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REVIEW

Preparatory attention in visual cortex

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Top-down attention is the mechanism that allows us to selectively process goal-relevant aspects of a scene while ignoring irrelevant aspects. A large body of research has characterized the effects of attention on neural activity evoked by a visual stimulus. However, attention also includes a preparatory phase before stimulus onset in which the attended dimension is internally represented. Here, we review neurophysiological, functional magnetic resonance imaging, magnetoencephalography, electroencephalography, and transcranial magnetic stimulation (TMS) studies investigating the neural basis of *preparatory* attention, both when attention is directed to a location in space and when it is directed to nonspatial stimulus attributes (content-based attention) ranging from low-level features to object categories. Results show that both spatial and content-based attention lead to increased baseline activity in neural populations that selectively code for the attended attribute. TMS studies provide evidence that this preparatory activity is causally related to subsequent attentional selection and behavioral performance. Attention thus acts by preactivating selective neurons in the visual cortex before stimulus onset. This appears to be a general mechanism that can operate on multiple levels of representation. We discuss the functional relevance of this mechanism, its limitations, and its relation to working memory, imagery, and expectation. We conclude by outlining open questions and future directions.

Keywords: visual search; top-down attention; biased competition; neuroimaging; search template

Introduction

Our daily-life visual environments, such as city streets and living rooms, contain a multitude of objects. Out of this overwhelming amount of sensory information, our brains must efficiently select, recognize, and act on those objects that are relevant to current goals. Consequently, visual stimuli compete for neural representation: when one object is favored, others are lost. Top-down attention is thought to be the process that biases this competition in favor of those stimuli that are relevant to current goals.[1] These top-down attention biases modulate visually evoked responses, as reviewed elsewhere.[2–5]

But attention does not always start at the moment a scene is processed by the visual system; it often starts before, when internal goals are established. For example, when crossing a road, we decide to look out for (i.e., attend to) cars before physically looking in both directions to inspect the scene for the presence of cars. This intuitive concept of *preparatory attention* was described by William James as "The image in the mind *is* the attention; the *preperception* [. . .] is half of the perception of the looked-for thing."[6] Preparatory attention (also referred to as *attentional set*, *attentional template*, or *search image*) has subsequently played an important role in theories of attention.[7–11] What are the neural mechanisms underlying preparatory attentional states?

One possibility that has gained substantial experimental support—and is the focus of this review—is that preparatory attention acts through the selective preactivation of the visual cortex, before stimulus onset and thus in the absence of visual input.[1,12] In this way, preparatory attention would bias visual processing in favor of objects sharing this attribute once the scene appears.[13] The existence of preparatory attention–related activity in the visual cortex has been relatively well established and accepted in

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the domain of spatial attention: focusing attention on a location in space is accompanied by increased baseline activity in parts of the visual cortex that are visually responsive to input at the attended location.[14,15]

In daily life, however, our goals are typically related to nonspatial attributes, such as when looking out for cars or when searching for our keys. Depending on what we look for and on the environment in which we find ourselves, these nonspatial attributes can range from low-level features to high-level object categories. Here, we use the term *content-based attention* (rather than *feature-based attention*) to refer to attention to nonspatial attributes of varying complexity. After briefly reviewing the behavioral consequences of spatial and content-based attention, we review evidence for spatial and content-based preparatory attention effects in the visual cortex from different cognitive neuroscience methods. This is followed by discussions of the ways in which preparatory attention may facilitate behavior, of preparatory attention effects at different levels of the visual hierarchy, and of similarities and differences between preparatory attention and related constructs, such as working memory (WM), imagery, and expectation. We conclude by outlining open issues and future directions.

The influence of spatial and content-based attention on behavioral performance

A large body of psychophysical work has demonstrated that voluntary spatial attention can improve performance in a range of perceptual tasks, including simple stimulus detection and localization, discrimination, and identification.[16] Perhaps most famously, Posner *et al.*[17] showed that prior information about the location of an upcoming stimulus provided by a symbolic cue (e.g., specific digits referring to specific locations) speeds up simple detection responses. The use of symbolic cues, which have no inherent spatial information but must be actively interpreted by the observer, is necessary to conclude that the effect indeed reflects voluntary rather than reflexive spatial orienting. Thus, observers can actively use prior information about the location of the upcoming stimulus to voluntarily direct spatial attention to the cued location. Further work adopting such spatial cueing paradigms demonstrated that spatial attention improves both response speed and perceptual sensitivity for a variety of different stimuli and tasks, from improving contrast sensitivity and luminance detection to orientation, letter, and form discrimination.[18–20]

Does content-based attention also, like spatial attention, improve discrimination and detection sensitivity? Most studies on the effect of prior information about stimulus content examined whether advance knowledge of certain basic stimulus features, such as orientation, color, or motion direction (often referred to as feature-based attention) can influence perceptual performance. As with top-down spatial attention, to conclude that such effects reflect voluntary attention rather than involuntary bottom-up processes (e.g., priming) it is necessary that information about the upcoming stimulus is provided by symbolic cues (e.g., words such as "vertical") on a trial-by-trial basis.[21] Studies following this approach provide clear evidence that prior information about a specific stimulus feature (e.g., approximate stimulus orientation) can improve discriminability of this particular feature (e.g., distinguishing specific orientations[22,23]). Additionally, when a target needs to be discriminated from highly similar distractors, such as in difficult visual search tasks, prior knowledge of target features improves performance.[24] Thus, similar to spatial attention, content-based attention improves stimulus discrimination and identification.

