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REVIEW

Flexibility in Attentional Control: Multiple Sources and Suppression

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In daily life, it is critical that we are able to direct our visual attention to information that is important for our tasks while avoiding distracting information. To control our attention, we engage "attentional templates" that reconfigure how incoming visual signals are processed in our brains. But what are these attentional templates and how do they work? Much of our understanding of the nature of attentional templates has been driven by the proposed mechanism linking attentional templates and working memory from the biased competition model [1] (Desimone and Duncan, 1995). Over the past 20 years, research inspired by this proposal has vastly increased our understanding of attentional control. This work has highlighted flexibility in attentional control, with multiple sources of control and flexible enhancement or suppression based on task demands.

INTRODUCTION

How do we find an object that we are looking for? From finding our keys on a messy desk to finding the right box of cereal on the grocery store shelf, in everyday life we are often engaged in goal-directed visual search tasks. Often, these search tasks are preceded by a cue. For instance, when we are driving, we see a bright "pedestrian crossing" sign before we approach a crosswalk. This cue allows us to create an *attentional template* for our search goal (*e.g.*, a pedestrian), which helps guide our attention to stimuli that match the template. Attentional templates are powerful because they fundamentally alter what aspects of the world our brain processes. Without engaging attentional control via attentional template, we would likely miss the information that is relevant to our goals. This could have frustrating (where *are* those keys!?) or dangerous implications (missing a pedestrian that blends in with the shadows of a tree).

Theories of attention dating back to William James [2] have stressed that attention is driven by two factors. First, bottom-up factors such as how salient an object appears compared to its surroundings (the bright yellow pedestrian sign will pop out from the gray and green surrounding objects as a feature discontinuity). Second, our internal top-down attentional templates that help guide attention toward relevant information in the environment (the pedestrian as a goal). These two factors are not assumed to be independent. Instead, psychologists believe that the two factors will interact with each other to determine which items will be attended [3]. Although the idea of attentional control via a template is ubiquitous

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†Abbreviations: ERP, Event-related potential; CDA, Contralateral delay activity.

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within the field of attention, we are still trying to understand the properties of the attentional template, as well as what alterations are made in the brain to instantiate the attentional template.

Over the last 20 years, many of the questions about attentional templates have been driven by proposals from Desimone and Duncan's [1] *biased competition* model of attention. Biased competition's key tenets are derived from research on single-cell neuronal recordings in monkeys examining neural output when stimuli are presented within a visually-responsive cell's receptive field (the area of the visual field that the cell represents). One primary tenet of the model is *competition:* the limited processing capacity of the visual system necessitates objects to compete for representation within individual cells' receptive fields. The "winner" of this competition gains access to enhanced processing, and attention is therefore an emergent property of the competition for representation. This concept was originally based on research examining how individual neuronal responses changed with spatial attention [4], demonstrating that the firing rate of a cell was driven more strongly by an attended stimulus than an unattended stimulus. The attended object won the competition and was able to dominate the neural response. This mechanism of competition has been supported by numerous findings from human neuroscience [*e.g.,* 5,6].

The second primary tenet of the model is *biasing*: the competition between objects can be influenced by current top-down goals. This concept can be appreciated in our daily experience—if I ask you the time, your goal will shift from reading these words to finding a clock and your attention will shift with your changing goals. Desimone and Duncan [1] focused on prior research examining neural evidence of this biasing. Chelazzi, Miller, Duncan, and Desimone [7] recorded from monkey inferotemporal cortex while monkeys performed a cued visual search task (see Figure 1) for a complex object (digitized magazine pictures). On each trial, the monkey would receive an object cue that indicated the search target. After a delay, two objects were presented and the monkey would receive a reward if they made a saccade to the cued item.

