), eSTST (Wyble, Bowman & Nieuwenstein 2009); and Boost Bounce models (Olivers & Meeter 2008). Those models, especially the STST and eSTST, focused more on the time course of encoding of information into memory, whereas RAGNAROC could be conceived as a spatial attention front-end to such models, replacing the simpler “blaster” mechanism that they employed. There has also been work on exploring the specific mechanism of how attention operates at the level of information processing, for example by showing that peripheral cues result in a combination of stimulus enhancement and noise reduction (Lu & Doshier 2000). The mechanism used here would be consistent with stimulus enhancement.

3.2 How it works

The focus of our modeling effort is to develop these ideas further, in close contact with a large body of empirical data, and also to extend the implications of such models to understanding the generators of attention-related ERPs. The RAGNAROC model simulates the consequences of attentional decisions rippling through the visual hierarchy, creating transient attractor dynamics that allow attention to lock-on (Tan & Wyble 2015; Callahan-Flintoft, Chen & Wyble 2018) to one or more locations. In this context, the term *lock-on* refers to a state in which top-down attentional enhancement at a given location amplifies feed-forward projections from stimuli at that same location to create a temporary attractor state that locks attention at a given location for a brief window of time. These lock-on states are similar in some respects to what was originally conceived of as *attentional engagement* (Posner REF), in that attention is strongly attached to the location of one (or more) stimuli through a combination of feedback dynamics. The model also simulates a natural process of disengagement from a given location due to the buildup of inhibition for sensory representations at attended locations.

RAGNAROC, a model of reflexive visual attention

Model outputs. The model simulates both the behavioral consequences of reflexive attentional deployment, measured in terms of accuracy and reaction time, while also simulating key ERP correlates of attention, such as the N2pc and the P_D components. ~~As a starting point, the model incorporates the convergent gradient field (CGF) model of Tan & Wyble (2015), which provided a partial explanation for reflexive attention with a focus on target enhancement and the N2pc component.~~

Stimulus Processing and Differentiation. In order to provide a theory of attention that can be applied to many different experimental contexts, we do not commit to the decoding of pixelwise representations. Instead, simulated neurons in each spatiotopic map represent the presence of attributes at locations with a granularity of 0.5 degrees of visual angle. These representations are segregated into distinct maps that are each specialized for particular kinds of stimuli, ~~as in an assumption that is common to other models~~ (Itti et al. (1998).

Localizing and attending important stimuli. ~~The RAGNAROC model~~RAGNAROC ~~is built with the assumption~~assumes that ~~attention must~~ n-essential function of the visual attention system is to determine the precise location of a to-be-attended stimulus from the coarse-grained location information carried by higher levels of the visual hierarchy (DiCarlo & Maunsell 2003), ~~and then deploy attention to the corresponding location. This is consistent with a broad range of findings as described above.~~ ~~We assume further that attention enhances the rate of processing of information at that location so as to enable the attended information to be encoded into memory more accurately and more rapidly. Such a model is consistent with findings that detection of a target facilitates the processing of a subsequent target at that same location (Wyble, Potter & Bowman 2009; Mounts 2000). This assumption is also consistent with the theory of biased competition (Chelazzi et al 1993) in which detection of a target allows neural responses from an attended stimulus to dominate responses from unattended stimuli.~~

The distinction between Targets and Distractors. RAGNAROC assumes that targets and distractors are distinguished based on differences in priority(defined below). ~~Another assumption of RAGNAROC is that most stimuli initially excite activity in the attention map because there is rarely a clear-cut distinction between targets and distractors for processes on the time-scale of reflexive attention. The attention map represents stimuli only in varying levels of attentional priority~~ (defined below), since a decision must be made to commit attention before

RAGNAROC, a model of reflexive visual attention

input from slower, more deliberate stimulus evaluations are completed. In this framework, targets (to the extent that the visual system perceives them as such) are successful at deploying attention because they elicit a more rapid priority signal at their location in the attention map. The decision process is, in effect, a race between competing representations, and the top-down attentional set plays a key role in helping task-relevant stimuli to win that race.

However, the outcome of this race-based decision process is not pre-ordained and the attention system is prone to deploying attention to highly salient distractors, ~~but task irrelevant distractors~~ on some fraction of trials. Thus, the model explains attentional capture experiments as a mixture of trial outcomes, which often exhibit successful deployment of attention to the target, but sometimes allow a distractor to win the competition. The variability in these outcomes is mediated by trial-to-trial variability.

Priority value. Each Stimulus in the visual field receives a priority value, which is a valuation of its ability to trigger the attentional system according to its likely importance according to a combination of physical salience, and top-down contributions from attentional set (Figure 3). Physical salience reflects the degree to which a given stimulus stands out from other nearby stimuli in terms of low-level features (e.g. color, orientation, luminance). Priority is also affected by the degree to which a stimulus matches the current attentional control settings, (Saenz, Buracas & Boynton 2002; Zhang & Luck 2009; Bundesen 1990 REF CHECK). These attentional control settings prioritize simple features like color, or more complex attributes such as conceptual categories (e.g. dinner food, animal, etc) by upweighting feedforward activity from some maps and downweighting feedforward processing from other maps. We assume that the ability to select certain stimulus attributes for task-relevant weighting is governed by pre-learned stimulus categories (e.g. contrasting letters vs. digits), but cannot easily be accomplished for arbitrary distinctions (e.g. select letters A, B, C from other letters). This follows from the work of Shiffrin & Schneider (1977) who demonstrated the ability to efficiently attend to previously learned categories, but not to arbitrary subsets of a category. Based on work suggesting that even conceptually defined target sets can be used to select information from RSVP (Potter 1976; Barnard, Scott, Taylor, May & Knightley 2004) or capture attention (Wyble, Folk & Potter 2013), it is assumed that prioritization can happen even at a conceptual level.

~~-~~Other potential contributions to priority that will not be considered here could involve whether stimulus attributes have been associated with reward (Anderson, Laurent & Yantis 2011), have

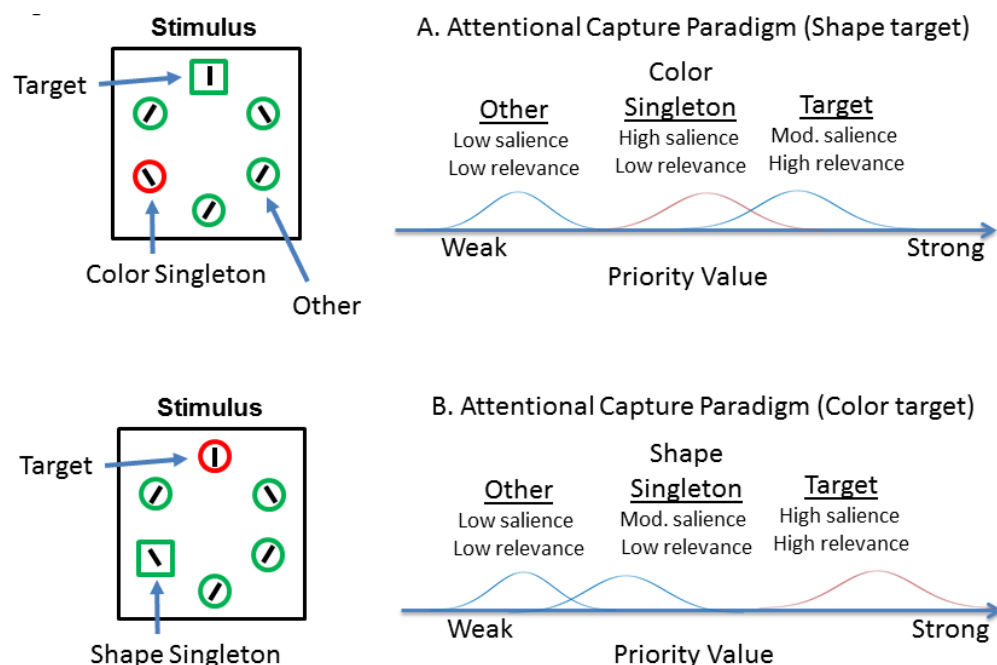


Figure 3. Illustration of how both intrinsic salience and top-down relevance cues can be mapped onto a single priority dimension. The figures illustrate canonical paradigms from attentional capture experiments. The top version of the paradigm uses a highly salient color singleton which results in priority values that are competitive with the less-salient target. When the target and distractor dimensions are switched, the shape singleton is not competitive with the color-singleton target.

been recently presented (Awh, Beloposky & Theeuwes 2012), were recently task relevant (Kadel, Feldmann-Wüstefeld & Schubö 2017) or are relatively novel in time (i.e. an oddball). Thus, a strength of the attention-map framework is to allow a broad variety of influences to affect how stimuli are prioritized.

Using Attentional control settings to prioritize targets: To help guide attention towards targets, it is assumed that attentional control settings prioritize certain stimuli as defined by the current task in a spatially nonselective manner (Saenz, Buracas & Boynton 2002; Zhang & Luck 2009; Bundesen 1990). These attentional control settings prioritize simple features like color, or more complex attributes such as conceptual categories (e.g. dinner food, animal, etc) by upweighting feedforward activity from some maps and downweighting feedforward processing from other maps. We assume that the ability to select certain stimulus attributes for task-relevant weighting is governed by pre-learned stimulus categories (e.g. contrasting letters vs. digits), but cannot easily be accomplished for arbitrary distinctions (e.g. select letters A, B, C from other letters). This follows from the work of Shiffrin & Schneider (1977) who demonstrated the ability to efficiently attend to previously learned categories, but not to arbitrary subsets of a category.

RAGNAROC, a model of reflexive visual attention

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3.2 RAGNAROC Architecture ~~of the model~~

3.2.1 A Hierarchy of Visual maps

The visual system is composed of a hierarchy of maps that each represent the visual field and are connected so as to preserve a spatiotopic organization that is rooted in a retinotopic representation at the earliest level (Figure 4). No claims about the number and complexity of this hierarchy are necessary here ~~as this is a model of general principals~~. Information propagates through the layers via feedforward excitation. The first layer of the model is termed Early Vision (EV) and simulates the earliest cortical regions in the visual hierarchy, which contains neurons with small receptive fields, such as V1. The second tier of layers is collectively termed Late Vision (maps LV1 and LV2) and contains neurons with larger receptive fields, corresponding to anatomical areas in the ventral visual stream that are thought to be specialized for different kinds of stimuli, such as V4 (color), FFA (faces), the EBA (body parts), the PPA (places), as well as distinctions between animate and inanimate stimuli, canonical size (Konkle & Carmazza 2013) and other distinctions that are as yet undiscovered. In our simulations, EV neurons have a simulated receptive field size of .5 degrees, while LV neurons have receptive fields of 3.5 degrees width.

The third layer of the model's hierarchy is the attention map (AM), which receives input from all of the subordinate LV maps⁷ and have the same diameter of receptive fields as LV neurons. Thus their receptive fields are extremely broad, because their input from the LV is already enlarged. The role of the AM is essentially to implement decision making across the visual field and to enact the consequences of that decision by sending modulatory projections down to the earliest level of the hierarchy. It does this by accumulating spatially imprecise activity from the subordinate LVs and then computing the spatiotopic location of the originating stimulus in the EV by summation. Convergent input from the LV maps initially forms an activation bump, centered at the location of each stimulus in the visual field. The correct localization of this bump

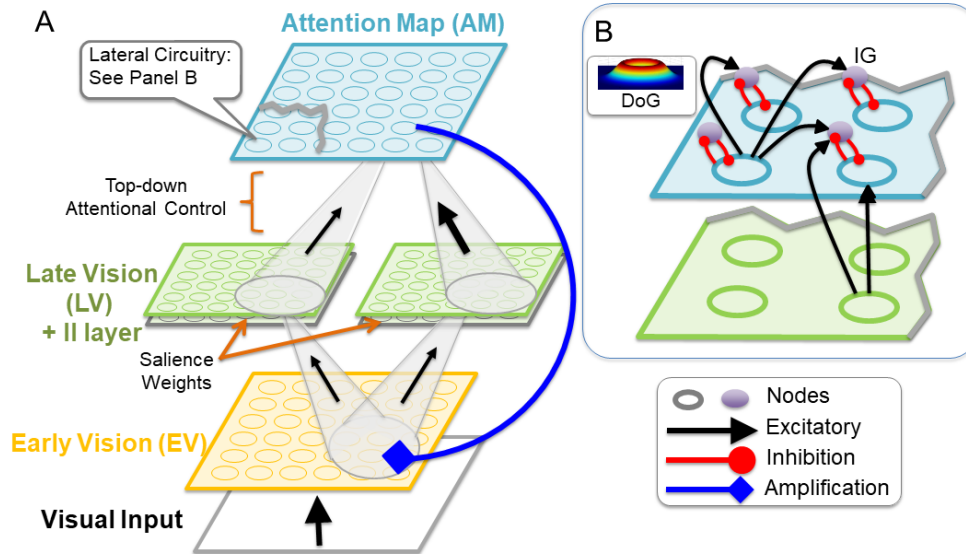


Figure 4. Illustration of the model's macro architecture (A) and the microcircuitry (B) of the attention map. In the hierarchy of visual areas, the cones reflect the set of neurons at a subordinate layer that excite a given neuron in the superordinate layer. Only two LV maps are shown here, but this architecture would generalize to additional levels. Differences in saliency are implemented as stimulus-specific differences in feed-forward excitation between EV and LV. Top-down selection is implemented as feature-specific weights for an entire LV map between LV and AM. The Attention Map returns a location-specific gain enhancement at a given location in the EV. The grey II layer represents feedback inhibition for each LV node. The inset in B shows how neurons are interconnected within the AM. The small grey circles are Inhibitory Gating (IG) neurons, each of which has a competitive inhibitory relationship with a principle neuron of the AM. The principle neurons excite one another with a spatial distribution defined by a Difference of Gaussians (DoG). This connection corresponds to the black curved arrows in panel B.

⁷ Direct projections from the EV to the AM could exist but they are not represented here for simplicity.

RAGNAROC, a model of reflexive visual attention

follows naturally from the activation dynamics of the model since the AM neuron that resides at the corresponding topographic locus of the centroid of LV activity will receive the largest amount of input from the LV.

When AM neurons are stimulated above threshold, a multiplicative attentional enhancement is applied to all neurons in the EV at the corresponding spatiotopic location. This modulation increases the strength of the feedforward input from that region of the visual field, which in turn increases the excitatory input to the AM. This dynamic creates a brief attractor state, in which the activated peak in the attention map is amplifying its own input. This condition we term a *lock-on* state and allows a precise, stable localization of attention despite the relatively coarse-grained spatiotopy in the receptive field of the neurons. Furthermore, the activated AM neuron inhibits other surrounding neurons in the AM, which narrows the spatial focus of the lock-on state.