Whether, like spatial attention, content-based attention also improves simple stimulus detection (i.e., without the need to recognize the stimulus) has been more controversial, with several studies failing to obtain evidence for an effect on such early levels of perceptual processing[17,20] (for reviews, see Refs. 21 and 25). One demonstration of an influence of content-based attention on perceptual selection is the finding that attentional capture by irrelevant distractors is contingent on the stimulus attributes observers look for.[26] For example, when looking for a target defined by color, abrupt-onset distractors do not capture attention, while color distractors do. Conversely, when looking for a target defined by abrupt onset, color distractors do not capture attention, while abrupt-onset distractors do.[26] Direct evidence for an effect of content-based attention on detection performance comes from recent work using accuracy-based measures of simple stimulus localization and detection, showing that content-based attention can enhance perceptual sensitivity.[27–29] For example, Stein and

Peelen[29] provided participants with prior information about the orientation of an upcoming grating through a word cue (e.g., "horizontal") and found that accuracy in detecting and localizing briefly presented, low-contrast targets was better when the orientation of the target matched the word cue, even though orientation was irrelevant to the detection task. The beneficial influence of content-based attention appears to reflect a general mechanism that can operate at different levels of abstractness of stimulus content, from simple stimulus features to basic-level object categories and even superordinate categories.[30,31]

These findings demonstrate that content-based attention can influence performance in even the most basic perceptual tasks, similar to spatial attention. This does not necessarily imply that content-based and spatial attention rely on identical cognitive and neural mechanisms. Indeed, there is psychophysical evidence that content-based and spatial attention modulate target processing in distinct ways, suggesting different effects on the neural population response.[23,32] Neuroimaging and neurophysiology studies, reviewed in the following sections, have established the neural mechanisms of preparatory spatial and content-based attention.

Neural evidence for preparatory activity in the visual cortex

Single-cell electrophysiology

An important source of evidence for attention effects in the visual cortex comes from single-cell recordings in monkeys. A well-established finding in this literature is that spatial attention increases the firing rate in neurons with receptive fields (RFs) covering the attended location.[4,12,16] Importantly, this effect starts while animals *prepare* to detect a target at a specific spatial location; that is, in the absence of stimulation and before stimulus onset. In one study, firing rates of neurons in areas V2 and V4 increased by 30–40% when monkeys covertly attended to a location inside the neurons' RF in preparation of a detection task, relative to when attention was directed outside the RF.[15] Spatial attention thus increases the baseline firing rates of visual cortex neurons in a spatially specific manner, providing evidence for preparatory spatial attention effects in the visual cortex.

Does a similar preparatory attention mechanism exist when the attended dimension is not location but a nonspatial stimulus attribute? To address this question, Chelazzi *et al.*[33,34] recorded activity of inferotemporal (IT) neurons in monkeys performing a memory-guided visual search task on complex stimuli, such as colored pictures, textures, and patterns. A picture cue indicated the behaviorally relevant object, and, after a brief blank delay, monkeys were required to saccade to the target object within an array of multiple objects. IT neurons are characterized by high-order visual-response properties, such as selectivity for complex visual patterns (colored shapes and textures) and large RFs.[35] Exploiting such properties, for each recorded cell the authors selected a "good" stimulus (evoking a strong response), a "poor" stimulus (evoking little or no response), and a "neutral" stimulus (evoking an intermediate response). During the delay between the cue and the search array, in the absence of visual stimulation, most cells (52%) showed sustained higher activity (30–40% above baseline levels) following the good stimulus cue relative to the poor stimulus cue. If the target changed on a trial-by-trial basis, this effect was observed during the delay following the offset of the cue; but, interestingly, if the target was constant throughout a block of trials and therefore could be predicted, this effect was observed even before cue onset. Control experiments showed that changing the type of response (from a saccadic movement to a lever release) did not influence the content-specific preparatory baseline increase. Furthermore, if the cue was no longer behaviorally relevant, the effects disappeared. These controls demonstrate that prestimulus baseline increases could not be attributed to specific behavioral responses or long-lasting sensory aftereffects, but rather reflected the maintenance of specific behaviorally relevant representations in preparation for a visual search task.

The studies reviewed here show that preparing to detect a stimulus in an array results in increased firing rates of those visual cortex neurons that code for the dimension that distinguishes the target from distractors, both when the dimension is spatial location and when it is a nonspatial attribute, thus revealing similarities in the neural basis of preparatory attention to space and content.