Chelazzi and colleagues [7] focused on the neural responses when two complex objects were in the cell's receptive field during the search, one that led to strong neuronal firing when presented alone (good stimulus) and one that led to weak firing when presented alone (poor stimulus). Prior research had shown when two objects were placed in the receptive field of an IT cell, the cell would have a lower response than the best object presented alone, indicating that the cell was being driven by both objects when there was no attentional task [8]. However, in the Chelazzi study [7] when the monkey needed to perform a cued visual search task by moving his attention to one of the objects to complete his task, something interesting happened. On trials where the monkey directed his attention to the good stimulus, the neuronal firing remained strong throughout the search period. However, when the monkey directed its attention to the poor stimulus, neuronal firing dropped off substantially 200 ms after the search array came on. It was almost like the receptive field had shrunk around the poor stimulus, with no indication that the good stimulus was even in the receptive field. This demonstrated that attention could bias the competition between the good and poor stimuli, leading to one stimulus driving the neuron's firing rate.

The Chelazzi and colleagues study [7] also found that when the good stimulus served as the search target, there was a sustained neuronal firing throughout the delay period. In this sustained firing rate, Desimone and Duncan [1] saw the potential for a mechanism behind the attentional template. The sustained firing rate had previously been shown in working memory tasks where information needs to be maintained for a short time before being tested. Desimone and Duncan concluded that the sustained activity derived from holding an item in working memory could be enough to *bias* the competition toward stimuli that match working memory, with the sustained activity adding to the bottom-up drive from the incoming object. They stated, "The top-down selection templates for both locations and objects are probably derived from neural circuits mediating working memory" (p. 217). With this conclusion, Desimone and Duncan created the first clearly proposed neural mechanism behind the attentional template.

In this review, I will focus on research over the last 20 years that has tested the second tenet of Desimone and Duncan's [1] model—the relationship between attentional templates and working memory. I will focus on the literature examining this mechanism in relation to *content-based attention* [6], which is differentiated from spatial attention.[1] (The term content-based attention seems more appropriate than feature-based attention, as it indicates that the template may be composed of one or more visual features or an object representation, given that the original biasing in biased competition came from com-

[1]Although many theories of attention suggest that location and features are just two paths to control attention, research from human electrophysiology suggests that the mechanisms supporting spatial and feature-based attention are very different [9]. Spatial attention can affect the first wave of processing of incoming visual information [10], and working memory effects on spatial attention are thought to conform to the strong linkage between working memory and attention proposed by biased competition [11]. However, the earliest effect of feature-based attention on ERPs occurs hundreds of milliseconds later [12], and is applied globally [13]. Given the fundamentally different mechanisms subserving attentional control effects in these two systems, it seems reasonable to consider them separately.

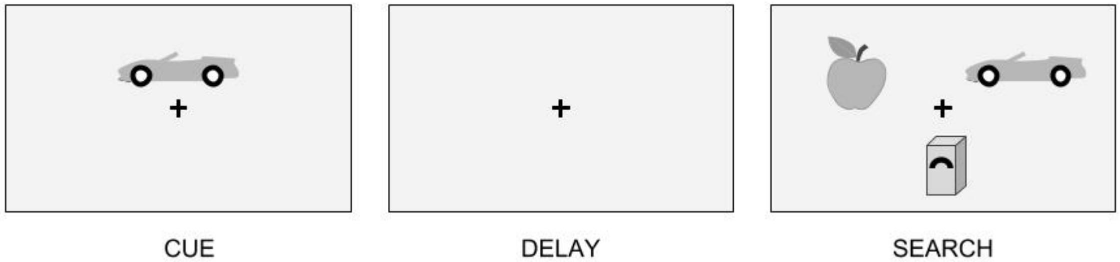

Figure 1. Example of the typical trial sequence in a cued visual search task. First, the cue is presented. Next, there is a delay period where the participant must remember the cue. Finally, a search array is presented, and the participant must look for the target. The response necessary can vary depending on the study, but typical responses include fixating gaze on the target, or pressing a button to respond to indicate target presence/absence, the location of the target, or indicating an aspect of the target (*e.g.,* facing left or right). Reaction times for the response determine how long it takes to find the target. The specific stimuli used also differ based on the study, and may include objects or simple features like colors. The cue may change on each trial or remain the same for a number of trials.

plex objects.) This review is not meant to be exhaustive[2], but rather to showcase examples of the impact of biased competition on our understanding of attentional control. We will focus on research that supports and challenges the link between working memory and attention, and conclude with a call for new theories that can help synthesize the existing empirical data and lead to new predictions to drive the field forward for the next 20 years.