Thus, the attention map integrates information from the subordinate feature maps to localize one or more targets and then projects an enhancement signal back down to earlier areas at the appropriate location(s). There have been a number of proposals for where such an AM might reside in the brain, including frontal cortex, parietal cortex and portions of the pulvinar nucleus (Shipp 2004). We note that a lateral, parietal location would be broadly consistent with the scalp topography of attention-related ERPs, which are typically larger above parietal cortex than directly over occipital, central or frontal areas (e.g. Tan, Wyble 2015). It is also possible that this functionality is distributed over several cortical areas, although that would come at the expense of intracortical white matter to mediate the competition.

3.2.2 Attentional gating circuitry

One of the key innovations in this model is the inhibitory control circuitry within the AM (the IG nodes in Figure 4B), which has been developed according to key findings in the literature. It allows attention to rapidly focus at a location, selectively inhibiting regions of the visual field that contain other visual stimuli. Moreover, the disinhibitory component of the circuit permits attention to be simultaneously focused at multiple locations when the stimuli are of similar priority.

To ensure that attention is **primarily** inhibited at regions of the visual field that contain stimuli (Gaspelin et al 2015; Cepeda et al. 1998), gating circuits (the IG neurons in Figure 4b) ensure

RAGNAROC, a model of reflexive visual attention

that inhibition is only delivered to neurons receiving excitatory input from the visual field. Each IG neuron is paired with one principal neuron in the AM. An IG only becomes activated when it receives lateral excitation from another AM neuron (i.e. the curved arrows at the top of Figure 4B) and concurrent excitation from any LV neuron at its own spatial location (i.e. the rising arrow from LV to AM in Figure 4B). As a consequence, only AM neurons that are receiving feedforward excitation from the LV can be inhibited by another neuron in the AM. This prevents the AM from inhibiting locations of the visual field that are empty, matching behavioral data regarding the suppression of attention (Cepeda et al. 1998; Gaspelin et al. 2015).

The disinhibitory component of this gating circuit acts to increase the stability of lock on states, such that once a decision to attend to a given location is reached, it is less likely that other stimuli will cause it to disengage. Each strongly active AM neuron inhibits its own IG neuron, a form of competitive inhibition that has been determined to have a similar stabilizing function in well-charted nervous systems such as the drosophila larva (Jovanic et al. 2016). With this circuit, multiple neurons in the AM can remain active, since they protect themselves from the inhibition generated by the other active AM neurons.

3.2.3 Free and fixed parameters

The model uses predominantly fixed-parameters according to a set of empirical constraints, which are listed below in section 4. These parameter values are invariant for all of the simulations provided below, except for a subset that vary in order to implement the experimental paradigm of each simulation (e.g. Timing and location). There are also two partially-fixed parameters that specify the physical salience and task-relevance (i.e. bottom-up and top-down) weightings of each stimulus type. The term partially-fixed reflects the fact that their relative values are determined by the experimental paradigms. E.g. in simulations of the additional-singleton paradigm (Theeuwes 1991), we allow the specific value of the distractor's salience to vary, but it has to remain higher than the salience of the target. Finally, there is one additional free parameter that defines the accumulator threshold for a behavioral response for each experiment. This parameter is constrained to have a single value for all conditions of a given experiment and prevents behavioral accuracy values from being at ceiling or floor. The specific values of all parameters will be provided for each simulation in the appendix.

3.3 Mechanisms of the model:

3.3.1 Equations

RAGNAROC, a model of reflexive visual attention

The model uses rate-coded neurons, governed by the activation equations of O'Reilly & Munakata (2001) as shown in the Appendix. In these equations the activation level of each neuron is governed by three currents: excitatory, inhibitory and leak. This level of abstraction is a compromise that captures the properties of neuronal synaptic interactions in broad strokes, while allowing rapid exploration of different model architectures. Moreover, the distinction between excitatory and inhibitory currents provides a mapping to current flows underlying EEG components. This set of equations has been used effectively in previous simulations of attentional processes at similar time scales (e.g. Bowman & Wyble 2007)

Each connection within the model is enumerated in Figure 5 and properties are described below. For simplicity, all maps have the same dimensionality and number of stages. Furthermore only two pathways are simulated here. The mechanisms used here generalize to more complex architectures with more layers and more pathways. All connections between or within layers are assumed to have either an identity projection (i.e. strictly topographic), a Gaussian spread, or a Difference of Gaussians (DoG).

The following numbers indicate connections specified in Figure 5.

1. Input to EV neurons: The EV represents the earliest stage of cortical visual processing in which neurons have extremely small receptive fields and color/orientation/frequency specific firing preferences. For the sake of simplicity, EV nodes are separated into different areas according to the kinds of stimuli presented, although in the brain these different neurons occupy the same cortical map. Input to a specific EV node is specified as a step function, since the simulations are of suprathreshold stimuli (i.e. a value changing from 0 to 1 while the stimulus is visible), which causes the corresponding EV node's membrane potential (MP) to charge up according to equations 1.1, 1.2 and 1.3, see appendix.

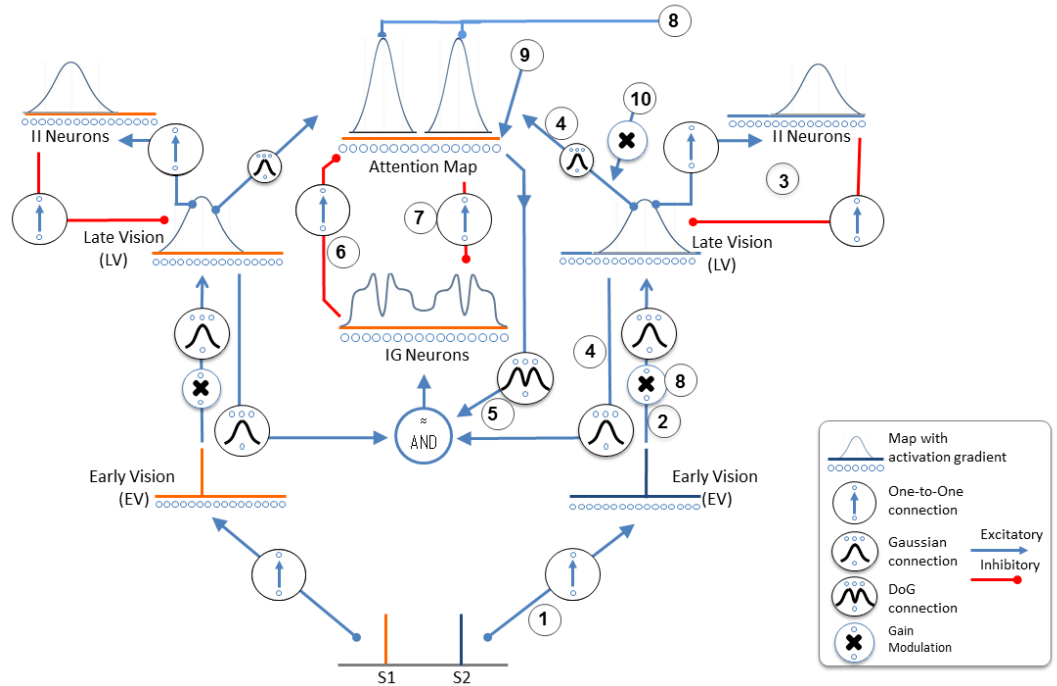


Figure 5. Illustration of the complete architecture for two distinct pathways during perception of two objects with highly distinct dimensions (e.g. form vs color). The left and the right side represent the same connections but for different stimuli. The bubbles indicate the spatial distribution and character of each connection. The traces above each layer illustrate a typical activation profile for that map in response to a stimulus. Note that attention affects both pathways, regardless of which stimulus triggered it. The numbers correspond to descriptors in the text.

2. Projection from EV to LV: When an EV node's membrane potential crosses threshold, it sends a feedforward excitation to an array of nodes in the corresponding LV maps. This projection is spatially weighted according to a Gaussian centered at the location of that EV node. The magnitude of this projection is the salience of the stimulus, and indicates its physical dissimilarity to other stimuli in the visual field according to the specific LV it projects to (e.g. a shape singleton would have a high salience in an LV map that is specific for form). Other accounts have shown how to compute salience for some classes of features such as color, orientation and luminance (Zelinsky 2008; Itti et al. 1998; Bruce & Tsotsos 2006). In RAGNAROC, we abstract over the process of computing salience to accommodate the broad diversity of tasks. [Computing LV activation corresponds to equations 1.4-1.6 in the appendix.](#)

3. Inhibitory feedback nodes in the LV: Each LV node has a dedicated inhibitory interneuron (labelled II), that provides feedback inhibition. This inhibitory feedback is crucial for emphasizing the onset of new information by causing the activity of any given LV neuron to drop after approximately 100ms, which is characteristic of single units in the visual system (e.g. Fig 9 of Chelazzi, Duncan, Miller & Desimone 1998). [Moreover, these II neurons cause attention to naturally disengage from a stimulus that remains constant on the retinal field. Computing II activation corresponds to equations 1.8 to 1.10 in the appendix.](#)
4. Projection from LV to AM: When an LV node crosses threshold, it projects feedforward excitation to an array of nodes in the AM according to a Gaussian profile centered at the location of the active LV node. LV nodes also excite IG nodes (see below) with the same Gaussian profile. The projections to both the AM and IG nodes include a parameter that represents the task-relevance (i.e. "top-down") weighting of each stimulus type, and is fixed for each LV map. [\(e.g. to represent an attentional set for a specific color, all LV nodes for that color have an increased feedforward strength to the AM\). Computing AM activation corresponds to equations 1.11 to 1.14 in the appendix.](#)
- 4.
5. Inhibitory Gating Nodes (IG): The IG nodes ensure that inhibition with the attention map only occurs at locations receiving input from an LV (see also Beuth & Hamker 2015). Each IG node is paired with a single AM node that it can inhibit. An IG node is excited by neighboring AM nodes according to a Difference Of Gaussians (DoG) activation profile. IG nodes are also excited by LV nodes. The total excitation of each IG node from these two sources (AM and LV) is capped such that concurrent AM and LV activity is required to raise an IG node above threshold. Thus, IG neurons exhibit the equivalent of a logical AND gate in that they require concurrent activation from two pathways in order to fire. [Computing AM activation corresponds to equations 1.16 to 1.21 in the appendix.](#)
6. IG inhibiting the Attention Map: When activated by convergent AM and LV input, an IG node inhibits its corresponding AM node. This is the basis of inhibitory

suppression of attention within the model [and corresponds to equation 1.12 in the appendix.](#)

7. Attention Map inhibiting IG: The inhibition from AM->IG has a high threshold of activation, so that once a lock-on state has formed at a given location, the corresponding AM node protects itself from inhibition. This disinhibitory circuit increases the stability of an AM lock-on state, since AM neurons can protect themselves from inhibition generated by neighboring AM nodes. [This inhibition corresponds to equation 1.19 in the appendix.](#)
8. Attentional Enhancement: Each AM node provides a gain modulation of synaptic transmission from EV to LV for all EV nodes at the same location. Note that enhancement of a given location in the EV occurs for the entire Gaussian spread of an EV neuron's feedforward projection, unselectively across all feedforward pathways. It is this modulation that creates the “lock-on” attractor between EV and AM since it allows an AM node to increase the gain on its own input. [This enhancement corresponds to equations 1.4 and 1.15 in the appendix.](#)
9. AM excitatory Bias: There is a uniform level of bias input to the entire AM, keeping these neurons slightly active in the absence of input. [This enhancement corresponds to equation 1.11 in the appendix.](#)
10. Noise input: Intertrial variability is added to the model as modulations of the weights between the LV and AM, which represents fluctuations in attentional control. The variability is constant for a given trial and varies between trials as samples from a Gaussian distribution. [REF](#)

3.4 Example Simulations

The following examples illustrate the model's dynamics in response to several stimulus scenarios.

3.4.1 The simplest case: Single stimulus

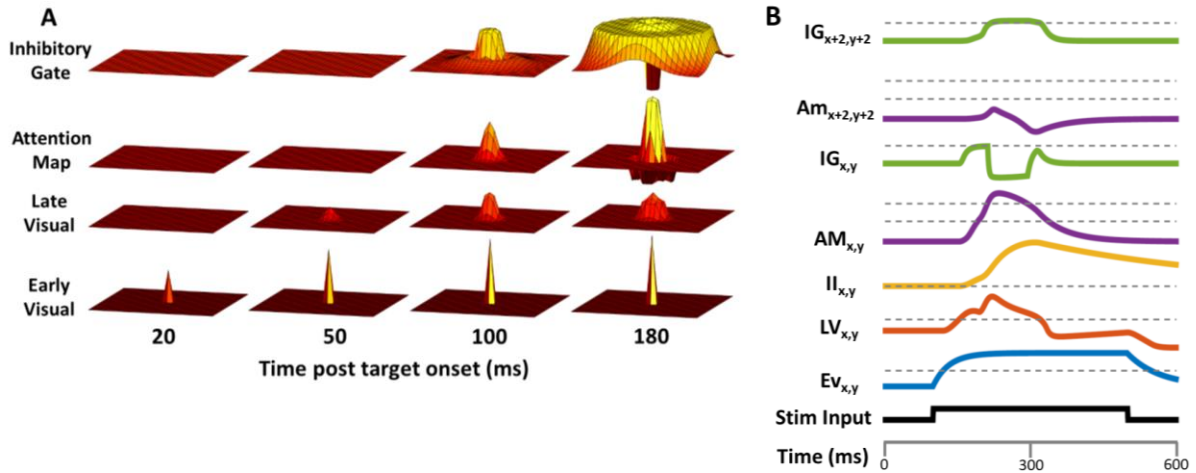


Figure 6. A. Evolution of a lock-on state across time and layers for a single stimulus. An initial feedforward wave of excitation from a single location in the EV triggers activation in the LV, which carries forward to a peak in the AM. Once the central peak of the AM activation crosses threshold, the surrounding IG neurons are activated producing surrounding inhibition in the AM. B. Illustration of the time course of activation for each kind of node within the model in response to a stimulus. Subscripts x,y indicate the location of the stimulus while $x+2,y+2$ indicate nodes at a neighboring location.