Functional magnetic resonance imaging

Human functional magnetic resonance imaging (fMRI) studies have built on these findings, investigating top-down attention effects in the whole visual system using more complex tasks. Initial studies focused on the effects of top-down spatial attention on visual cortex responses. A key finding was that covertly attending to a location in space, in the absence of visual stimulation, results in topographically specific blood oxygen level–dependent (BOLD) signal increases: voxels in the visual cortex containing a representation of the attended location (as established by retinotopic mapping) increased their activity levels before stimulus onset.[14,36–39]

Subsequent fMRI studies investigated whether similar effects may be found for attention to nonspatial attributes, such as low-level features, object shape, and object category.[40–54] In an early study, Chawla *et al.*[40] revealed feature-specific activity increases in preparation of a feature-detection task. A cue instructing subjects to attend to either color or motion elicited BOLD activity increases in motion-sensitive areas (V5) in the "attend motion" condition and in color-sensitive areas (V4) in the "attend color" condition. Therefore, during the preparatory phase, neuronal activity increased above baseline levels in brain regions specialized for the analysis of that specific stimulus dimension. Studies employing more complex stimuli extended these results to attention to other object attributes.[41,45–48,52,53] For example, Stokes *et al.*[53] used multivariate pattern analysis (MVPA) to provide evidence for shape-specific preparatory activity patterns in the lateral occipital complex: classifiers trained to discriminate activity patterns elicited by different visually presented shapes ("X" versus "O") could differentiate which of these shapes participants were subsequently preparing to detect in visual noise. In another study,[47] participants were instructed, using word cues, to detect faces or houses. Activity in face- and house-selective regions of high-level visual cortex increased in response to the cue in a category-selective manner. To study whether such anticipatory responses play a role in more naturalistic visual search tasks, Peelen and Kastner[46] measured brain activity patterns in participants who were cued to detect cars or people in cluttered natural scenes. Results showed that activity patterns in the object-selective cortex (OSC) distinguished the two preparatory states. Importantly, the strength of this effect in the OSC (but not in the early visual cortex (EVC)) predicted both the speed and the accuracy with which participants detected the objects, linking preparatory fMRI activity to behavioral performance.

Taken together, fMRI studies have provided convincing evidence for preparatory spatial attention and preparatory content-based attention in the visual cortex. Using a variety of tasks, and targeting different levels of representation (from low-level features to object category), studies have consistently demonstrated that attention to nonspatial stimulus attributes evokes activity in those parts of the visual cortex that are selectively responsive to these attributes. Multiple studies have shown a positive correlation between the magnitude or selectivity of prestimulus activity in the visual cortex and behavioral performance.[41,42,46,47,52,53]

Magnetoencephalography/electroencephalography

A well-known limitation of fMRI is its slow temporal resolution, making it insensitive to oscillatory neural activity occurring at subsecond resolution, which is increasingly recognized as playing an important role in attention.[2,55–58] Magneto- and electroencephalography (MEG/EEG) studies, capitalizing on the excellent temporal resolution of MEG/EEG, have provided intriguing evidence for the involvement of oscillatory activity in preparatory attention. In the context of spatial attention, several studies have found evidence for retinotopically specific alpha-band (7.5–12.5 Hz) activity modulations during the prestimulus period: the power of activity in the alpha band is increased over occipital sensors contralateral to the to-be-ignored location and decreased over occipital sensors contralateral to the to-be-attended location.[59–71] Alpha activity increases may reflect the suppression of irrelevant and potentially distracting information, reducing excitability and gating the transmission of information to further processing stages.[63,65,72] Alternatively, top-down changes in alpha activity may be a secondary consequence of target upregulation,[73] with alpha activity decreases reflecting increased spatial attention[71] and enhanced neuronal excitability.[74]

Interestingly, recent studies show that these preparatory alpha inhibition/release mechanisms operate similarly for content-based attention. For example, Snyder and Foxe[75] measured EEG activity while participants performed a feature-detection task similar to the task used in the fMRI study by Chawla *et al.*[40] reviewed above. They asked subjects to pay attention to the color or motion of a random dot display via a word cue and found that prestimulus alpha activity increased over ventral visual regions when color was the irrelevant feature; conversely, alpha activity over dorsal regions increased when motion was the irrelevant feature, consistent with how the visual system segregates the processing of motion and color information to dorsal and ventral regions, respectively.[76,77] Another study[78] showed that prestimulus alpha power over the dorsal visual cortex increased when participants maintained a representation of face identity (putatively engaging the ventral visual cortex), relative to when they retained a template of their orientation (putatively engaging the dorsal visual cortex) in preparation of a discrimination task. Finally, Knakker *et al.*[79] investigated attentional selection of spatially overlapping face/word stimuli, cueing the relevant category before stimulus onset. In line with the left-hemisphere lateralization of word processing, prestimulus alpha power increased over the right occipitoparietal cortex when words were attended relative to when faces were attended.

Together, these results provide further evidence for preparatory attention effects in the visual cortex, now measured as changes in oscillatory activity in the alpha frequency band. They suggest that prestimulus alpha modulations in the visual cortex may constitute a general mechanism of attentional selection, where increases in alpha power index functional inhibition and decreases in alpha power reflect release from inhibition. Like the behavioral, neurophysiology, and fMRI results reviewed above, results from MEG/EEG reveal a remarkable similarity between spatial and content-based preparatory attention mechanisms.