MULTIPLE SOURCES OF ATTENTIONAL INFLUENCE

One of the testable predictions from Biased Competition [1] is the strong connection between working memory maintenance and attentional templates. According to biased competition, the enhanced neural activity from working memory maintenance is the mechanism behind the attentional template. Many studies in the 2000's examined whether working memory maintenance is equivalent to an attentional template by measuring whether items that match the contents of working memory were attended more than other items in the visual field. In other words, this research determined whether working memory "guided" attention. Some studies assessed working memory guidance by determining whether a working memory item will be attended when there is no task, or when attending to the memory-matching item is compatible with the goals of the current task. In these studies, participants performed a working memory task, and were presented with multiple items during the delay interval, one of which could match the contents of working memory. These studies have consistently shown that working memory representations are attended more frequently than other representations [18-22]. However, these studies do not lead to the conclusion that the influence of working memory representations on attention is involuntary, because the results would be equally compatible with an alternative interpretation that individuals are directing their attention to memory-matches voluntarily. One reason to voluntarily direct attention to memory-matching items during search would be to serve as an aid in the concurrent task of maintaining the memory representation [23].

Many other studies made a stronger test of the involuntary influence of working memory on attention by measuring whether memory-matching items will be attended even though they are not beneficial for (or distract from) the current task. Using this stronger test of the link between working memory and attention, many still found that items matching representations in working memory were selectively attended [19,24-28]. Some of these studies found it took longer to respond to the search target (longer reaction times) when a memory-matching distractor was present in a search array, in contrast to when no memory-matching distractor was presented. Longer reaction times when a memory match is present were in line with the conclusion that the memory-matching item was attended prior to finding the search target. Others measured eye-movements and found memory-matching distractors were fixated, *i.e.,* overtly attended, more than other distractors [25]. Based on the evidence that memory-matching items were selected even though attending to

[2]One notable omission is a discussion of the specific brain areas related to content-based attention. A recent review of animal neurophysiology related to the neural mechanisms of attention [14] highlighted the fact that we know more about the neural basis of spatial than content-based attentional control. However, recent work supports the role of prefrontal cortex as the source of top-down content-based attention [15,16], for a recent review see [17].

them did not match the goals of the current task, a review paper from 2008 concluded “guidance of selection from working memory occurs automatically, even when it is detrimental to task performance” (p. 342; [29]). These findings were compatible with the strong linkage between working memory and attention proposed by the biased competition theory.

In contrast, other studies failed to find evidence that working memory representations guide visual selection using similar behavioral methods [23,30-31]. Some of these studies even showed a speeding of search for another target when working memory distractors are present in the array, suggesting that the items can be actively avoided. It was difficult to reconcile these behavioral findings with the support for automatic working memory guidance of attention described above.

In order to provide more informative evidence about the working memory guidance of attention, other researchers turned to electrophysiological measures. While reaction time measures reflect all attentional allocations as well as decision related processes, the biased competition model [3] suggests that the bias from working memory should be present very early on in attentional processing because the impact of working memory is present even before visual stimuli are presented. Electrophysiological measures can be used to examine these early covert attentional processes. Carlisle and Woodman [32] used the N2pc event-related potential (ERP) component, derived from EEG measurements, to examine these early attentional priority signals. The N2pc is an index of covert visual attention that appears approximately 200 ms following stimulus presentation that is more negative contralateral to the attended hemifield, appearing hundreds of milliseconds before a behavioral response. Using this index of early covert attention, Carlisle and Woodman showed no N2pc to the working memory matching items which were consistently distractors in the search task. This provided evidence that attention was not influenced by working memory alone. In fact, there was a significant positivity contralateral to the hemifield containing the memory-matching distractor, which could be in line with active suppression (*e.g.,* the Pd component; [33]). Furthermore, in another experiment where the working memory representation served as the visual search target, early N2pc signals showed clear attention to these goal-relevant working memory matches. While alternative ERP work using different search displays supported working memory guidance of attention [34], Carlisle and Woodman [35] later replicated and extended upon this work confirming the dependence on goals. This electrophysiological research suggested that working memory can be used to create an attentional template when the information is goal-relevant, but holding an item in working memory alone does not create an attentional template. The differential influences of working memory on attention based on the participant’s goals conflict with a direct mechanism linking working memory to attentional templates.