Notable inflection points are when the $AM_{x,y}$ node crosses its lower threshold, which triggers enhancement of the LV activation. This drives the $AM_{x,y}$ node more strongly such that it passes its second threshold, allowing it to suppress the $IG_{x,y}$ node. At this point attention is fully locked on to location x,y , since processing is enhanced at that location, and the IG has been inhibited.

When a single stimulus of sufficient priority is presented to the EV, it triggers a *lock-on* of attention at its spatiotopic location, which is a self-excitatory attractor state resonating between EV and the AM through the LV. Figure 6a illustrates the impulse response function in the AM elicited by a single stimulus. Figure 6b illustrates the time course of activation of each of the layers of the model centered at the location of the stimulus.

3.4.2 Transition to the lock-on state

We demonstrate that the lock-on state has the characteristics of an attractor by illustrating that a broad range of stimulus values evoke a bump in the AM of similar size and duration (Figure 7a). The rapid growth of this neuron's activation is due to the attentional enhancement of feedforward activity from the EV after the corresponding node in the AM crosses the threshold value. The decrease in peak amplitude is a result of the drop in LV activity due to feedback inhibition from II.

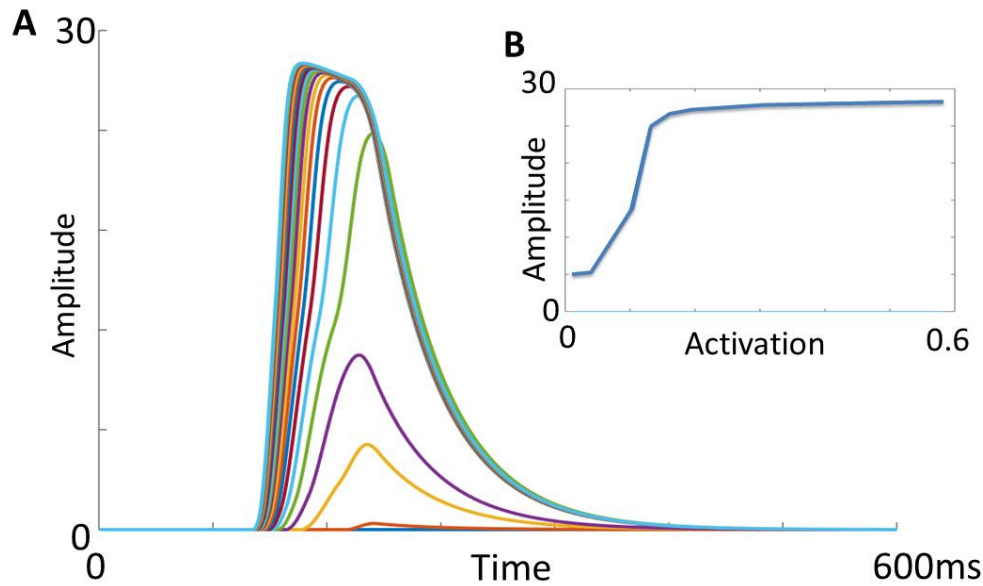


Figure 7: Illustration of the time course of activation of a neuron in the AM centered at the location of a stimulus for varying amounts of activation strength of a stimulus from .01 to .6 in increments of .03. The inset plots peak amplitude as a function of activation strength. The takeaway point is that a lock-on state is an attractor, such that many different values of strength map onto the same amplitude of activation.

3.4.3 Two stimuli

Figure 8 depicts a comparison of AM activity for either one(A) or two stimuli(B,C). In the case of two stimuli, if one of them is of substantially higher priority, it will inhibit the AM at the location of the other (B). However if both stimuli are of very similar priority and nearly simultaneous, the two of them will always enter lock-on states simultaneously leading to a fully parallel deployment of attention (C). In such a case, each AM inhibits its paired IG (not shown in this figure), and the two lock-on states protect themselves from inhibition by the other.

3.4.4 Sequential stimuli

When stimuli onset sequentially, the first stimulus will typically be able to activate its Lock-on state and suppress activity of the second. In this way, a first target (T1) with a relatively low priority value can suppress attention to a second target (T2) since the temporal advantage of T1 allows it to establish a lock on state before the T2 has a chance.

3.5 Competitive Inhibition helps to stabilize attentional focus

The competitive inhibition between AM and IG neurons was developed to meet empirical benchmarks and this particular case highlights a virtue of modelling biological systems, which is

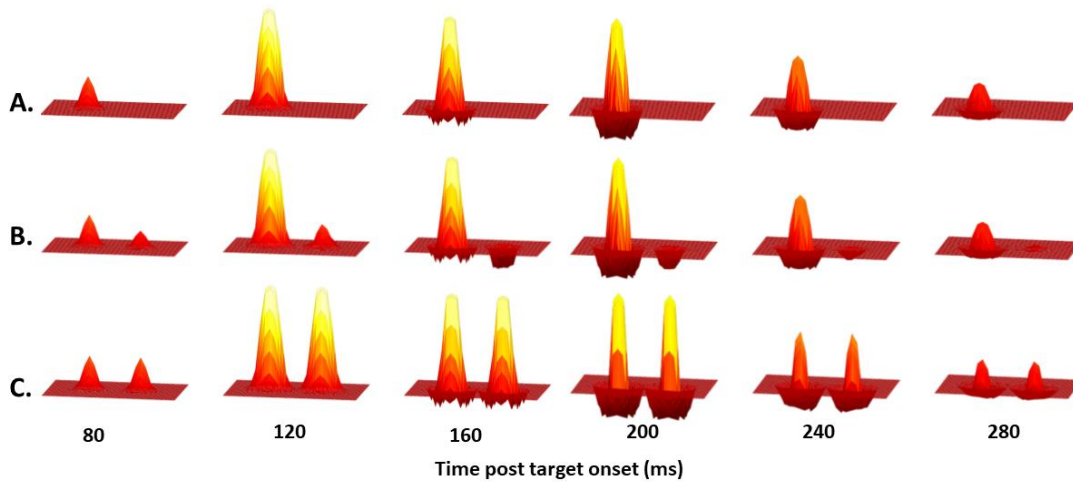


Figure 8. Evolution of activity in the attention map over time for a single stimulus (A), and the same stimulus accompanied by a stimulus of lower priority (B). In the case where two stimuli have equal priority (C), attention is recruited at both locations.

the ability to understand the value of particular mechanisms. RAGNAROC gives us the tools to understand that competitive inhibition improves the functionality of attention by increasing the stability of one or more lock-on states, allowing attention to be simultaneously deployed more easily, in accord with empirical findings such as Bay & Wyble (2014) and Goodbourn & Holcombe (2015). To illustrate the effect of competitive inhibition on the attentional state, Figure 9 compares the intact model (bottom two panels) to one in which the AM->IG inhibition has been removed (top two panels). This change preserves the center-surround inhibition, and the selective inhibition but does not allow AM nodes to competitively block their own inhibition. The figure illustrates how the duration of lock-on states for two temporally proximal stimuli is compromised without the inhibition.

With the inhibition intact (bottom two panels), it is much easier for simultaneously (or nearly so) stimuli to evoke robust lock-on states because each protects itself from such interference. However within about 50ms, the window of attentional simultaneity has expired because the T1 lock-on starts to inhibit nearby activity in the AM. This makes it difficult for T2 to establish its own lock-on state if it onsets between 50 and 100ms after the T1. The time course of this transition from simultaneous to sequential attention is in agreement with behavioral data showing the onset of attentional inhibition following a T1 onset (Mounts 2000, Experiment 2). The advantage of protecting the lock-on state of the T1 at the expense of the T2 is to reduce the volatility of attentional decisions in the case of dynamic or rapidly changing stimuli.

RAGNAROC, a model of reflexive visual attention

In contrast, when the competitive inhibition is removed (top two panels), the AM activations evoked by two stimuli always compete against one another, such that only T1 or T2 can be fully attended even when the stimuli onset simultaneously.

3.6 Mapping model activity onto measurable data

In order to compare the model against empirical benchmarks, it is necessary to map model activity to behavioral measures of accuracy and reaction time, as well as EEG correlates of attention such as the N2pc and P_D. Figure 10 illustrates which activity states in the RAGNAROC model are used for generating data.

3.6.1 Model configuration

For each experiment, physical salience values and task-relevance weightings are configured for different kinds of stimuli in the task. To provide variability, task-relevance weightings are varied at random over repeated simulations, while the physical salience values remain fixed. Task-relevance weights are initially varied according to a uniform distribution of possible values for each kind of stimulus in the task. For example in a salient-singleton attentional capture paradigm (Theeuwes 1992), the target stimulus has a physical salience value of .15 and a range of task-relevance weightings from .17 to .37 in 12 steps of .018. The singleton distractor has a physical salience of .3 and a range of relevance weightings from .07 to .27 in 12 steps of .018. The model is run for all possible combinations of these weightings, (e.g. 144 total simulations in this example). The simulations are then bootstrapped to form the simulated data set of an entire experiment. The bootstrap involves resampling 10,000 times according to a normal distribution (with mean centered at the median attention weight and a standard deviation of .75) under the

assumption that there is trial to trial variability in the attentional set of the observers that is normally distributed. For this bootstrapping, the normal distribution is mapped onto the bins of the uniformly distributed task-relevance weightings over a range of ± 3 standard deviations. This bootstrapping determines both the simulated behavior (accuracy and RT, as appropriate) and the EEG traces for a given experiment. This is the only source of variability in the model when simulating EEG. For simulations of behavior, an additional source of noise is added during the bootstrapping, as described below.

3.6.2 Simulating Behavior

RAGNAROC simulates the successful detection or response to a target with a thresholded accumulator. The accumulator sums the time course of activation of all LV neurons that are activated over baseline (.5)

for the target. For every trial, the area under the curve (AUC) is calculated for the entire time course of activation. A trial is considered accurate if this AUC exceeds a threshold value that is calibrated for each task, but is not allowed to vary for different conditions within a task. This threshold is a free parameter fit for a given task to achieve a particular accuracy value in one baseline condition chosen for each task. In order to introduce more variability and make

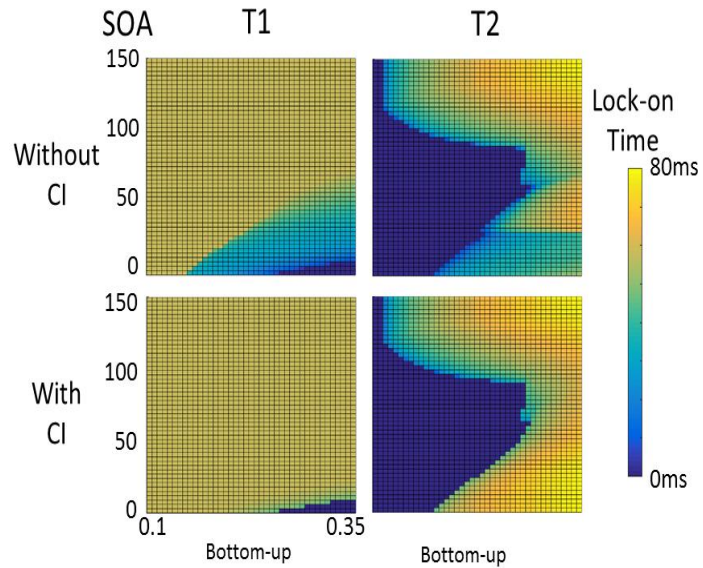


Figure 9 Illustration of the robustness of lock on states to each of two stimuli where the second stimulus varies in the strength of bottom-up strength value of the T2 (horizontal axis) and temporal latency (vertical axis). Each point represents the total duration for which the AM neuron at the location of the stimulus (T1 or T2) is above threshold. The key takeaway is that without competitive inhibition (CI), T1 and T2 compete destructively at short SOAs such that neither elicits a robust lock-on state. With inhibition intact, both stimuli can achieve a lock-on state if presented with nearly identical onsets. However at longer SOAs T1 suppresses T2 enforcing a serialized deployment of attention. In this simulation, T1 and T2 were presented 4 degrees apart and have a duration of 120ms. Note that the T1 bottom-up weighting is fixed for all simulations and only the T2 weighting is varied. The distinction between T1 and T2 becomes notional when they are simultaneous.

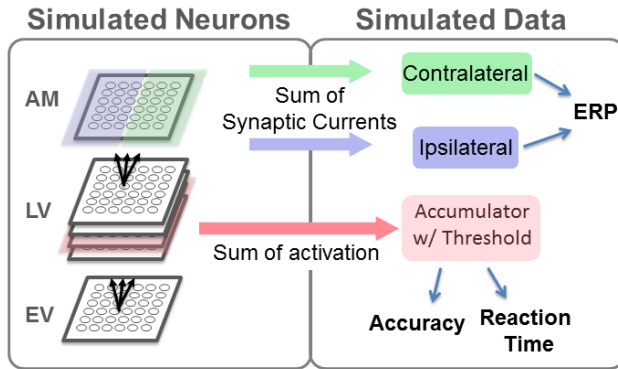


Figure 10 Activity within the RAGNAROC model is used to construct simulations of data in the form of behavioral accuracy, behavioral reaction time and EEG components. Behavioral data are extracted from the late vision area, which is assumed to drive the formation of memory representations and response decisions through mechanisms that are outside of the scope of the model. Simultaneously, synaptic currents within the attention map are measured to generate simulated ERPs such as the N2pc and the PD.

simulations less sensitive to the particular threshold value, each simulated trial is jittered with random noise. This is done by adding 15% of the baseline condition's average AUC times a random scalar (ranging from 0 to 1 from a uniform distribution) for each trial. Reaction times are calculated as the time step at which the accumulator crossed threshold.

3.6.3 Simulating EEG

To translate from simulated neurons to EEG correlates is a hard problem that, in its most

exact form, would require compartmental-level modeling of cortical neurons including all of the synapses in each layer, a fairly complete understanding of the neuroanatomy for each individual subject, and a model of the electrical properties of the tissue layers above the cortex (dura, fluid, skull, muscle, skin).

However, it is possible to make effective progress with a much simpler model, given some starting assumptions to simplify the forward model for generating scalp potentials. Here, these assumptions are (1) that the attention map exists over a region of cortex situated in posterior-lateral parietal areas of cortex (2) that EEG potentials are largely driven by excitatory synaptic input on pyramidal neurons oriented perpendicular to the scalp (Nunez & Cutillo 1995) (3) that an increase in this synaptic current within the attention map produces (on average) a negative voltage at the scalp and (4) An additional weighting parameter that determines the relative contribution of excitatory and inhibitory synaptic currents for all simulations. The advantage of such a simple model is that it provides fewer opportunities to overfit the observed EEG.