Transcranial magnetic stimulation

The neural evidence reviewed so far is correlational in nature, showing various neural correlates of preparatory attention in the visual cortex. An important question is whether preparatory neural activity is directly (i.e., causally) related to subsequent attentional selection and behavioral performance or whether this activity is purely epiphenomenal. Transcranial magnetic stimulation (TMS) is a useful tool to address this question because it allows for the disruption of neural activity with sufficient temporal and anatomical resolution to ensure that activity is disrupted before stimulus onset and at location- or content-selective brain regions hypothesized to be involved in preparatory attention. A challenge of this technique, however, is that any disruption by TMS is short-lived, potentially allowing for the reinstatement of top-down attention signals. Nevertheless, several recent studies have used this approach to provide evidence for a causal relationship between preparatory neural activity in the visual cortex and behavioral performance.

Studying preparatory spatial attention, Romei *et al.*[80] applied rhythmic TMS over occipitoparietal areas at alpha frequency (10 Hz) before stimulus onset, thereby entraining oscillatory activity at this frequency. Relative to TMS at control frequencies (5 and 20 Hz), such alpha stimulation had a retinotopically specific inhibitory effect: it impaired target visibility in the visual hemifield contralateral to the stimulated hemisphere but enhanced it ipsilaterally. The spatial and frequency specificity of these results provide strong evidence that preparatory oscillatory activity in retinotopically organized visual cortex is causally involved in stimulus detection.

TMS has also provided evidence for causal involvement of content-based preparatory activity in attentional selection. In two experiments, Reeder *et al.*[81] followed up on an earlier fMRI study that localized preparatory activity for naturalistic visual search to a region in the posterior temporal cortex (pTC).[46] Applying TMS over this region 100 or 200 ms before stimulus onset, while participants were preparing to detect cars or people in natural scenes, impaired search performance relative to TMS over control regions (vertex and EVC). Importantly, these effects were specific to category-level search: relative to prestimulus TMS over the EVC, prestimulus TMS over the pTC impaired the accuracy of category-level search, while no difference was observed in a control task in which participants detected individual exemplars based on lower-level features.

These TMS results indicate that preparatory activity in the visual cortex directly facilitates subsequent stimulus detection; inhibiting this activity (or entraining inhibitory activity) results in impaired behavioral performance in detection and visual search tasks. Given the unique value of this technique in providing causal evidence, more TMS studies are needed to characterize the causal role of spatial and content-based preparatory attention. Furthermore, systematically varying the timing of the TMS pulse relative to scene onset would allow for testing when top-down signals can be reinstated after these have been disrupted.

How does preparatory activity facilitate perception?

The studies reviewed here provide evidence that preparatory activity in the visual cortex facilitates the attentional selection, detection, and recognition of visual stimuli. How might preparatory activity facilitate these processes? One possibility is that the processing of the cue automatically primes the representation of the target object or, in the case of spatial attention, its location, leading to enhanced visual sensitivity. Automatic priming is particularly relevant to consider for facilitatory effects observed in studies using exact image cues that depict the target object or when the target dimension is blocked so that the target is repeated across trials.[21] But a priming account cannot be fully excluded in studies using symbolic cues (e.g., a word indicating the target object) either: activating the semantic representation of the object (reading the word) may spread to sensory systems, thereby potentially facilitating the perceptual processing of the primed object.[27] However, automatic priming (or spreading of activation) does not fully explain the spatial and content-based preparatory attention findings reviewed here. For example, studies have shown that sustained preparatory activity in the visual cortex is only observed when the cue is actively maintained in preparation for a subsequent visual task[33,34,49] and that preparatory activity in response to a symbolic cue reflects the specific requirements of the subsequent detection task.[81] These and other findings are not in line with automatic priming accounts.

Rather, we interpret findings of preparatory visual cortex activity as primarily reflecting voluntary attention-related activity. This activity has a clear purpose: it serves to bias processing in favor of attended items,[1] such that items that are attended gain a competitive advantage proportional to the degree to which they match the internal attentional state. In the context of a visual search task, top-down attention biases have been shown to highlight relevant locations in the scene in parallel, preceding saccades to these locations.[82] These findings confirm predictions of the guided search model, in which spatial attention is serially directed to locations in a scene based on an activation map that integrates top-down and bottom-up feature maps.[83] Content-selective preparatory attention in the visual cortex may thus constitute a neural correlate of the top-down feature map. The finding that preparatory attention activates the same neural populations that respond to bottom-up visual input supports the hypothesized integration of top-down and bottom-up feature maps.

Importantly, however, to be most effective in guiding attention to targets, preparatory attention would need to be directed to those representations that optimally distinguish the target from the distractors rather than simply activate the representation of the target.[84–88] We would thus predict that preparatory attention effects in the visual cortex for the same target differ as a function of the expected distractor set (e.g., scene context). For example, different shape features are diagnostic of the presence of people in a forest as compared with a desert. Finding evidence for distractor-dependent preparatory activity would provide further support for the idea that preparatory activity reflects attentional processes rather than automatic priming, which would not be influenced by distractor properties.