Another challenge to the proposal that working memory maintenance is the mechanism behind attentional templates comes from findings suggesting attentional templates can be held in long-term memory. To examine whether working memory was necessary for successful visual search, Woodman and colleagues [36,37] had participants perform a visual search task while working memory was occupied. If working memory is necessary to house the attentional template, loading working memory with other items should interfere with search efficiency. One common way to examine search efficiency is to look at how reaction times increase with increasing search set sizes, the search slope. For highly efficient searches, adding more items does not alter search reaction time significantly and search slope is close to zero. For inefficient searches, the search slope will be larger than zero. In Woodman and colleagues’ study [37], when the visual search target changed on each trial, the working memory load interfered with visual search as indicated by an increasing the search slope (the slope of reaction time by number of items in the visual search). This suggested working memory was necessary for visual search. However, in a second experiment, where the visual search target remained the same across a large number of trials, the working memory load had no impact on the search slope. This suggested working memory is only needed for visual search when the target changes frequently, and in situations with a stable target it was inferred that long-term memory may be used as an attentional template (see also [38]).

Subsequent electrophysiological research sought to confirm when working memory was being used to house the search template. This work measured an ERP index of working memory, the contralateral delay activity (CDA; [39]). Participants received a visual cue indicating the search target for the upcoming search task, and the CDA was measured during the delay period to determine if participants were maintaining the cued attentional template in working memory. A CDA working memory component was found prior to visual search when the target changed frequently, but not when the target remained the same [40-43], replicating the conclusions of the prior behavioral work [37]. This suggested that working memory could hand off the template to long-term memory if the target remained unchanged over many trials. In one experiment, this handoff of the attentional template between working memory and long-term memory seemed to happen within the first seven trials of repeated search [41], as indicated by a significant reduction in the CDA across seven trials of repeated search. The timing of this handoff is similar for easy and difficult search tasks [44]. As the CDA decreases, another component, the P170, comes online suggesting an increased reliance on long-term memory representations [43]. Interestingly, after the template "handoff" to long-term memory, it seems that working memory attentional templates can also be reactivated on highly rewarded trials [45]. On these highly rewarded trials, both the CDA and the P170 were present, suggesting it is possible to simultaneously utilize working memory and long-term memory templates. Long-term memory representations should also be critical in hybrid visual search tasks where participants must look for one of many possible search targets on any one trial [46], although the access to long-term memory may occur after a potential target is fixated [47]. Overall, the evidence that long-term memory can be the source of attentional templates suggests that there are multiple sources of top-down attentional control.

The idea that templates may be maintained in long-term memory was used in order to try to generate a single explanation for the earlier conflicting evidence that says working memory *can* influence attention with the evidence that it does not always do so. Olivers and colleagues [48] proposed two states within working memory. When an item is maintained in the 'active state', it creates an impact on attention. However, when an item is maintained in the "accessory state," it has no impact on attention. When the visual search target was consistent across many trials, presumably the attentional template was maintained in long-term memory [37,41] and any other item maintained in working memory was capable of occupying the "active state" leading to attentional guidance toward working-memory matching items in the visual field. However, when the visual search target varied across trials, the target representation would have to be maintained in working memory and would occupy the "active state." Any other items in working memory would be relegated to the "accessory state" and have no impact on attention. This proposal was a modification of biased competition's [1] proposed mechanism in that only one item in working memory has an influence on attention. This distinction helped to rectify the conflicting results and describe when working memory should influence attention and when it should not (but see [23,32,35] for results that show no influence of working memory on attention with consistent targets).