Given these assumptions, RAGNAROC simulates lateralized EEG components associated with attention by summing synaptic currents across each half of the AM, and taking the difference of

RAGNAROC, a model of reflexive visual attention

those sums relative to the side of the visual field that a particular stimulus was presented on. This is analogous to the measure of potentials such as the N2pc and P_D, which are calculated as the difference in voltage between electrodes contralateral and ipsilateral to the side of the display containing a target (or a distractor in some cases).

The synaptic currents are computed separately for each neuron as its excitatory current, minus its inhibitory current, with a floor of zero. The intuition behind this implementation is that excitatory currents are the primary drivers of the large dipoles that are observable at the scalp, and inhibitory inputs often shunt those excitatory currents by creating high conductance areas of the cell membrane closer to the soma (Koch, Douglas & Wehmeier 1990)

The AM receives a uniform input to elevate all of the neurons above their resting potential. This provides a baseline level of excitatory current that is uniformly distributed across the attention map and therefore drops out during the subtraction of ipsilateral from contralateral. Activation or inhibition of nodes within the AM causes deviation away from this baseline level of current. When this current is summed across the halves of the attention map, laterally asymmetric differences in activation produce changes that are comparable to the N2pc and P_D components⁸. Note that using the sum of currents across a hemifield to simulate voltage means that increases in current for some neurons might be effectively invisible to the simulated EEG signal if there

⁸ For the sake of simplicity, we assume here that there is a constant level of resistance across the AM, such that voltage is directly proportional to current.

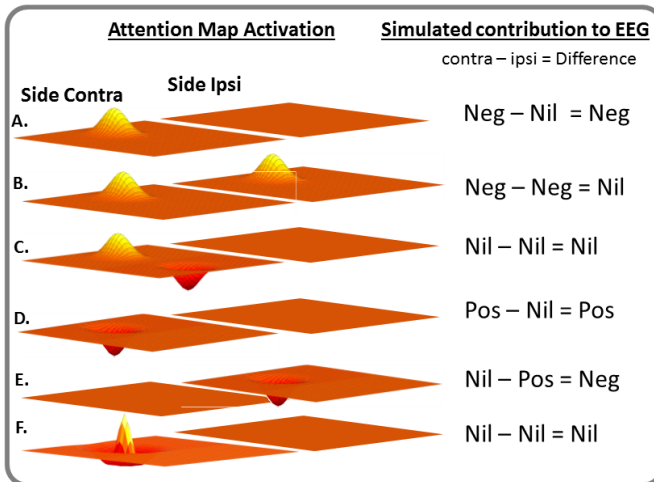


Figure 11 Illustration of how different patterns of activity on ipsi and contralateral sides of simulated cortex can summate to produce either positive, negative or nil voltage differentials. Note that in F, the currents generated by the activity in the peak is effectively cancelled out by the surrounding inhibitory surround producing an effective Nil in the contralateral side. Note that “Nil” in this context doesn’t necessarily mean exactly 0, but sufficiently small that it is not detectable at a given level of experimental power.

are also corresponding decreases in current for other neurons in the same half of the attention map (Figure 11). Furthermore, any negativity in the simulated voltage difference between the contralateral and ipsilateral sides of the map could be caused either by an increase in activity in the contralateral side, or a decrease in activity on the ipsilateral side. It is important to remember that there are only two possible polarities of a component, positive or negative, but there are (many!) more than two neural processes that could result in a scalp potential at a given latency. Therefore one cannot uniquely ascribe a given functional property to an ERP on the basis of a given polarity/latency.

This ambiguity in the interpretation of simulated EEGs is not a shortcoming of the model, but rather reveals a complication inherent in the interpretation of all ERPs. This complication underscores the importance of understanding EEG signals at the level of their neural sources and the role of computational models in understanding those sources.

3.6.4 Simulation of the N2pc

In RAGNAROC, any lateralized stimulus that has the highest priority produces a simulated ERP that resembles an N2pc (Figure 12a). The onset and peak of the N2pc is caused by the initial activation bump in the AM. When the lock-on state is established, the AM activates its neighboring IG neurons, which adds an inhibitory region in the immediate surround. When the central peak is surrounded by inhibition, the sum total of synaptic currents on the contralateral side of the AM nearly cancel out and sometimes even reverse briefly producing a positivity. Thus, while RAGNAROC is in general agreement with the theory that the N2pc reflects

processes associated with spatial attention, it suggests a more specific temporal relationship, which is that the N2pc reflects, in large part, the processes of localizing a target prior to attentional deployment, as in the CGF model (Tan & Wyble 2015).

Thus, the model explains that the end of the N2pc does not indicate the end of attention, but rather the onset of surround suppression. This simulation provides a straightforward explanation for the brief duration of the N2pc, which is typically brief and followed by a positive swing (Brisson & Jolicouer 2006)

3.6.5 Simulation of the P_D

The P_D is an EEG component thought to reflect inhibition of distracting information in the visual field. In RAGNAROC, a P_D can emerge whenever there is sufficient inhibition of activity in the attention map and this occurs in at least two ways. First, whenever two stimuli compete for attentional control and one of them loses, the AM is suppressed at the location of the loser (Figure 12b). This suppression reduces synaptic currents in the hemifield containing that stimulus and results in a net positivity in contralateral scalp electrodes. However, a P_D also occurs when the surround suppression encircling an attended stimulus is large enough that it causes a net reduction in current for that half of the visual field. This imbalance would be reflected as a P_D trailing an N2pc, and could occur even in the absence of a suppressed distractor (Figure 12a, see also Töllner, Zehetleitner, Gramann, & Müller 2011).

These are the essential aspects of simulating behavioral effects as well as lateralized EEG components in the early time range following the onset of a stimulus array. In the next section we illustrate how specific empirical effects emerge in specific experimental contexts through these mechanisms.

4. Simulations of Empirical Constraints

4.1. Constraints in model development

As in previous papers (Tan & Wyble 2015; Swan & Wyble 2014), the model is parameterized according to a set of extant findings in the literature. Once the model is able to simultaneously accommodate those findings with one set of fixed parameters, it can be used to generate insights about the underlying system and testable predictions for future work. The philosophy of this approach is to allow a large number of empirical constraints to inform the model's design, with as little parametric flexibility as possible. Here we list a series of behavioral and electrophysiological findings that we consider to be crucial for defining the functionality of

RAGNAROC, a model of reflexive visual attention

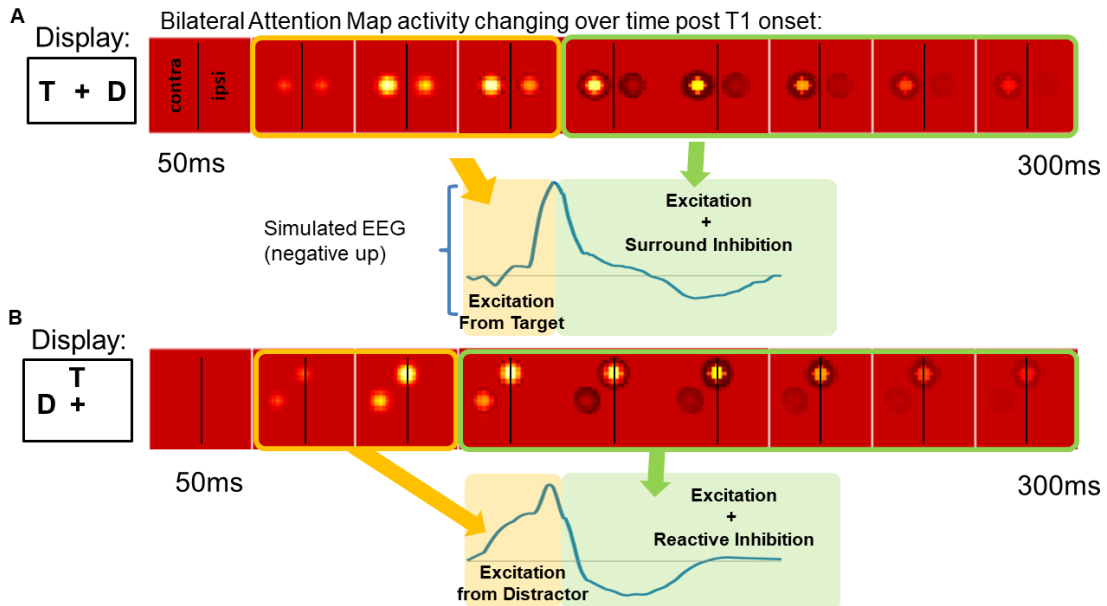


Figure 12 Illustration of how activation levels within the attention map produce simulations of N2pc and Pd components for commonly used experimental paradigms. Note that this is not intended to predict that distractors always elicit an N2pc. .

reflexive attention. Each of these findings is simulated with the same set of parameters, except for the configural parameters described in 3.2.3. The supplemental describes the exact set of parameters for each simulation. Given the large diversity of experimental paradigms that provide the constraints, the fits to the existing data are evaluated for their qualitative similarity to the data.

4.2 Behavioral constraints:

1. Covert spatial attention is triggered rapidly in response to a target or highly salient stimulus. This effect is measurable as an enhancement of accuracy and reduced reaction time for stimuli presented just after a cue, at that same location. The time course of this enhancement peaks at about 100ms SOA (Nakayama & Mackeben 1989). Note that this transient form of attention is short lived even when the cue stays on the screen. It is difficult to precisely estimate the duration of this effect because it is followed by slower, more volitional forms of attention that sustains the attentional effect to differing degrees in differing paradigms. However, there have been consistent findings of enhanced perception at brief cue-target (Yeshurun & Carrasco 1999; Müller & Rabbitt 1989; Cheal & Lyon 1991) or target-target intervals that attenuate at longer cue-target intervals. Targets elicit such attention as well (Wyble, Potter, Bowman 2009). RAGNAROC simulates the transient attention effect of Nakayama and Mackeben (1989) as a

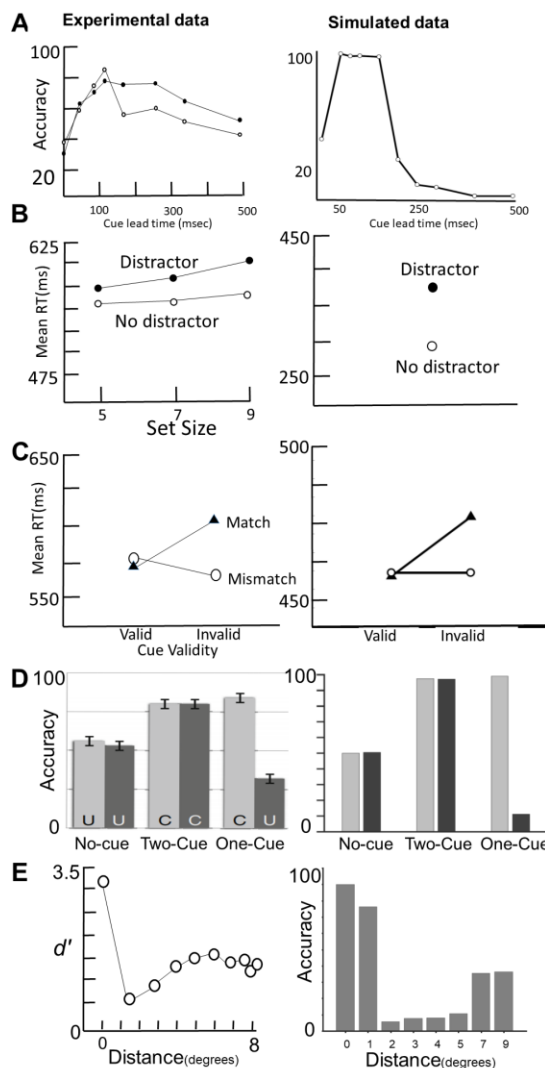


Figure 13 Behavioral constraints and simulations. (a) Accuracy of reporting a target indicates the transient nature of reflexive attention (N = 2, Nakayama & Mackeben 1987). (b) Reaction time to report a shape singleton target is increased in the presence of a salient color distractor (Experiment 3 from Theeuwes 1992). (c) A singleton affects the reaction time to report a target only if it matches the type of target (Folk Remington & Johnston 1992; Experiment 3). (d) The benefit of a valid cue, relative to a no-cue condition, is not diminished when two cues are used, suggesting simultaneous deployment of attention to two locations with minimal cost (Bay & Wyble 2014). (e) Accuracy of reporting a second target is affected by proximity to a preceding target with a spatial gradient (Mounts 2000). Note that the empirical data is reported as d' , but model accuracy is reported as accuracy since it lacks a mechanism for guessing.

brief window of elevated accuracy in reporting a target when it follows another stimulus at the

RAGNAROC, a model of reflexive visual attention

same location because the second stimulus benefits from the lingering lock-on state created by the first stimulus. (Figure 13a, the two traces in the data plot indicate different subjects)

2. This rapid deployment of attention is reflexive, which means that it is vulnerable to capture by a non-target stimulus that is either highly salient (Theeuwes 1992) or contains a target-defining attribute (Remington, Folk & Johnston 1992). This reflexive form of attention occurs even to locations that are known to always be task irrelevant (Lamy, Leber & Egeth 2004; Krose & Julesz 1989). Also, highly-salient distractors will trigger this form of attention regardless of instruction, or lengthy practice sessions (Theeuwes 1992; [but see Kim & Cave 1999 for a counter example](#)). RAGNAROC simulates the attentional capture effect of Theeuwes (1992) as a longer reaction time for a target in the presence of a distractor (Figure 13b). See the discussion section for an in depth discussion of precisely what causes the slower RTs in a capture paradigm.

3. Attention can be biased towards stimuli containing certain features or attributes, provided that there exist well-learned, cognitively accessible distinctions between target-defining features and other stimuli (e.g. letters can be selected among digits but an arbitrary subset of letters cannot be efficiently selected from other letters without substantial training, Schneider & Shiffrin 1977). This target-defining attentional set is implemented across the entire visual field such that, for example, establishing a control setting for red at one location prioritizes red at all locations (Zhang & Luck 2009). RAGNAROC simulates attentional set as capture costs that are mediated by task-set from Folk, Remington & Johnston (1992). See Figure 13c.

4. Attention can be deployed to two or more locations at the same time when stimuli are presented in parallel, but behaves more like a spotlight when targets are presented sequentially (Bichot et al. 1999; Dubois Hamker & VanRullen 2009; Bay & Wyble 2014). RAGNAROC simulates divided attention as an attentional benefit that is similar in size regardless of whether one or two locations are cued (Bay & Wyble 2014). See Figure 13d.