In summary, we interpret visual cortex activity in preparation for challenging detection or discrimination tasks as reflecting a voluntary attention mechanism that serves to prioritize the processing of the target, allowing the observer to efficiently achieve behavioral goals. Nevertheless, more work is needed to directly link preparatory activity in the visual cortex to subsequent attentional selection, for example by demonstrating that preparatory attention reflects the demand for attentional selection (e.g., degree of clutter[89]) and that it reflects properties that optimally distinguish targets from distractors.

Preparatory attention across the visual hierarchy

Throughout this review, we have seen similarities between spatial and content-based preparatory attention and among different levels of content-based preparatory attention, including attention to orientation, color, shape, and object category. As such, preparatory attention appears to be a general mechanism that operates across levels of the visual hierarchy: preparatory activity is observed in those regions (or neurons) that represent the

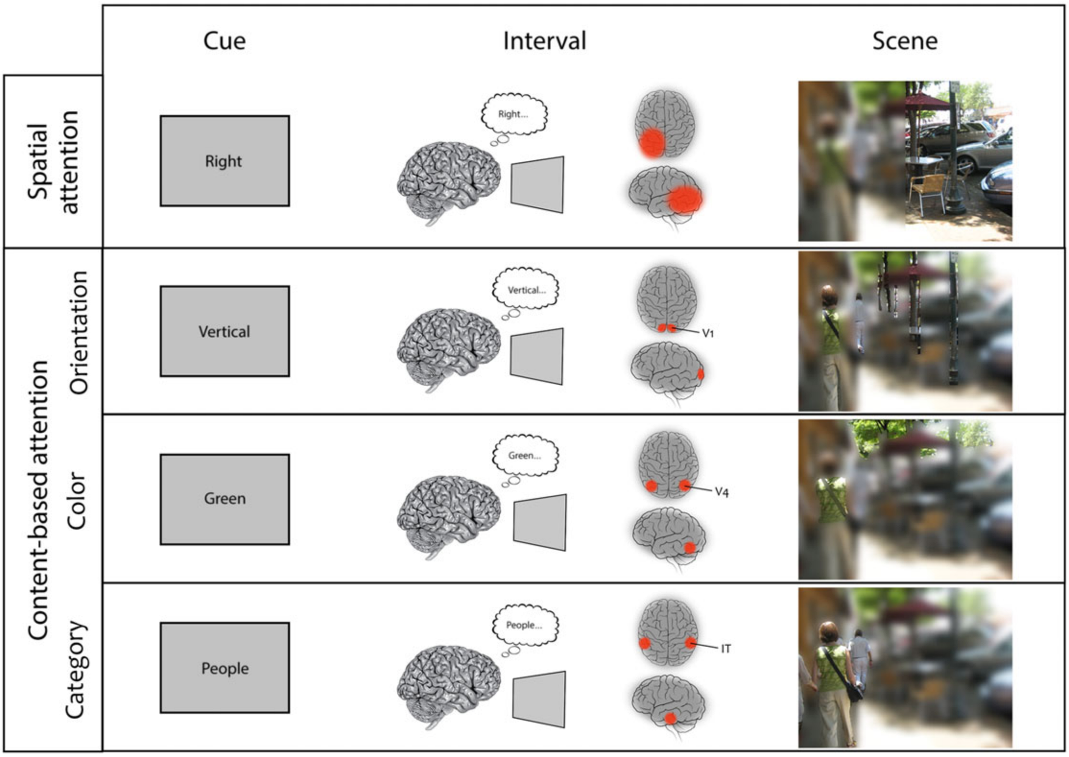

Figure 1. Schematic overview of three stages of attentional selection (from left to right) based on different goals (different rows). Goals are prompted by words indicating the task-relevant dimension (left panels). Preparatory attention is the process of internally activating task-relevant representations in the visual cortex (middle panels), leading to attentional selection in subsequently presented scenes (right panels). Preparatory attention to different stimulus attributes recruits corresponding neural populations in the visual cortex: retinotopically specific activity for spatial attention, orientation-selective activity in the primary visual cortex for attention to orientations, color-selective activity in the visual cortex (e.g., V4) for attention to colors, and category-selective activity in high-level visual cortex (e.g., the inferior temporal (IT) cortex) for attention to object categories.

task-relevant stimulus, ranging from low-level feature representations in the EVC to object category representations in the high-level visual cortex (Fig. 1). Furthermore, preparatory attention is observed not only for anatomically coarsely organized dimensions (e.g., space) but also for dimensions that are organized at a finer anatomical scale, such as object shape[53] or object category.[46]