One implication of the proposed two-states in working memory is that only a single item maintained in working memory should have an impact on attention. This proposal has led to another wave of research about how many items in working memory can influence attention. Currently, some evidence supports a single item in working memory that can impact attention [49-52] by showing no impact of other items in memory on attention. Other studies suggest multiple items in working memory can influence attention [53-55]. This debate is still ongoing and will likely drive continued research over the coming years.

At the same time that researchers were trying to uncover the relationship between working memory and attentional control, another set of research emerged focusing on the long-term influence of reward on attentional processing. Anderson, Laurent, and Yantis [56] showed that if participants are rewarded for finding a search target on a set of trials, an attentional bias would remain for the rewarded color on a subsequent task, even though the reward structure was removed. The bias from prior reward also occurred when the later task involved rewarding a new target [57]. Could this influence of reward on attention be driven by a working memory mechanism, as proposed by biased competition? This bias from prior reward has been shown to last for over six months [58], making it very unlikely that working memory drives the effect. This long-term effect of reward on attention does not fit clearly with the simple dichotomy of bottom-up or top-down factors influencing attention [59]. While this line of research was not specifically aimed at testing the relationship between working memory and attentional control, it adds to the previously discussed evidence suggesting that there are multiple sources of attentional impact.

Overall, the proposed mechanism of attentional templates from biased competition [1] has led to a wave of research on the intersection of working memory and attention. While this research has suggested that working memory maintenance alone is not sufficient or necessary for the generation of the attentional template, much research does indicate that the mechanism of top-down control involves preparatory attentional processes to bias the incoming visual signals toward our goals (for a recent review, see [6]). Although some debates are still ongoing, this detailed analysis of the sources of attentional control has certainly expanded the field. We now have a clear recognition that the internal factors that influence attention include working memory, long-term memory, and prior reward. Future research will need to learn how these internal factors interact to guide attention.

FLEXIBILITY AND ATTENTIONAL SUPPRESSION

Another line of research branching from the work linking attentional templates and working memory examines the flexibility in the attentional template. The mechanism of attentional control within biased competition [1] suggests a clear and consistent linkage between holding an item in working memory and an attentional enhancement. Because the activity from maintaining an item in working memory is the bias, one could generate a prediction stating that the only way to shift the amount of attentional impact from working memory would be to reduce the memory activation. In this way, attention could be like a switch- the attentional bias is on if information is maintained in working memory or off if working memory is unoccupied. While most theories of attention generally focus on enhancement [60,61], the direct linkage between an increase in baseline firing rate and attentional bias within biased competition [1] makes enhancement an absolute necessity if attentional templates are exclusively derived from working memory maintenance.

If holding a representation in working memory is sufficient to create an attentional template [1,28], then it should not matter how relevant the working memory item is for the search—it should always have a similar attentional enhancement effect. Carlisle and Woodman [62] assessed this claim by providing participants with a visual cue prior to a search task, but varying the likelihood between subjects that the cue (held in working memory) would be the search target (20 percent, 50 percent, or 80 percent). If working memory matches are given an attentional advantage, we would expect to see faster reaction times when a memory match is the target (reaction time benefit) compared to when no working memory matching item is in the array. Similarly, we would expect to see slower reaction times if the working memory item is a distractor (reaction time cost). The researchers then examined reaction time costs and benefits based on the likelihood that the memory match would be the search target. They found that the costs and benefits increased with increasing likelihood that the cue indicated the search target. Performance on the memory test was very similar for the three likelihood groups, suggesting that the differential impact on attention was not due to differences in memory quality between the conditions (although these results might depend on a single item being maintained in working memory, see [63,64] for a different perspective). This suggests a flexibility in how the information in working memory can be used to influence attention, breaking the direct linkage between working memory and attention (see also [65]). Instead of attentional control being like a switch that is on or off, it may be more akin to a dial that can be fine-tuned to task demands.