5. Presenting a cue or target at one location causes subsequent targets presented at spatially proximal locations to be harder to perceive. This suppression is diminished with increasing spatial distance (Mounts 2000; Dubois et al. 2009). RAGNAROC simulates attentional suppression surrounding an attended region using two sequential targets as in Mounts (2000). See Figure 13e.

6. In the presence of a target, inhibition is localized at the spatiotopic location of non-target stimuli, in comparison to empty locations in the visual field. Thus, probe stimuli will be harder to perceive when they occur in the locations of singleton distractors in comparison with blank areas (Cepeda et al. 1998) or non-singleton distractors (Gaspelin, et al. 2015; Figure 2c). Moreover, this effect is dependent on the attentional set of the subject. It is present only when targets are defined by specific features, rather than by being a form singleton. RAGNAROC simulates increased suppression of attention at locations containing salient distractors when the top-down weightings from LV->AM are strongly biased towards for the target are increased the target (Figure 14 bottom two panels). When these weightings are weaker, the reverse pattern is obtained such that salient distractors evoke attentional enhancement rather than suppression (Figure 14, top two panels).

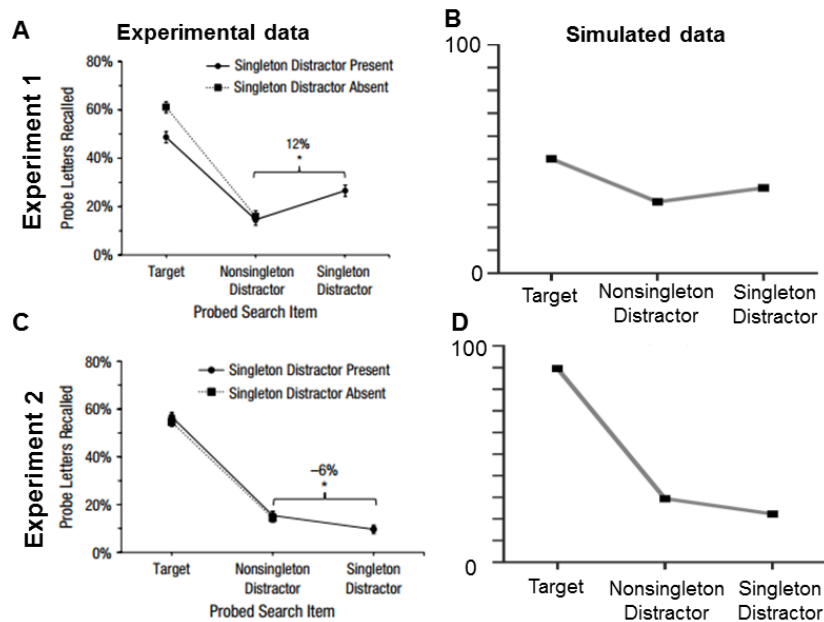


Figure 14 Experimental data from Gaspelin, Leonard & Luck (2015) alongside simulations. In panel A the data are from a condition in which the target was a shape singleton, but the subject did not know which of two shapes would be the singleton or the distractor. In this condition, report of the probe at the singleton color distractor was elevated. The model simulates this effect (B) as the result of weaker top-down attention which allows the salient distractor to successfully trigger attention on a large enough proportion of trials that report of the probe letter at that location is elevated. In panel C, the participant knows exactly what shape will contain the target and attention is inhibited at the location of the singleton distractor. This is simulated (D) by adopting stronger top-down settings, which allows the target to inhibit the distractor on nearly every trial, such that the probe letters at that location are reported less often across the entire block of trials.

4.3 EEG Constraints

Data concerning the N2pc (also referred to as the PCN by Tollner, Muller & Zehetleitner 2012) and P_D components will be taken as constraints as well.

4.3.3 Specific EEG Constraints:

1. Presenting a target in either hemifield produces a brief negativity in EEG recorded on the contralateral, posterior side of the scalp called the N2pc (Luck & Hillyard 1994; Eimer 1996) or PCN (Töllner, Zehetleitner, Gramann & Müller 2011). This negativity typically peaks at about 250ms after target onset and is observed even in the absence of distractors on the same

side of the display (Tan & Wyble 2015). RAGNAROC simulates this effect as a contralateral negative voltage for a target on one side of the visual field (Eimer 1996). See Figure 15a.

2. Multiple targets in the same location in immediate succession will produce an N2pc only to the first target in the sequence, even for trials in which both targets were reported. Thus, the lack of a difference between the waveforms in one and two-target trials does not reflect a failure to attend or encode the second target (Tan & Wyble 2015; Callahan-Flintoft et al. & Wyble 2017; Callahan-Flintoft & Wyble 2018). When the two targets are presented in different locations of the visual field, there will be an N2pc to each of them in turn (Tan & Wyble 2015). This single-N2pc effect is only present when the two targets are presented within roughly 150ms and at exactly the same location. When the duration between targets is extended, a second N2pc is observed for the second target, even when it is in the same location as the first and also regardless of whether subjects know that the second target will appear in the same location as the first (Callahan-Flintoft & Wyble 2018; See Figure 15c).

3. Multiple N2pcs can be evoked in rapid succession (e.g. at 10-100ms intervals), with no delay [when targets are presented at different locations](#). When presenting a lateral target at intervals of 10, 20, 50 and 100ms relative to a preceding target, an N2pc is evoked with a target-relative latency that is very similar (i.e. within 10ms) to that evoked by the first target. This finding indicates that deploying attention to one target does not affect the time course of attentional engagement to a second target within this short time frame (Grubert, Eimer 2014, Experiment 1). At longer separations, an attentional blink may be observed but the blink is not within the scope of the mechanisms of RAGNAROC See Figure 15d.

4. The N2pc/PCN is often followed by a positive contralateral potential called the P_D (Hickey et al. 2009; McDonald, Green, Jannati & DiLollo 2012) or Ptc (Hilimire, Mounts, Parks & Corballis 2010). This positivity has been particularly associated with the occurrence of a highly salient lateral distractor, although this positivity can occur without such a distractor (Töllner et al. 2011; Hilimire, Hickey & Corballis 2011). RAGNAROC simulates this effect as a positive voltage after the N2pc for a lateralized target (Töllner, et al. 2011). See Figure 15e.

5. A laterally presented salient distractor can produce an N2pc, and this N2pc will be larger if the distractor is presented without an accompanying target (Kiss, Grubert, Petersen, & Eimer 2012; Hilimire, Hickey & Corballis 2012; McDonald, et al. 2012). RAGNAROC simulates this

effect as a negative contralateral voltage after a lateralized distractor (McDonald et al. 2012). See Figure 15f.

6. Specificity of the attentional set affects the degree to which targets and distractors produce N2pcs. When the task set does not predict a specific stimulus shape (e.g. when the task is to find the shape singleton), the distractor can elicit an N2pc (Hickey, et al. 2006; Burra & Kerzel 2013) because the top down weighting is less efficient, which allows a salient distractor to have higher relative priority. Furthermore, a target presented on the midline will reduce the distractor induced N2pc by competing with it for attention (Hilimire, et al. 2011; Hilimire & Corballis 2014; Figure 3c). Similarly, in the same condition an N2pc induced by a lateral target

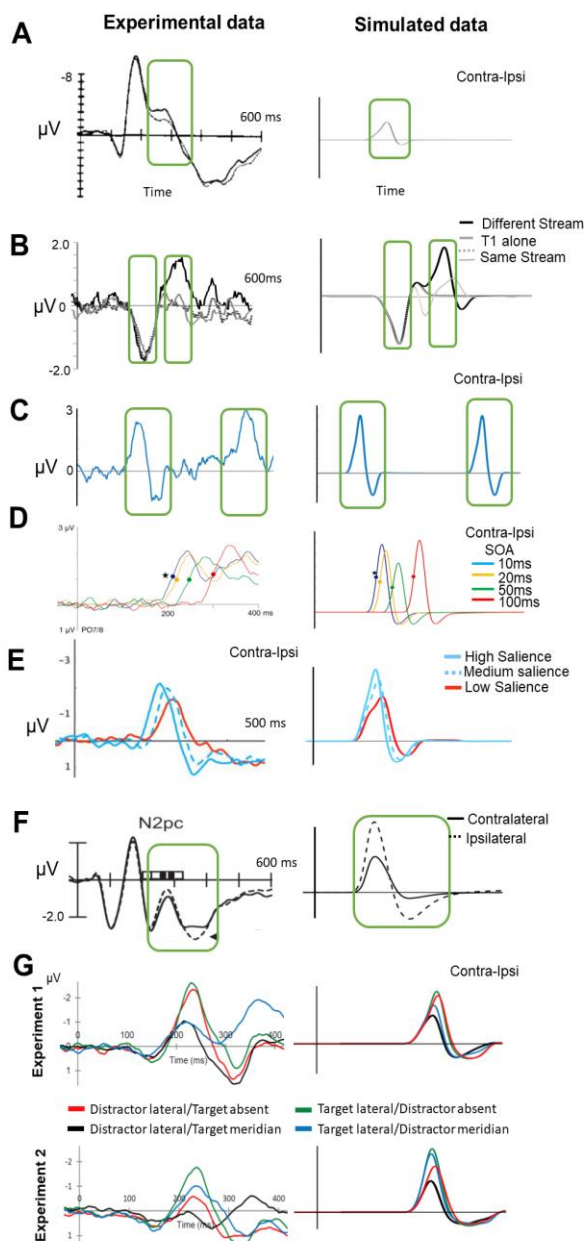


Figure 15 EEG constraints and simulations. Note that polarity is oriented according to the original source and thus switches between panels (a) A laterally presented target causes a brief contralateral negativity, even if it has a long duration (Eimer 1996; green window added to emphasize the time frame of the N2pc). (b) The N2pc to a second target is muted if it occurs very soon after and in the same location as a preceding target (Tan & Wyble 2014). (c) The second N2pc is of normal size if the two targets are far apart in time (Callahan-Flintoft & Wyble 2018). (d) When two highly-salient, unmasked targets are presented in rapid sequence at different locations, the N2pc to the second target is not much delayed (Grubert, Eimer 2014). (e) The N2pc is often followed by a deflection in the positive direction, particularly when there are nearby salient distractors, or in this case when the target itself is highly salient (Töllner, et al. 2011). (f) A laterally presented distractor can trigger an N2pc (McDonald et al. 2012). (g) With a highly predictable or salient target, the distractor produces a minimal N2pc and has little effect on the target's N2pc (Exp 2). When the target set is less specific the distractor has a greater effect on the target N2pc (Exp 1, Hilimire & Corballis 2014).

RAGNAROC, a model of reflexive visual attention

is reduced by a centrally presented distractor (Hilimire & Corballis 2014). When the task set is a *predictable singleton*, then distractors produce a much weaker N2pc and the target induced N2pc is barely affected by the presence of a salient distractor. RAGNAROC simulates this effect as a specific ordering of N2pc amplitudes for different stimulus configurations across two different specificity manipulations (Hilimire & Corballis 2014). A similar result is obtained when the task is manipulated such that the distractor is of higher or lower salience than the target. For example, when the task is to detect a form singleton, a highly salient color singleton will reduce the target's N2pc, but this is not true when the task is to detect a color singleton, and the distractor is a form singleton (Schubö, 2009). See Figure 15g.

5.0 Discussion: what have we learned?

The RAGNAROC model describes a set of neural mechanisms that explicates how attention reflexively responds to new visual input, and makes rapid decisions about which locations in the visual field to enhance and which to suppress. The decisions are mediated by attractor states and competitive inhibition that help to ensure that the decisions are stable and accurately targeted at the correct location. It is argued that this reflexive attentional system plays a key role in many experimental paradigms, and constitutes the first form of decisive filtering of visual information after it enters the brain.

As a model, RAGNOROC is both an architecture, as well as a specific set of parameters that are calibrated against several decades of data that specify the time course of reflexive attention. Presumably, this time course reflects an adaptation imposed by other constraints of the visual system. For example, the operation of reflexive attention has to occur within the time span of a visual fixation, while the eye's position is relatively stationary. During the time window of a single fixation, the representations throughout the visual hierarchy would be roughly in spatiotopic register, making it easy to determine which information is associated with the same object across different maps.

With the model developed and parameterized, the next steps are to use it as a tool to learn more about the underlying system, and to assert a series of testable predictions that can measure the validity of the model relative to the human system. We begin with a series of lessons that were learned through the model's development and then proceed to some more specific predictions.

RAGNAROC, a model of reflexive visual attention

Lesson 1. Attention does not draw a clear distinction between targets and distractors.

Experimental paradigms in experimental psychology often designate stimuli as targets or distractors according to their physical attributes and it is tempting to assume that the mind of the participant adopts the same crisp distinction. However, the visual system is presumably maintaining vigilance for all possible kinds of stimuli (e.g. consider whether the participant would react to an unexpected flash of light in an experimental context). To accomplish this feat of general vigilance, even during a highly explicit visual attention experiment, the visual system must evaluate all stimuli to determine which, if any, should be attended. This idea was critical in two-stage models of attention (Treisman REF, Hoffman 1979), which posited explicitly that stimuli had to be evaluated in sequence to determine whether they were targets. RAGNAROC extends this idea to reflexive attention mechanisms such that, assumes that stimuli compete with a common currency of relative priority. Therefore, within the confines of the attention map, for at least the first two hundred milliseconds of processing, there is no categorical distinction between targets and distractors. Rather, all stimuli compete, and attention is deployed to the winners, and the losers are suppressed (though priority is biased towards stimuli that bear target-defining attributes). The implications of this idea become more interesting when we think about tasks with multiple targets of varying priority. In such cases, the reflexive attentional system may initially allocate attention to the highest priority target and treat the other targets as distractors.