This raises the question of whether there are any limits on what can be selectively attended. Treisman[10,90] proposed several diagnostic criteria for defining features that are separately attended, including the criterion that neural populations are selectively tuned to the feature (also see Ref. 91). In Treisman's model, the question of which object attributes count as features is an empirical question and partly depends on the experience of the observer. For example, extensive experience with particular objects or object categories might increase (and create) neural selectivity for the features characterizing these objects,[92] resulting in efficient attentional selection.[93,94] This is exemplified by the efficient detection of familiar object categories (e.g., animals, vehicles, people, cars) in natural scenes. In these tasks, attention is unlikely to be directed to a specific low-level feature, yet detection is highly efficient when preparatory attention is available.[31,95,96] One possibility is that, through experience, neurons in the high-level visual cortex have become selectively tuned to these object categories.[97,98] Alternatively, experience may increase the efficiency of attending to a set of features that together are diagnostic of the presence of the category,[10] thus reflecting efficient parallel attentional guidance by multiple separately represented features.[11] More work is needed to establish what these features are, particularly for naturalistic visual search.[99]

Drawing on the analogy with spatial attention, Maunsell and Treue[3] note that efficient implementation of feature-based attention might require a topographic organization of the feature, which would limit the potential set of features that can be attended. A related factor that may determine the efficiency with which features guide attention is the spatial specificity of the feature representations in the visual cortex; activity in feature-selective neurons with small RFs (i.e., low-level features represented in the EVC) is most informative about the feature's location. This is confirmed by behavioral studies showing that attentional selection is most efficient when attention can be directed to low-level features, for example when search is for a specific image as compared with a broader category.[100–103]

However, this does not rule out that content-based attention can also act on object representations at higher levels of the visual hierarchy.[104] This may be necessary in many real-world situations in which targets are viewed from different angles and distances. Furthermore, low-level features are often shared by other objects in a scene and may thus not be diagnostic of the target. Therefore, we expect that in naturalistic environments attention acts on intermediate-level shape representations that are to some extent invariant to changes in viewpoint and scale.[105] These representations may be located in areas beyond the EVC yet still show coarse retinotopic specificity.[106–109] A currently debated topic is whether preparatory attention can also be directed to conceptual-level representations, such as superordinate categories like furniture or food.[110–116] In the current framework, this would be possible as long as there is a set of mid- or high-level shape (or texture, or color) features that characterize the category. For abstract categories that lack such characterizing visual features altogether, preparatory attention in the visual cortex is unlikely to be an efficient mechanism of attentional guidance.[24,102]

Relation between preparatory attention and other cognitive processes

The observation of visual cortex activity in the absence of sensory stimulation is not a unique feature of preparatory attention but has also been found in tasks designed to study WM maintenance, mental imagery, and expectations. Such top-down activation of content- and location-specific visual representations may thus represent a general mechanism supporting multiple cognitive processes. However, the exact nature of top-down driven visual cortex activity may differ between tasks and paradigms, as described below. Thus, despite sharing certain neural mechanisms, preparatory attention, WM, mental imagery, and expectations may not simply be different labels referring to the same phenomenon but rather at least partially distinct cognitive processes.

Working memory

Several authors have highlighted the overlap between the constructs of attention and WM.[117–119] This similarity is evident in the tasks used for studying preparatory attention and WM. In a typical WM task, a memory cue needs to be maintained over a retention interval with no sensory stimulation. Some attribute of the memory cue is then compared to a memory probe. Thus, in both preparatory attention and WM tasks, some task-relevant attribute of a cue needs to be maintained during a delay period. Accordingly, whenever there is a temporal delay between setting a search goal and target detection, attentional preparation involves WM.[120] Conversely, attention can dynamically modulate WM content to prioritize task-relevant internal representations during the retention interval.[45]

Given this close relationship between the two constructs, it may not be surprising that visual cortex activity has been found both during attentional preparation and during WM maintenance. Indeed, there is evidence from monkey electrophysiology that delay period activity in the IT cortex supports the temporary maintenance of content-specific representations for stimuli, such as colors,[121–123] orientations,[124] shapes,[125] colored textures and patterns, images,[126–128] and other complex stimulus dimensions.[129–132] For example, using a delayed match-to-sample task with colors, Fuster and Jervey[122,123] found that, during the retention interval, a set of IT neurons exhibited content-specific delay activity, presumably reflecting the maintenance of a specific color in WM. Furthermore, cooling of this area impaired both neural firing during the retention period and WM performance.[121,133] Similarly, MVPA of human fMRI data has revealed color- and orientation-specific delay activity during WM maintenance, even in early visual areas.[43,49,134] Finally, TMS over the visual cortex modulates WM performance[135,136] and influences subsequent attentional selection.[137] The tight link between preparatory attention and WM maintenance is consistent with theoretical frameworks, such as the biased competition model. Here, an attentional template is thought to be held active in WM[138–142] until the successful completion of the task.[86]

However, although attention is often biased by WM content,[143–146] not all information held in WM influences the deployment of attention,[147–150] demonstrating that the two constructs can be dissociated.[151] For example, the capacity of preparatory attention may be smaller than the capacity of WM.[152] Other studies have shown reduced sustained delay activity for WM content that is not immediately relevant (or attended),[153,154] indicating the existence of "activity-silent" storage mechanisms.[155–157] Also, the specific kind of information carried by delay activity in the visual cortex presumably differs between tasks typically used to study preparatory attention and WM. In WM tasks, this representation needs to enable an efficient comparison of the memory cue with the memory probe. When preparing to search for a target in a multielement display or in a cluttered scene, by contrast, the attentional template needs to optimally distinguish the target from the distractors. Such task-specific goals and strategies, as well as differences in advance information and expectations, seem to require at least partially different neural mechanisms. A flexible coding scheme of top-down induced visual cortex activity may thus support both preparatory attention and WM, with the actual neural implementation depending on specific task parameters.