An extreme prediction of flexible use of working memory would be using the contents of working memory to suppress an item. This prediction would be strong evidence against the idea that working memory maintenance activity alone determines the nature of the attentional template. While previous attention research has discussed the idea that attentional suppression of distractors may happen during the visual search process as a natural consequence of enhancement of targets [66,67], little research has focused on the concept of active attentional suppression [68].

Within the previous literature, there have been a few hints that active distractor suppression is possible. Downing [30] and Woodman and Luck [23] found that reaction times were faster when a memory-matching distractor was present in a search array compared to when it was absent, suggesting participants might be ignoring that item. Carlisle and Woodman [32] found evidence of a contralateral positivity to memory-matching items when participants knew the items would always serve as a distractor, indicating the possibility of an active suppression process via the Pd ERP component [33]. Similarly, working memory-matching distractors presented during a delay period of a working memory task led to a Pd [69], although this effect was not measured during an active visual search task.

A suppressive effect was also found in an fMRI study utilizing multi-voxel pattern recognition to examine the activation of three object categories [70]. Two categories served as potential target categories during the experiment, while a third category served as a control. The researchers compared the activation of the three object categories to look for evidence of attentional influences. They found stronger activation of the current target category than the control category, as expected. However, they also found that the distractor object category (which had been a target on previous trial, but was now a distractor) actually showed *less* activation than the control category. This suggested that the previous target category may have actually been suppressed in order to facilitate processing of the new target category, although it was not clear if this would be an active suppression process or an automatic component of switching search targets.

While hints of suppression have been shown in behavioral, ERP, and fMRI studies, only recently has research been designed to examine active attentional suppression. Arita, Carlisle, and Woodman [71] provided participants with a color cue prior to a visual search task where they looked for a shape-defined target among Landolt-C's. The search array contained objects of two colors, with all objects of one color appearing in one visual hemifield. In one block, the color cue indicated the color of the target. This cue was called a positive cue, as it could be used for the typical attentional enhancement in visual search tasks. In another block, the cue indicated the color of distractors, a negative cue that could be used to suppress. In the final block type, the color was not informative about targets or distractors in the upcoming array, a neutral cue. Importantly, both the negative cue and the positive cue were equally informative because the array contained half items of the target color and half items in a distractor color. Using either cue eliminated the need to search through half of the items in the search array. If participants can use a negative cue maintained in working memory to suppress distractors, we would expect to see reaction time benefits following negative cues compared to the neutral cues. Arita and colleagues [71] found that both the positive and negative cues led to significant reaction time benefits compared to the neutral cues (although the benefits were smaller for the negative cues). These results suggested that participants were able to use the negative cue to create a "template for rejection" and suppress the distractors, providing the first evidence of an active suppression mechanism within attentional control.

Some research has challenged the proposal that active attentional suppression is possible. Alternative explanations for the results include a location-based strategy, since the two items were always presented in opposite hemifields [72,73]. However, a recent study containing behavioral and ERP tests did not confirm these location-based strategies [74] (but see [75]), and instead supported the active suppression account. Further support for active suppression comes from a recent fMRI study examining BOLD responses following the presentation of positive, negative, or neutral cues but prior to the onset of the search array [76]. Differences in this time period should reflect the attentional preparation for the visual search task. They found differential activation between the cue types from the occipital pole to the lateral occipital area, and also in the superior parietal lobule extending into the precuneus. Behavioral performance also supported the active suppression of negatively cued colors, with significantly faster reaction times following negative than neutral cues. Negative templates seem to be represented differently in cortex [77], suggesting the possibility of separate mechanisms underlying negative and positive templates. On the whole, this research suggests that information in working memory can be used both for enhancement and suppression. Attentional control may be seen as a dial that can be turned up (enhancement) or turned down (suppression) based on task demands.