Lesson 2: Visual Attention as a decision in continuous spaceprocess

In RIn many attentional models, the attention or priority map at the top of the hierarchy accumulates information from subordinate maps to find locations of maximal priority. RAGNAROC, illustrates another crucial function of such a priority map, which is the ability to implement decisions about where to attend within a continuous spatial dimension. A lock-on state in RAGNAROC is essentially a decision to commit attention to a given location within the spatiotopic coordinate frame of the visual system. The lock-on dynamics (including the enhancement at the attended location, the surround suppression and the suppression of the IG neurons) all serve to generate a commitment to attend to one or more locations anchor that decision. This anchoring ensures that once attention is committed, it will stay engaged for at least a brief window of time (roughly 100ms or so), rather than shifting abruptly from one location to another. These bursts of attentional lock-on provide stability to reflexive attention over the time span of typical visual fixations, and allow the entire visual stream to momentarily

RAGNAROC, a model of reflexive visual attention

synchronize representations across the multitude of maps distributed throughout the ventral and dorsal streams. This is one means to address the classic notion of binding (Treisman REF). -

~~Such synchronization could be important for creating a robust representation of a stimulus to drive memory and other task-related cognitive functions.~~ Without the extra circuitry, reflexive attention would be prone to jumping rapidly from one stimulus to another, leading to jumbled and mismatched representations in the various maps of the ventral stream.

Even more interesting, however is that RAGNAROC is able to implement these decisions over a many possible spatial configurations. For example, the activity in the AM could be confined to a single point, spread across multiple points, or be distributed across one or more large regions.

~~Thus, the AM in RAGNAROC illustrates how a neural sheet can make decisions in a continuous space, rather than among discrete alternatives as are typical in the case of race or diffusion models (Ratcliff & McKoon 2008).~~

Lesson 3: What does the N2pc/ P_D complex reflect?

A typical approach in theoretical work is to assign specific roles to particular EEG components. For example the N2pc is thought to reflect attention evoked by a target in some form while the P_D reflects inhibition evoked by a distractor. However, as we note above, there are cases in which targets elicit P_D components and distractors elicit an N2pc. This modeling approach illustrates why it is important to consider that there is a many-to-one mapping between current sources and ERPs. The neutrality of a scalp potential at a given latency could indicate a period of neural inactivity, but it could also be the case that there are strong underlying dipoles that happen to cancel one another out at that particular moment in time. It is therefore crucial to ultimately understand ERPs at their source level if we want to fully incorporate them into the inference process. In a similar fashion, there are several ways in which neural activity evoked by a stimulus could lead to a negativity or positivity. For example, RAGNAROC illustrates why the N2pc is often followed by positive rebound after about 100ms, even though the stimulus stays on the screen (Brisson & Jolicouer 2007). Furthermore, the model explains why this rebound can increase to the point of producing a trailing positivity as target salience is increased (e.g. Tollner et al. 2011) despite there being no specific distractor.

Lesson 4. Experiment outcomes are a mixture of different trial outcomes

In RAGNAROC, trial-to-trial variability in the simulations accounts for uncontrolled sources of variability (e.g. spontaneous fluctuations in attentional focus on the part of the subject) and is

RAGNAROC, a model of reflexive visual attention

essential for simulating different levels of accuracy. More importantly, the model clarifies how differences in the magnitude of an effect could reflect variation in the frequency of a given outcome, rather than differences in the size of the effect within each trial, a point that was also emphasized by Zehetleitner et al. (2013). For example, a given experiment that exhibits a weak attentional capture effect by a salient distractor, may in fact have a very strong capture effect, but only on a minority of trials. Likewise, a manipulation that produces a stronger N2pc in one condition may be altering the proportion of trials that contain an N2pc rather than the amplitude of the N2pc itself. [van Zoest, Donk, & Theeuwes \(2004\) demonstrate that this point with eye movements.](#)

Lesson 5. Understanding reaction time costs in attentional capture

The term attentional capture typically refers to a behavioral phenomenon of slowed responses to a target due to the presence of a distractor, but what exactly causes the reduced performance? In RAGNAROC, there are three possible patterns of attentional allocation when a target and at least one distractor are presented together. First, the target might trigger attention and suppress attention to the distractor(s); second, the target and distractor might trigger attention together; and third a distractor might trigger attention and suppress attention to the target. Each of these three possibilities produces a different RT for the target.

RAGNAROC predicts that RTs would be fastest when the target is attended and the distractor is suppressed because this reduces interference caused by distractor processing. When both the target and the distractor are attended (i.e. simultaneous attention), RTs to the target would be slightly slowed because simultaneous lock-on states, while stable, are often slightly smaller compared to a case in which the target is clearly dominant. The final case produces the slowest RTs because the target is not enhanced by attention which reduces the strength of evidence for that target.

The RAGNAROC model predicts that any given experimental block of an attentional capture experiment is composed of a combination of these three outcomes, with proportions determined by the relative priority of the targets and distractors. Thus, even in a paradigm that has minimal evidence of attentional capture at the group level, the distractor may nevertheless trigger the deployment of attention on a subset of trials depending on variation in the subject's attentional focus.

Lesson 6. Architectural answers to the bottom-up/top-down attentional capture debate

One of the most enduring discussions in the attentional literature is whether bottom-up stimuli are always able to capture attention, or are top-down attentional control signals able to override bottom-up salience. Driving this debate are classic findings that some kinds of distractors elicit capture costs consistently, even though they are never task relevant (Theeuwes 1991). In others studies, capture effects seem to be entirely contingent on top-down settings (Folk, Remington & Johnston 1992). This debate has continued without a clear resolution.

In the model, there is a sense to which bottom-up selection occurs prior to top-down guidance because of the anatomical ordering of early vs later stages of processing. Differences in physical salience are represented at the junction between EV and LV, and differences in task-related attentional set are represented between the LV and AM. This means that a difference in physical salience will often manifest in the AM prior to a difference in task relevance simply because the EV neurons are earlier in the processing hierarchy, which allows them to determine which stimuli in the LV will cross threshold first. Figure 16 compares the time course of activation

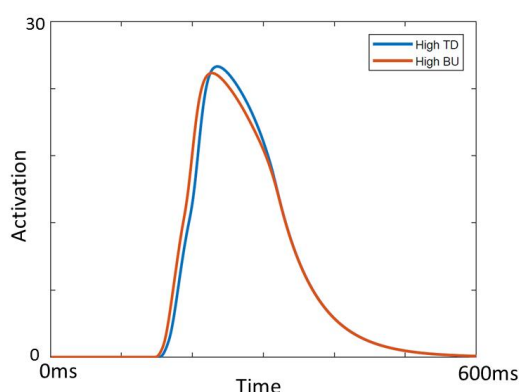


Figure 16. Simulation of the time course of attention map activation for two stimuli that have similar attentional priority, except that one has high salience and a low bottom-up weighting (BU: .2, TD: .15) while the other has the reverse (BU: .15, TD: .2). Of note, despite the higher peak of the high-TD stimulus, the high-BU stimulus has an earlier peak. This is an overlay of two traces; the two stimuli were simulated separately and had the same onset.

bumps generated by highly-salient, irrelevant stimuli, to less-salient but task relevant stimuli. Thus, the model exhibits a form of precedence that is in general agreement with Theeuwes Atchley & Kramer (2000). Moreover, this result is not due to specific parameter values, but rather is an outcome of the model's feedforward architecture. Since salience differences are thought to be processed earlier in the hierarchy (Zhaoping 2002), highly salient stimuli will tend to activate their corresponding LV nodes earlier than less salient stimuli. However, this temporal advantage does not mandate that salient stimuli will always be attended first, since a strong top-down weighting can ensure that a task-relevant, but lower-salience stimulus

RAGNAROC, a model of reflexive visual attention

will establish a lock-on state more quickly than an irrelevant, higher-salience stimulus.

Lesson 7. Architectural answers to the singleton-detection mode debate

Another crucial issue in the attentional capture debate has been the idea that the singleton detection mode allows the system to select unique information for any attribute dimension (e.g. the red item among green items). The advantage of such a mode is that it does not need to be configured in advance for a specific value, preferring equally a red among green items or a green among red items. It has been suggested that subjects use singleton detection when looking for a target that has a unique property, such as a color or form singleton (Bacon & Egeth 1994). However, a limitation of singleton detection mode is that it cannot be directed towards a specific dimension. Thus, using singleton mode to detect an oddball shape will also prioritize an oddball color.

Models like RAGNAROC make singleton-detection mode straightforward; it is simply the lack of a strong top-down set, which thereby allows stimuli with high physical salience to dominate the computation of attentional priority. This explains the observation that singleton detection mode cannot be specific for a given dimension. Moreover, since singleton mode is effectively the absence of a top-down set, it is the default search policy (Bacon & Egeth 1994; Lamy & Egeth 2003).

Lesson 8: Architectural answers to the distractor suppression debate

Competing accounts of inhibitory control in reflexive attention pit the notion of a suppressive surround (Mounts 2000; Cutzu & Tsotsos 2003; Tsotsos 2011) against accounts in which inhibition is selectively deployed to distractor locations (Cepeda et al. 1998; Gaspelin et al. 2015). RAGNAROC illustrates how readily a single model can exhibit both behaviors depending on the paradigm that is being used. A spatial gradient in AM->IG connectivity simulates the surround inhibition effect of Mounts (2000). However, within that surround field, inhibition is selectively applied to the locations of stimuli as a function of their spatiotopic distance to the lock-on state.

RAGNAROC thus explains why the Mounts paradigm and other paradigms which also surround the initial target with distractors such as Cutzu & Tsotsos (2003) were so successful in eliciting the inhibitory surround, while other paradigms have no clear pattern of inhibitory surround (Wyble & Swan 2015). In the Mounts paradigm, the first target is surrounded by a large number

RAGNAROC, a model of reflexive visual attention

of simultaneously presented distractors. This display is followed immediately by a second display that is used to probe the state of attention. According to the RAGNAROC, the dense field of distractors in the first display of Mounts (2000) plays a key role in revealing the shape and size of the inhibitory gradient, since each of those distractors will elicit inhibition in their location, and this inhibition will affect the following target. For paradigms in which the initial target is not surrounded by a dense field of distractors (e.g. Wyble & Swan 2015), the IG neurons in the large area surrounding the target are not stimulated by input from the LV and therefore the only inhibition that is actually expressed in the AM is that immediately surrounding the target's lock-on state.

Lesson 9. The Competition for attention can result in a tie.

The conventional notion of spatial attention is that it behaves like a spotlight, focusing on only one location at a time. This explanation provides a ready explanation for cueing costs and attentional capture effects, since attention directed at one location can therefore not be at another. However there is also mounting evidence that attention can be deployed simultaneously at two distinct locations (Bay & Wyble 2014; Bichot Cave & Pashler 1999; Kyllingsbaek & Bundesen 2007; Kawahara & Yamada 2012; Goodbourn & Holcombe 2015; [see also the possibility of having multiple attention pointers or FINSTs \(Pylyshyn & Storm REF\)](#)). Of these, Goodbourn & Holcombe provide what is arguably the most compelling evidence of the simultaneity of attentional deployment by measuring the time course of selection at two discrete locations and finding essentially no lag for one vs two simultaneously cued locations. The RAGNAROC model provides an explanation for these seemingly incompatible sets of findings. The circuitry in the attention map is designed to encourage a competition between simultaneous items, however it is a competition in which there can be multiple winners, which allows simultaneous attention for two stimuli of approximately equal priority.

Lesson 10. Reflexive Attention may have almost unlimited capacity.

A common assumption of cognitive theories is that attentional limitations play a key role in determining performance in complex tasks. However, attention is a broad concept and it is often difficult to understand exactly what forms such limits take. In many cases, attention is equated with the ability to "process" information, which includes some mixture of identification, decision making, response generation, and memory encoding.

RAGNAROC, a model of reflexive visual attention

RAGNAROC embodies a specific definition of attention, which is the reflexive enhancement of feedforward excitation at a given location in the visual field deployed reflexively in response to a stimulus. In the model, this form of attention has no clearly defined limit in terms of the number of attended locations, since the model only simulates an increase in gain at a given location and that increase could occur at an almost arbitrary number of locations. The variability in the representations of multiple items coupled with the suppressive interactions in the AM makes it unlikely that more than a few locations would be attended in this way, but it is possible in principle. Thus, the model proposes that the earliest stage of attentional selection may operate without strict capacity limits. Of course, subsequent stages of processing are surely limited. For example, even if four stimuli produced simultaneous lock-on states, encoding them all into memory at the same time would produce interference. Parallel selection at early stages does not necessarily entail parallel processing at later stages.

Lesson 11. Attention can be suppressed without suppressing the representations

It is often suggested that distractors are inhibited during the selection of target information. Models like RAGNAROC elucidate an important distinction between suppressing the representation of a stimulus itself vs suppressing attention at the stimulus' location. Suppressing a stimulus representation entails direct inhibition of the neurons that represent the attributes and features activated by that particular stimulus (e.g. Reynolds & Heeger 2009; Beuth & Hamker 2011) with the potential to eliminate the active representation of that information from the nervous system. On the other hand, suppressing attention at the location of a stimulus, as in RAGNAROC, preserves the original information of the stimulus at the earliest layers of the visual system.

It is, unfortunately, difficult to clearly distinguish between the two implementations of suppression using observations of accuracy or reaction time, since both forms of inhibition will reduce the ability to respond to a stimulus. However this difficulty illustrates an advantage of the modeling approach, since models are able to clarify distinctions of implementation that are not otherwise obvious (see also Lu & Doshier 1998 for an illustration of how models of noise exclusion can provide a more specific inference about the mechanisms of attention with the use of psychometric curves). Moreover, the model illustrates why it would be advantageous to suppress attention, rather than the representation. Suppressing the representation of a stimulus would require an enormous number of long-range connections to deliver inhibition to the

RAGNAROC, a model of reflexive visual attention

appropriate neurons throughout the set of LV maps. Suppression of attention is much simpler to implement, since the inhibitory circuitry is entirely self-contained within the AM.

6: Review of other theories

There is an enormous literature of theories and models of visual attention. With a term as broad as attention, it is impossible to identify a canonical set of effects that all models should strive to explain and therefore a point-by-point comparison with other models is impossible. Speaking broadly, the RAGNAROC model occupies a relatively unique position in the modeling landscape by focusing on the neural mechanisms associated with reflexive attention at a short time scale and explaining the N2pc/ P_D complex as the result of an impulse response function across a field of neurons. Other models have touched on the idea of simulating the N2pc (Fragopanagos, Kockelkoren, & Taylor 2005) but have not provided a complete picture of neural firing that would translate into a lateralized potential, nor linked to such a diversity of findings.

This review will cover a subset of models that focus on the mechanisms of spatial attentional selection to point out commonalities and also points of divergence.