Mental imagery

Voluntary generation of a mental image of an object or an event is associated with visual cortex activity that mimics activity during actual perception of the same stimulus.[158–167] Similar to preparatory attention and WM maintenance, mental imagery thus also involves visual cortex activity that is purely top-down driven, generated in the absence of sensory stimulation. There are several lines of evidence for a functional and neural overlap between mental imagery and WM.[164] Mental imagery is one strategy to complete visual WM tasks, and more vivid imagery is linked to better performance in visual WM tasks.[168,169] Furthermore, an MVPA-based fMRI study found that classifiers trained on grating orientations held in WM could accurately decode which grating orientations participants formed and rotated in mental imagery.[158] This demonstrates that similar patterns of visual cortex activity support WM maintenance and mental imagery.

Considering the overlap between imagery and WM and the link between WM and preparatory attention, could preparatory visual cortex activity in attention tasks reflect mental imagery? This depends on the definition of mental imagery, an intuitive concept that has been notoriously difficult to pin down.[170] Although it is difficult to imagine mental imagery without attention, preparatory attention is unlikely to reflect mental imagery defined in a narrow sense—as vivid conscious experience of specific mental images. In studies testing for this type of imagery, participants are instructed to create and/or transform a specific mental image, whereas in preparatory attention studies participants are asked to prepare for detecting or discriminating a stimulus; in these tasks there is no incentive to put effort into consciously creating a vivid mental image (and this is not the experience one has when performing these tasks). Furthermore, in many daily-life situations, creating a specific mental image of the target object would be inefficient because targets in real-world scenes rarely match an exact image. Recent studies have confirmed that a vivid mental imagery strategy is inefficient for search in natural scenes.[46,81] And, as discussed above, preparatory attention would need to take into account both target and distractor properties rather than only reflecting the target object. However, when defining mental imagery in a broad sense, as "thinking about how something looks," this term would encompass processes such as WM and preparatory attention. In this case, it is important to note that preparatory attention-related activity has been shown to be directly relevant for subsequent task performance; that is, findings of preparatory activity are not just (i.e., epiphenomenal) imagery.

Expectation

Until recently, the terms attention and expectation were often used more or less interchangeably.[14,17,29,171] Indeed, spatial attention and content-based attention have often been studied by manipulating prior expectations about the likely location or content of an upcoming stimulus. Following the terminology adopted in the present review, preparatory attention refers to situations where these expectations are relevant for an upcoming search, detection, or discrimination task. In this framework, visual cortex activity elicited by expectations about task-relevant stimulus attributes is a neural correlate of attentional preparation.

Interestingly, recent research has experimentally dissociated the two constructs. In particular, expectation has been defined as the (implicit or explicit) knowledge of the probability of occurrence of a stimulus, independent of its task relevance. Attention, by contrast, refers to the relevance of a stimulus for an upcoming task, independent of its probability.[172] Defined in this way, expectation and attention have distinct effects on stimulus-evoked visual cortex activity: attended stimuli elicit stronger responses than unattended stimuli, whereas expected stimuli elicit weaker responses than unexpected stimuli.[173] Preparatory effects of expectation and attention may also differ,[73,174] but more work is needed to directly compare the distinct influence of content-specific expectation and attention on visual cortex activity before stimulus presentation.

Conclusions and future directions

Taken together, the studies reviewed in this paper provide overwhelming support for the idea that preparatory attention involves changes in visual cortex activity. These changes cannot be attributed to bottom-up responses because they are also observed in the absence of visual stimulation and when using symbolic or auditory cues. Intriguingly, preparatory attention effects appear highly similar for spatial and content-based attention: these types of attention similarly affect behavior and are similarly reflected in increased baseline activity in neural populations coding for the attended (spatial or nonspatial) attribute, and both are accompanied by changes in the power of activity in the alpha frequency band. Finally, both location- and content-specific preparatory activity are critical for behavior, as the strength and selectivity of this activity are correlated with behavioral measures and their disruption leads to impairments in behavioral performance. Preparatory attention is thus reflected in the top-down activation of visual cortex neurons coding for attributes distinguishing targets from distractors. This may serve as an internally generated bias that modulates the processing of subsequent visual input in favor of stimuli sharing the attended attribute—the top-down component of the biased competition model of attention[1]—thereby guiding spatial attention to likely target locations.[11,83] Research over the past 25 years has provided converging evidence for preparatory attention by employing different methods, species, and tasks, as reviewed here. This research has provided new insight into the basic mechanisms of preparatory attention and has started to reveal how these mechanisms may operate in more naturalistic situations.[104] The research reviewed here also raises many further questions that remain to be addressed. We highlight some of these questions below.