If working memory can be used for enhancement and suppression, one might question if one item in working memory might be used for enhancement while another item could be used for inhibition. Dube, Basciano, Emrich, and Al-Aidroos [78] used a preview search paradigm to assess this question. In a preview search task, participants are shown a subset of the distractors on some trials, and reaction times on the previewed trials are compared to reaction times on non-previewed trials. Previous work showed that working memory is used to create the preview benefit, as the benefit is reduced once working memory capacity is reached [79]. Dube and colleagues [78] followed up on this research by determining whether preview search was observed with a variable search target, which should be held in working memory [41]. Dube and colleagues found a preview search benefit for variable search targets, suggesting inhibition can occur when the target template is maintained in working memory. At the same time, they also found larger attentional capture effects when a distractor color singleton (a single item with a different color) matched the target template being maintained in working memory than when it did not match. This capture showed enhancement based on the target template features, while the preview effect showed inhibition based on the contents of working memory simultaneously. This research provides another example of inhibition within visual search and suggests that multiple items in working memory may influence attention in divergent ways.

Other recent research has examined a learned distractor suppression process. In these studies, participants performed a search task that sometimes contains a salient singleton distractor. This salient singleton should capture attention based on bottom-up attentional factors, and indeed this is what was found early in the experiment. Surprisingly, when the color of the salient singleton remained the same across a large number of trials, reaction times were faster when the salient singleton was present than when it was absent [80]. This indicated the participants learned to suppress the salient singleton. When the salient distractor changed to a different color in a second block, evidence of capture was shown early on in the block with a similar pattern of learning leading to suppression by the end of the block. The lack of transfer across singleton colors suggested that the learning was restricted to a specific feature value. Recent eyetracking evidence provided compelling evidence of the ability of participants to avoid the salient singleton [81], by showing that participants looked at the salient distractor *less* than the other non-salient distractors in the display (see also [82]). This surprising finding shows that the learned suppressive effect can counteract the low-level visual salience of the singleton item.

While it was originally thought that participants could not generalize across distractor colors, more recent evidence suggests that generalization is possible. Vatterott, Mozer, and Vecera [83] showed that although generalization across salient colors did not occur when a single salient distractor color was presented in a block, when participants were shown a mix of three salient distractor colors, their experience generalized. In a later block with a new distractor color, the group that had only been exposed to a single color were captured by a new color, but the mixed color group was not captured. In addition, Won and Geng [84] showed evidence of generalization to nearby distractor colors. While the learned suppression effect is now well established (see [85] for a recent review), the exact mechanisms behind this process are less clear. Future research will need to examine whether there is overlap between the cued active attentional suppression described above and learned

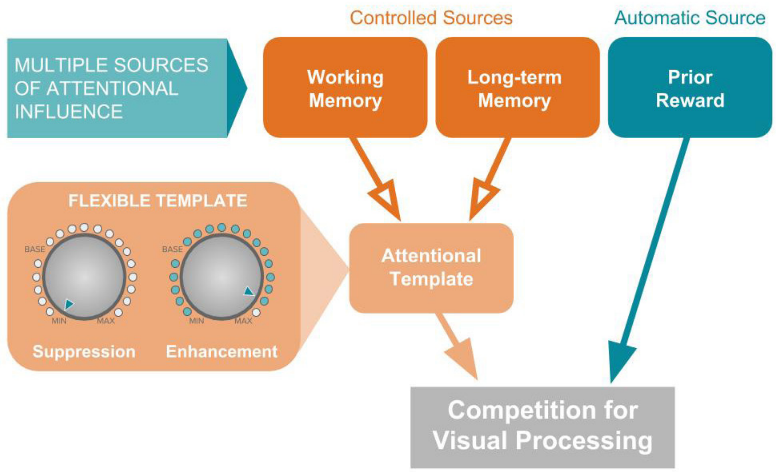

Figure 2. Multiple sources of attentional influence and flexibility in controlled attentional processes. Working memory and long-term memory can both be the source of the attentional template. This template can lead to both enhancement and suppression, like a dial that can be turned up or down based on current task demands. Reward has an automatic influence on attention that is not driven by current task demands or goals.

attentional suppression.