~~This excludes, for example, models of the attentional blink, which typically focus on how processing of information affects attentional selection.~~

Models inspired by neurophysiology. There is a family of models and theories of visual attention inspired by single unit neurophysiology in monkeys. Some of the research in this domain explores the properties of attention in spatial and feature domains. For example, the normalization model of Reynolds & Heeger (2009) proposes that the neural response to any given stimulus is downweighted by the activity of nearby stimuli. Thus, when one stimulus is attended, other stimuli in the vicinity will evoke less activity, all else being equal. The normalization model provides a straightforward, neurally plausible mechanism for the effects of attention at the level of single-unit data. Beuth & Hamker (2015) provide a more detailed account of how attention can be mediated at the level of cortical representations. Such models interface directly with single-unit data from a variety of cortical areas, although they do not explain the decision-making aspect of attention that is the focus of RAGNAROC. Instead, attention is directed by other mechanisms that are outside the scope of those models, making them complementary to this model. However, we consider it an open question as to whether the suppression of attention is best explained at the circuit level within earlier cortical areas, as in

RAGNAROC, a model of reflexive visual attention

Reynolds & Heeger (2009) and Beuth & Hamker (2015) or at a superordinate level as in RAGNAROC.

Biased Competition. Another well known theory of attention is biased competition, in which stimuli compete with one another for representation in a neural system with overlapping receptive fields and the competition is biased in favor of neurons that respond preferentially to task-relevant information (Desimone & Duncan 1995). There is an important point of correspondence between the biased competition (BC) and the RAGNAROC accounts, which is that both incorporate an initial period of non-selective processing before the deployment of attention begins. In RAGNAROC, this is the time during which information feeds forward through the hierarchy to reach the AM. The RAGNAROC and BC models differ in the mechanism of enhancement, since the BC implements attention as a contraction of receptive fields around the target stimulus. The difference is key because at the core of BC is the idea that representational space is a limited resource, which strongly limits the ability to attend to multiple locations at once. In RAGNAROC, this first stage of attention has fewer limits and thus can be deployed to multiple locations in certain situations. With that being said, the effect of attention in RAGNAROC would manifest as a contraction of receptive fields around a given stimulus, since an attended stimulus would dominate nearby representations in LV.

Theory of Visual Attention. The Theory of Visual attention (Bundesen 1990) is a mathematical abstraction of the process of attending to and perceiving one or more stimuli in a single display. In TVA, there are two ways to prioritize certain kinds of information selection: *filtering*, and *pigeonholing*. *Filtering* involves upweighting the priority for certain features, which increases the rate at which stimuli possessing those features attract attention. This is similar to attentional control settings in RAGNAROC. The *pigeonholing* mechanism relates to how efficiently certain kinds of information are categorized, which allows them to be reported and remembered. The TVA model thus represents two distinct types of attentional control setting, which might also be described as key feature and response feature (Botella, Barriopedro, & Suero 2001). The RAGNAROC model differs from the TVA model in that it provides a more complete model of the neural mechanisms associated with the computation and use of priority to direct spatial attention. The TVA model, on the other hand, provides a concise mathematical formulation of how two different kinds of filters interact to facilitate perception. A Neural implementation of TVA has been proposed (Bundesen et al. 2011), however it is less clear how such a model would scale up to a full working specification, since it requires a large scale winner-take-all

RAGNAROC, a model of reflexive visual attention

implementation to complete attentional selection. Given the similarity of the role of priority within the two models, it could be fruitful to consider the RAGNAROC as a neurophysiologically plausible front-end for computing the priority-based competitive selection process and the TVA as a clearer specification of subsequent processing.

Guided Search. To better understand a number of complex patterns in the visual search literature, the Guided search model (Wolfe 1994) simulates how top down goals interact with bottom up salience signals to determine likely target locations. Like RAGNAROC, this model attempts to explain how the visual system mediates the balance between salience and task relevance. Its focus is on a longer time scale than reflexive attention, and incorporates both overt and covert forms of attention. RAGNAROC is complementary to this model, by explaining attentional dynamics at a short time scale, and with a greater emphasis on inhibitory processes.

Feature Map Models. Another class of models simulates spatial attentional effects across sheets of neurons corresponding to different visual features. Perhaps the most canonical of such models is the salience model of Koch & Ulfman (1985), which is architecturally quite similar to RAGNAROC. A descendent of this model is often invoked as a benchmark in computer vision algorithms (Itti, Koch & Niebur 1998).

In such models, feature detectors in multiple channels (i.e. luminance, color, motion flicker) project to a master salience map that ultimately makes decisions about where attention will be deployed using a simple winner take-all mechanism, coupled with a form of memory that erases salience values at recently-visited locations. Like RANGAROC, this model uses salience as a common currency across all stimuli in the visual field, and would be able to simulate capture effects. The Itti, Koch & Niebur (1998) model has been foundational in understanding how simple mechanisms can reproduce complex gaze behavior when iterated over many distinct feature dimensions and levels of scale. Also, because the Itti et al. model simulates responses to pixelwise visual data, and can be compared against visual fixation data from human subjects, it set the stage for a generation of further modeling efforts.

Itti et al.(1998) and RAGNAROC address phenomena at different time scales. The former is intended as a model of gaze behavior on time scales of a second or more, involving multiple fixations. RAGNAROC is developed to understand how covert attention deployment is computed anew with each visual fixation or significant change to the visual display. Moreover,

RAGNAROC, a model of reflexive visual attention

the salience map in Itti et al.(1998) lacks the inhibitory mechanisms to suppress distractors without first attending to them. The two models are thus complementary; they operate at distinct time scales, emphasize different kinds of processes and simulate fundamentally different kinds of data.

Other models provide more direct simulations of neural processes of enhancement in neural sheets. The Selective Tuning model by Tsotsos (1995; 2011) implements a form of inhibition in which detection at an upper level of the hierarchy produces surround inhibition at earlier layers of the hierarchy. This model is perhaps the most well-formulated attention model that has ever been proposed since it proposes a gating control circuitry that allows information to be effectively linked across differences in spatial invariance. Selective Tuning would reach several of the benchmarks described here, but does not propose a reactive control circuit. It applies inhibition in a region surrounding a target, irrespective of the presence of distractors. Moreover, in the full architecture, decisions to deploy attention are made independently for different stimulus dimensions and it is not precisely formulated how cross-dimensional competition between stimuli would be implemented at the time scale of reflexive attention (see p121, Tsotsos 2011).

Resonance models

~~There is a variety of models by Grossberg and colleagues based on the overarching principle of adaptive resonance. One of the more recent of this series have proposed neural architectures for attentional control using an attentional shroud (Fazl, Grossberg & Mingolla 2009), which is essentially a means to delineate the boundaries of an object and then ensure consistent focus on that object during learning.~~

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~~These ideas are both similar to the notion of the lock-on states described here, which also emerge through properties of spatial topography. are also shaped by the boundaries of the stimulus. The shroud model does not contain an explicit mechanism for inhibiting distractors, and its success in attentional focus in very complex displays could be offered as an example that distractor inhibition is not necessary. However in~~

~~terms of hitting the empirical benchmarks described here, it is not clear how well inhibitory effects would be simulated.~~

The class of interacting neural sheet models includes a large number of others that make important contributions to understanding particular empirical phenomena. For example, Zirnsak, Beuth & Hamker (2011) simulate the temporal dynamics of attentional competition in response to one or more stimuli; Lanyon & Denham (2004) simulate eyegaze during visual search as a product of interacting attentional systems. Another class of models simulates how neglect symptoms arise from damage to the attentional system (Heinke & Humphreys 2003) at longer time scales than are considered here.

The enormous variety of such models and their success at addressing such a broad range of phenomena across varying time scales illustrates the practical generalizability of the hierarchical attention architecture.

7. Predictions:

RAGNAROC is part of an ongoing investigation that involves a cyclic iteration between theory and experiment. Driving this cycle are *a-priori* predictions, that provide a roadmap for future experimental work to diagnose the model's validity. By publishing these predictions in advance of testing them, we minimize the file drawer problem, which occurs when model tests are selected for publication after the results are known. Furthermore, our goal here is to specify an ambitious set of predictions, with the goal that some of them should be inaccurate. Since all models, being abstractions of the real system, are wrong by definition, the prediction/testing cycle should be most efficient when there is a mix of true and false predictions. True predictions give evidence that the model has at least some resemblance to the underlying system. However, it is the false predictions that are truly valuable, for they indicate where the model is inaccurate, and thereby guide further development of the theory.

7.1 Competition within the attention map

This set of predictions concerns the essential architecture of the model. Failure to validate them would require at a minimum, significant parameter or architectural changes. In RAGNAROC, the competition for attention exists between all stimuli, and the priority values of the stimuli are the common currency with which they compete. Since the attention map does not represent the distinction between targets and distractors, the following predictions should obtain:

Prediction 1. Lower priority targets will elicit AM suppression

In RAGNAROC, input to the attention map does not distinguish between targets and distractors. A counterintuitive prediction of this assumption is that when a display contains two targets with sufficiently different priority values, the lower priority target will lose the competition and be treated as a distractor. This would mean that it elicits a weak N2pc when presented laterally, followed by a clear P_D component as if it had been a distractor. In terms of behavior, the location of the low-priority target should exhibit the same lower probability of probe letter reporting as the salient distractors of Gaspelin et al. (2015). Target priority could be manipulated either by varying the salience of targets or their proximity to the task-defined attentional set in some feature dimension, such as color (Becker Folk & Remington 2013).

Prediction 2. Higher priority distractors will more often elicit a lock-on state

One of the most fundamental predictions of RAGNAROC is that all stimuli are evaluated by the attention system prior to the deployment of attention, which occurs after a competition is resolved within the attention map. Therefore, if a display consists of only distractors of three or more clearly discernable levels of salience (e.g. by adjusting their relative luminance), the distractors will elicit N2pc and P_D components as if the most salient distractor were a target and the next most salient distractor were the key distractor in the additional singleton paradigm. The most salient distractor will also capture attention resulting in improved accuracy and reduced reaction times for probes (e.g. Gaspelin et al. 2015) at its location. Conversely, probes at the second-most salient distractor location will be less well perceived than distractors at the location of the least salient distractor. This prediction stems from the fact that the amount of inhibition delivered to the location of a lower-priority stimulus in the AM is proportional to its priority. Testing this prediction would require embedding distractor-only trials within a larger set of trials that contain targets as well. Some of these trials would contain probe letters as in Gaspelin et al. (2015)

Note that there is conflicting evidence about the ability of distractors to elicit an N2pc. Distractors that are highly salient on a different dimension than the target (e.g. color singleton distractors with shape singleton targets) elicit an N2pc, while a difference in salience along the same dimension (color) does not; Gaspar & McDonald 2014).

Prediction 3. Salient Distractors can sustain an existing lock on state

RAGNAROC, a model of reflexive visual attention

One of the most counterintuitive predictions of RAGNAROC is that once an attentional lock-on state has been established by a target, it can be sustained by a distractor because the attention map is agnostic about target/distractor categories. Attentional control settings bias attention towards the target, but distractors also have excitatory connections to the AM; they just have reduced priority. Thus, in a similar manner as two sequential targets can maintain a lock-on state (Tan & Wyble 2015), a target followed by a distractor should also maintain the lock-on state. The prediction can be tested by presenting either three targets in sequence (i.e. letters among digits), at an SOA of about 120ms, or two targets separated by a single distractor that is similar to other distractors (i.e. a black digit), or two targets separated by a highly salient distractor (i.e. a red digit). It should be observed that for three targets in a row, the second and third targets elicit small-amplitude N2pcs that peak early (roughly 30ms earlier than the relative latency of the T1's N2pc). If the middle of the three targets is replaced by a highly salient distractor, the last target's N2pc should still be early and small in amplitude. However in the case of two targets separated by a non salient distractor, that last target should evoke an N2pc of normal amplitude and latency since the lock-on state will have partially dissipated during the 300ms lag between the onset of the two targets. In behavior, the salient intervening distractor should result in more accurate report of the following target relative to the non-salient distractor condition, since the highly salient distractor sustains the lock-on state across the temporal gap between the targets.

7.2 Unified Attentional Map:

A central theme of the RAGNAROC architecture is that the competition for reflexive attention is confined to a small region of neural tissue this is sensitive only to stimulus priority. This allows the entirety of the visual system to participate in scene analysis, and yet make rapid, efficient and stable decisions about the allocation of attention. The priority map allows the priority signals generated by different stimuli to compete, taking into account their salience, task relevance, emotional/reward history, or any other potential factor that influences how a given stimulus should be prioritized. This idea of a single, superordinate attention map is also shared by many models of visual attention (Itti Koch et al 1998; .. Zelinsky2008) but not others (Tsotsos 2011).

Prediction 4: EEG correlates of lock-on occur regardless of stimulus type

A core finding of the lock-on state presents a straightforward means to test this architectural prediction. In Tan & Wyble(2014), it was found that two targets in the same location produced

only an N2pc to the first target, which RAGNAROC explains as a carryover of the attentional lock-on state from one target to the next in the attention map.

However, in that study, both targets were of the same kind (letters among digit distractors). If there is a single priority map, the carryover of lock-on from one stimulus to the next should occur even when T1 and T2 are of different types. Callahan-Flintoft & Wyble (2018) provided support for this prediction already by showing that targets could be defined by combinations of shape or color without disrupting the lock-on effect. It is nevertheless possible that the prediction may be falsified if the two targets were even more distinct. For example, RAGNAROC predicts that even if subjects are simultaneously looking for letters and faces of a particular gender, then two sequential targets (either letter-face or face-letter) should produce a clear N2pc only for the first of the two targets. Letters and faces should provide a strong test for the hypothesis since previous work has suggested that they are processed through sufficiently distinct channels in the visual system that the attentional blink evoked by a digit T1 has little effect on a face T2 (Awh et al. 2004). A failure to confirm this prediction would suggest that there are subdivisions of the priority map for stimuli that are highly distinct.

7.3 Lock-on states in visual cueing:

The RAGNAROC model implements a reflexive form of attention that should be common across many visual attention paradigms, including visual cueing. Thus, we should be able to predict behavioral and ERP effects for cueing experiments as well. Ansorge, Kiss, Worschech & Eimer (2011) have demonstrated that cues evoke clear N2pcs at moderate cue-target SOAs (200ms), as we would expect.

Prediction 5. Lock-on states in visual cueing, valid trials

The RAGNAROC model predicts that a lock-on state is sustained from one stimulus to the next. Thus, from a behavioral perspective, RAGNAROC explains cueing benefits at short SOAs, if one assumes that a valid cue initiates a lock-on state that carries forward in time to enhance the target. The model also generates EEG predictions for cueing experiments. Since the N2pc is caused by the formation of a new lock on state, then a validly cued trial with a short SOA should result in an N2pc appearing only for the cue, and not the subsequent target.

RAGNAROC, a model of reflexive visual attention

At longer SOAs (e.g. 500ms or more) between the cue and target, the lock-on state elicited by the cue would have disintegrated before the target appeared, with the result that both the cue and the target would produce a typical N2pc.

Prediction 6. Lock-on states in visual cueing, invalid trials

When a cue and target are not in the same location, then the cue and target will each elicit an N2pc at all SOAs, since the lock-on state elicited by a cue is spatially specific. Thus, a target in an invalid trial needs to build a new lock on state, which elicits a new N2pc. A failure to confirm these predictions would undercut the applicability of RAGNAROC's simulation of attention related EEG components to cueing studies.

8.0 Conclusions

Reflexive visual attention is a cornerstone of our visual system's ability to meet the challenge of rapidly choosing which information to selectively process, which pits stimuli that are inherently salient against those that are relevant for an ongoing task. A variety of experimental paradigms have provided a wealth of data that we have distilled into a common architecture for controlling the selection and suppression of information. The goal of the RAGNAROC model is to build a theoretical bridge between different paradigms (e.g. visual cueing and capture), and also between different kinds of data (e.g. behavior and EEG). While designing the model to hit its empirical benchmarks, we have developed circuits that implement competing attractor states to stabilize the deployment of attention within a continuous spatial dimensions.

Moving forward, the model's predictions are intended as a roadmap for further empirical investigation of reflexive attention and for creating links across paradigmatic boundaries. Testing these predictions will provide diagnostic data regarding the model's validity, but more importantly, will drive further development of the model.

[CHECK More here? Discuss attending to one spatial location first, prior to attending to another, unless two stimuli appear simultaneously]

We can use this model to make inferences about the fact that attention can process multiple items in parallel.

While RAGNAROC is intended as a model of reflexive attention that can be deployed covertly, future work could extend these mechanisms as a partial explanation of the time course of eye movements in visual displays. Doing this would require an additional set of assumptions regarding how activity in the attention map drives the decision to commit visual saccades. Recent work that explores the time course and spatial distribution of initial saccades in visual search paradigms (e.g. Gaspelin, Leonard & Luck 2017) indicates that initial saccades are directed towards the location of salient distractors when the distractor's location is not suppressed, but are directed away from salient distractors when that location is suppressed. These findings suggest that activity in the attention map contributes to the initial decision of where to commit an overt attentional response.

The neural attractor framework of RAGNAROC could be incorporated as a front-end onto models of higher order cognitive phenomena. For example, in models of the attentional blink, the time course of target processing is often the central question, and such models have little to say about the time course of reflexive attention. Combining models such as RAGNAROC with models of the attentional blink (e.g. Olivers, & Meeter 2008; Wyble Bowman & Nieuwenstein 2009; Taatgen, et al. 2009) has the potential for expanding our understanding of the spatial and temporal dynamics of attention out to the order of multiple seconds. The model also has the potential to benefit from recent innovations in computer-vision models by allowing us to simulate the spatial and temporal dynamics of attention to real-world video data under different task instructions.

Ultimately, the goal of models like this is to fill in the explanatory gaps left by broad-sweeping theories of attention. By framing the scope of this model as covert, reflexive forms of attention, our goal is to provide a stable platform for thinking more concretely about the entire suite of attentional mechanisms that are inherent in the visual system, and how they might be linked to specific correlates.

Acknowledgements:

This work was performed with the support of NSF grant 1734220 to B. W. Author B.W was responsible for the writing. C.C.F did most of the modelling with assistance from B.W.. Author

RAGNAROC, a model of reflexive visual attention

T.M. developed the non Matlab version of the model for dissemination on Jupyterhub with assistance from B.W. Authors H.C. and H.B. were responsible for conceptual input and advice. The authors also wish to thank, in particular order, Dirk Kerzel, Alex Holcombe, and Nick Gaspelin, for helpful comments.

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Appendix

MATLAB Code for running the simulations is available on the OSF at <https://osf.io/rwynp/>

Appendix 1, Equations

Early Visual layer:

These are the activation equations for each neuron in the EV layer, and note we represent each possible stimulus (T1 and T2) as having distinct EV neurons to reflect the fact that two distinct stimuli will activate distinct groups of neurons in V1 even if presented at the same location. These equations match those specified by O'Reilly & Munakata (2001) where **Input**, represents the presence of an input stimulus at a given location and time point (either 1 or 0) and **EV** represents the activation level of that neuron. **dt_{VM}** is a time constant that dictates the rate of change of a neuron by scaling the excitatory, and leak currents. **EE** and **EL** are the reversal potentials for excitatory and leak currents.

$$EV_{excite}(x, y, t) = dt_{VM} * (EE - EV(x, y, t)) * Input(x, y, t) \quad (1.1)$$

$$EV_{leak}(x, y, t) = dt_{VM} * (EL - EV(x, y, t)) \quad (1.2)$$

$$EV(x, y, t+1) = EV(x, y, t) + EV_{excite}(x, y, t) + EV_{leak}(x, y, t) \quad (1.3)$$

Late Visual layer:

The LV neurons have essentially the same dynamics except that they receive input from a region of EV neurons and the value of the input is scaled by a square-masked Gaussian profile, (**GRF**) for computational efficiency.

The variable **Attn** is the current value of attention as determined by activity at the corresponding location in the AM. **EI** is the reversal potential of the inhibitory current. **ItoIT** is a parameter that determines the strength of the feedback inhibition interneurons for each neuron. **BU_{type}** is a parameter that reflects the physical salience of a given stimulus type. The construct $\lfloor 0$ is a zero-bounded floor to prevent currents from going negative, which adds stability to the simulation at discrete time steps.

$$LV_{excite}(x, y, t) = dt_{VM} * (EE - LV(x, y, t)) * BU_{type} * \sum_{x'=-mask}^{mask} \sum_{y'=-mask}^{mask} GRF(x', y') * Attn(x + x', y + y', t) * (EV(x + x', y + y', t) - Thresh_{EV})_0 \quad (1.4)$$

$$LV_{inhib}(x, y, t) = dt_{VM} * (EI - LV(x, y, t)) * IItoIT * (II(x, y, t) - II_{Thresh})_0 \quad (1.5)$$

$$LV_{leak}(x, y, t) = dt_{VM} * (EL - LV(x, y, t)) \quad (1.6)$$

$$LV(x, y, t+1) = \max\{EI, LV(x, y, t) + LV_{excite}(x, y, t) + LV_{inhib}(x, y, t) + LV_{leak}(x, y, t)\} \quad (1.7)$$

The II neurons govern the feedback inhibition of the LV neurons following a similar dynamic as the EV.

$$II_{excite}(x, y, t) = dt_{VM-II} * (LV(x, y, t) - LV_{thresh})_0 * ITtoII \quad (1.8)$$

$$II_{leak}(x, y, t) = dt_{VM-II} * (EL - II(x, y, t)) \quad (1.9)$$

$$II(x, y, t+1) = II(x, y, t) + II_{Excite}(x, y, t) + II_{Leak}(x, y, t) \quad (1.10)$$

Attention Map:

The AM neurons receive input from all LV maps (1-*n*) scaled by the same masked Gaussian profile **GRF**. **LAI** is a parameter that controls the magnitude of inhibitory suppression from the IG to the AM neurons. **TD_{type}** is a parameter that determines the top-down task relevance for a given stimulus.

$$AM_{excite}(x, y, t) = dt_{VM} * (EE - AM(x, y, t)) * \sum_{type=1}^n \sum_{x'=-mask}^{mask} \sum_{y'=-mask}^{mask} GRF(x', y') * (LV_{type}(x + x', y + y', t) - Thresh_{LV})_0 * TD_{type}$$

[REF add attention bias of .2 to this equation](#)

(1.11)

$$AM_{inhib}(x, y, t) = dt_{VM} * (EI - AM(x, y, t)) * (IG(x, y, t) - IG_{thresh})_0 * LAI \quad (1.12)$$

$$AM_{leak}(x, y, t) = dt_{VM} * (EL - AM(x, y, t)) \quad (1.13)$$

$$AM(x, y, t+1) = \max\{EI, AM(x, y, t) + AM_{excite}(x, y, t) + AM_{inhib}(x, y, t) + AM_{leak}(x, y, t)\} \quad (1.14)$$

$$Attn(x, y, t) = \max\left(1, \log\left(AM(x, y, t) - AM_{threshLow} + 1\right)_0 * Attnweight\right) \quad (1.15)$$

The IG neurons within the Attention Map receive joint input from the LV and the AM. For each IG neuron, the input from each of those two sources has a ceiling value (**MaxInputtoIG**). Thus, the input from the LV and the AM to each IG neuron is computed separately.

$$IG_{exciteLV}(x, y, t) = \max(MaxInputtoIG, \sum_{type=1}^n \sum_{x'=-mask}^{mask} \sum_{y'=-mask}^{mask} GRF(x', y') * (LV_{type}(x + x', y + y', t) - Thresh_{LV})_0 * TD_{type}) \quad (1.16)$$

$$IG_{exciteAM}(x, y, t) = \max(MaxInputtoIG * \sum_{x'=1}^{dim_x} \sum_{y'=1}^{dim_y} (AM(x', y', t) - Thresh_{AMLow})_0 * DoG(x', y') * AMtoIG) \quad (1.17)$$

DoG is the difference of two Gaussians as specified below.

$$IG_{excite}(x, y, t) = (IG_{ExciteLV}(x, y, t) + IG_{ExciteAM}(x, y, t)) * dtVM_{IG} * (EE - IG(x, y, t))_0 \quad (1.18)$$

$$IG_{inhib}(x, y, t) = dtVM_{IG} * (AM(x, y, t) - Thresh_{AMHigh})_0 * AMtoIG_{inhib} \quad (1.19)$$

$$IG_{leak}(x, y, t) = dtVM_{IG} * (EL - IG(x, y, t)) \quad (1.20)$$

$$IG(x, y, t+1) = \max\{EI, IG(x, y, t) + IG_{excite}(x, y, t) + IG_{inhib}(x, y, t) + IG_{leak}(x, y, t)\} \quad (1.21)$$

$$GRF(x, y) = e^{-0.5(x^2 + y^2)} \quad (1.22)$$

$$DoG(x, y) = -1 * \left[2e^{-0.5(x^2 + y^2)}_{outerGaussian} - e^{-0.5(x^2 + y^2)}_{innerGaussian} \right]_0 \quad (1.23)$$

EEG Scalp Voltage

$$EEGVoltage(t) = \left[\sum_{x=1}^{xdim} \sum_{y=1}^{ydim} (AM_{excite_EEG}(x, y, t) + AM_{inhib}(x, y, t))_0 \right] \quad (1.24)$$

$$AM_{excite_EEG}(x, y, t) = dt_{vm} * (EE_{EEG} - AM(x, y, t)) * \sum_{type=1}^n \sum_{x'=-mask}^{mask} \sum_{y'=-mask}^{mask} GRF(x', y') * (LV_{type}(x + x', y + y', t) - Thresh_{LV})_0 * TD_{type} \quad (1.25)$$

Fixed Parameters:

$$dt_{vm} = .015$$

$$dt_{vm_II} = .0025$$

$$dt_{vm_IG} = .04$$

$$EE = 30$$

$$EL = 0;$$

$$EI = -10;$$

$$EE_{EEG} = 65;$$

Weights

$$TD_{type} = \text{Free Parameter}$$

$$BU_{type} = \text{Free Parameter}$$

$$ITtoII = .02$$

$$IItoIT = 6.5$$

$$AMtoIG = .4$$

$$AMtoIGinhib = .25$$

$$LAI = .45$$

$$Attnweight = 2$$

$$AMexcitebias = .2$$

$$MaxInputtoIG = .35$$

Thresholds

$$Thresh_{EV} = 7$$

$$Thresh_{IT} = 5$$

$$Thresh_{II} = 0$$

$$Thresh_{IG} = 8$$

$$Thresh_{AMLow} = 14$$

$$Thresh_{AMHigh} = 22$$

RAGNAROC, a model of reflexive visual attention

Misc

outerGaussian = .07

innerGaussian = .2

Appendix 2, Fitted Parameters

Sim Name	Type1BU	Type2BU	Type3BU	Type1TD	Type2TD	Type3TD
Bay & Wyble	0.3	0.3	N/A	0.17	0.12	N/A
Nakayama	0.15	0.15	N/A	0.18	0.18	N/A
Theeuwes (with salient D)	0.15	0.3	N/A	0.27	0.17	N/A
Theeuwes (without salient D)	0.15	0.05	N/A	0.27	0.17	N/A
Mounts	0.3	0.3	N/A	0.24	0.24	N/A
Gaspelin exp 1 (singleton search)	0.15	0.19	0.15	0.2	0.15	0.2
Gaspelin exp 2 (feature search)	0.15	0.19	0.15	0.4	0.15	0.2
LatDMidlineT	0.15	0.17	N/A	0.5	0.2	N/A
Tan & Wyble	0.15	0.15	N/A	0.2	0.2	N/A
Tollner (low)	0.17	0	N/A	0.15	0	N/A
Tollner (med)	0.2	0	N/A	0.15	0	N/A
Tollner (high)	0.23	0	N/A	0.15	0	N/A
Hillimire (unpredictable)	0.15	0.15	N/A	0.22	0.22	N/A
Hillimire (predictable)	0.15	0.15	N/A	0.4	0.25	N/A
Eimer Grubert	0.6	0.6	N/A	0.7	0.7	N/A
High TD	0.15	0	N/A	0.2	0	N/A
High BU	0.2	0	N/A	0.15	0	N/A

Sim Name	Mean	SD	Threshold
Bay & Wyble	3	0.75	10,891
Nakayama	3	0.75	6,997
Theeuwes (with salient D)	3	0.75	19,522
Theeuwes (without salient D)	3	0.75	19,522
Mounts	3	0.75	11,493
Gaspelin exp 1 (singleton search)	3	0.75	8,667
Gaspelin exp 2 (feature search)	3	0.75	8,667
LatDMidlineT	3	0.75	N/A
Tan & Wyble	3	0.75	N/A
Tollner (low)	3	0.75	N/A
Tollner (med)	3	0.75	N/A
Tollner (high)	3	0.75	N/A
Hillimire (unpredictable)	3	0.75	N/A
Hillimire (predictable)	3	0.75	N/A
Eimer Grubert	3	0.75	N/A
High TD	N/A	N/A	N/A
High BU	N/A	N/A	N/A