ATTENTION IN MEDICINE

How does the study of the cognitive processes associated with attentional control relate to medicine? General executive functions include aspects of inhibition and selective attention, and deficits in executive functions have been highlighted in multiple mental health disorders including addiction, ADHD, and Schizophrenia [86]. Learning more about the processes associated with selective attention, and especially active attentional suppression, may help to clarify what processes are disrupted in these disorders. In order to properly characterize what cognitive functions are disrupted in clinical conditions, we must first have a clear understanding of how the cognitive processes work in typical individuals. This section will touch on two examples of the intersection of our understanding of attention and aspects of medicine.

Individuals with Schizophrenia have long been understood to have deficits in attention. However, these deficits have frequently been assessed with one type of attentional test, the continuous performance test [87]. The continuous performance task is most associated with attentional vigilance, which is sustained task performance over a long period of time. We know that there are multiple facets of attention [88], with vigilance just being one aspect of the attentional system. More recent research has parcelled out the various components of attention to try to understand the specific attentional factors that are affected in Schizophrenia. For instance, individuals with schizophrenia seem to have a specific deficit in attending to a lower-salience potential target in the presence of a high-salience distractors, but intact processing when the task demands require focusing on higher salience items [89]. The speed of attention as measured by ERPs [90] to a salient visual target was also intact in individuals with Schizophrenia. These studies highlight that although individuals with Schizophrenia have deficits in attention, not all attentional processes are impaired. Examining these individual components of attention helps to paint a clearer picture of which specific components of attention are impaired in Schizophrenia [91].

Another place where attention research has been applied to the field of medicine is in understanding the attentional processes required for radiographers to successfully detect abnormalities. When decomposing the tasks of radiographers, it seems clear that the process is similar to a visual search task: Radiographers need to look for an abnormality (target) among potential distractors (normal tissue). Radiographers can identify an abnormality above chance, even prior to locating the abnormality [92]. Different radiographers utilize different search strategies, and these strategies can lead to differential rates of finding abnormalities [93]. Applying the knowledge and techniques gained from our understanding of visual search in typical psychology experiments to address the real-world challenges of medical image screening is an important and ongoing challenge [94]. These examples from translational research on attention deficits in Schizophrenia and attentional processes involved in medical image screening provide a few examples of why understanding basic attentional processes have important implications for medicine.

CONCLUSIONS AND OUTLOOK

Theories and models of attention help us understand how attention works. Broadbent [95] provided one of the first models of attention and suggested it could be used both as a formal theory and as a "useful mnemonic for the results of a number of experiments." Desimone and Duncan's biased competition model [1] followed this tradition and summarized research findings while making inductive assumptions about the broader attentional system. This work invited further examination into the relationship between working memory and attentional control, and we have Desimone and Duncan's exceptional work to thank for this progress.

This review has showcased examples of the impact of Desimone and Duncan's [1] biased competition on our understanding of attentional control. Research has confirmed the biased competition proposal that information in working memory can be used to control attention [48], and we now know that long-term memory [41] and reward [56] also have important influences on attention. We have also discovered that the attentional templates are far more flexible than previously appreciated [62]. The extreme example of negative templates suggests information in working memory can be used to actively suppress memory-matching stimuli [71,74,76]. This flexibility suggests that our attentional control system may be like a dial that can be turned up to enhance items matching a template or turned down to suppress items matching a template. This research led to substantial shifts in our understanding of the internal factors related to attention (Figure 2).

As our understanding of the factors influencing attention has expanded, the time is ripe for a new attentional theory that integrates these findings into a comprehensive theory. This new theory should summarize what we know about the multiple factors that drive attention and explain the flexibility of attentional control highlighted by negative templates. In addition, the theory should follow the example of Desimone and Duncan [1] and make bold, neurally plausible proposals about how these factors interact to drive our attentional processing. These proposals will create new research questions to drive attention research for the next 20 years.

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