Finally, we should note that, although we have emphasized the similarities between preparatory content-based and spatial attention, there are several fundamental ways in which these dimensions differ. Space is a core principle of neural organization that is replicated across regions, not only within the visual system but across the brain as well. This makes it relatively easy to connect corresponding locations across visual, attention, and motor systems.[3] Indeed, spatial attention may be closely related to motor planning,[175–177] whereas content-based attention does not have this relationship with the motor system. Ultimately, through eye movements, attentional selection takes place in space.[178]

What is the source of preparatory attention in the visual cortex?

An important question that has increasingly generated interest concerns the source of top-down activity in the visual cortex: which regions drive preparatory activity in the visual cortex? What is the mechanism of communication? A large body of research has implicated a network of regions in the frontal and parietal cortices in the top-down control of spatial attention (for reviews, see Refs. 2 and 179–183). Several studies find that a similar network may also control attention to nonspatial attributes.[184–188] For content-based attention, the prefrontal cortex (PFC) has been considered a putative source region, as neurons in the monkey PFC carry information about the attended stimulus during the prestimulus period.[189–191] In humans, the inferior frontal junction has been identified as a candidate source region of content-based attention.[192,193] Many open questions remain, however. What is the role of parietal cortex regions implicated in WM?[194] Are there different sources for attention to different types of content (e.g., low-level features versus categories)? How are source regions connected to the visual cortex so as to selectively modulate activity in overlapping neural populations? What is the role of rhythmic synchronization in the communication between source and target regions?[56,180]

Under what circumstances is preparatory attention in the visual cortex observed?

The top-down activation of the visual cortex in preparation for a detection or discrimination task is a voluntary and effortful process that comes at a metabolic cost. This raises the question of the circumstances under which preparatory attention in the visual cortex is observed. For example, how does this depend on the motivational state of the observer? What is the role of the perceptual load of the search display?[195,196] Specifically, are preparatory attention effects still observed when there is little competition and the target is easy to find? For a full understanding of the functional relevance of preparatory attention, it would be important for future studies to investigate the circumstances that trigger preparatory attention in the visual cortex and whether (or how) this differs for spatial and content-based attention.

How does preparatory attention function in the real world?

Most studies reviewed here used highly simplified stimuli and artificial tasks; in the real world we are not cued to detect a stimulus in a briefly flashed display. Real-world scenes are rich and cluttered, yet despite this clutter visual search in natural scenes is highly efficient.[197] It will be of great interest to investigate the extent to which optimized attentional preparation contributes to this efficiency.[104] For example, scene context provides information about the likely visual appearance of objects at different locations in the scene (e.g., as a function of depth), information that may be incorporated by preparatory attention mechanisms. Furthermore, knowing the category of a scene (e.g., through rapid processing of scene gist[198]) gives information about the likely distractor objects found in the scene, information that can be used to optimize the attentional template.[104] Another important difference between attention in typical experimental paradigms and attention in the real world is that the real world is a continuous and dynamic environment. When looking out for targets in real-world scenes, the attentional template needs to be maintained across saccades and be protected against intervening stimuli, a process that may rely on the PFC.[190] Finally, it is still largely unknown how semantic and episodic memory influence preparatory attention.[199] To conclude, now that the basic mechanisms of preparatory attention are relatively well established, as reviewed here, it is important to bring this knowledge to more naturalistic situations, investigating how preparatory attention mechanisms function in real-world environments.

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Conflicts of interest

The authors declare no conflicts of interest.

References

1. Desimone, R. & J. Duncan. 1995. Neural mechanisms of selective visual attention. *Annu. Rev. Neurosci.* **18:** 193–222.
2. Buschman, T.J. & S. Kastner. 2015. From behavior to neural dynamics: an integrated theory of attention. *Neuron* **88:** 127–144.
3. Maunsell, J.H. & S. Treue. 2006. Feature-based attention in visual cortex. *Trends Neurosci.* **29:** 317–322.
4. Reynolds, J.H. & L. Chelazzi. 2004. Attentional modulation of visual processing. *Annu. Rev. Neurosci.* **27:** 611–647.
5. Reynolds, J.H. & D.J. Heeger. 2009. The normalization model of attention. *Neuron* **61:** 168–185.
6. James, W. 1890. *The Principles of Psychology*.
7. Bundesen, C. 1990. A theory of visual attention. *Psychol. Rev.* **97:** 523–547.
8. Duncan, J. 1989. Boundary conditions on parallel processing in human vision. *Perception* **18:** 457–469.
9. Tinbergen, L. 1960. The natural control of insects in pinewoods. *Arch. Neerl. Zool.* **13:** 265–343.
10. Treisman, A. 2006. How the deployment of attention determines what we see. *Vis. Cogn.* **14:** 411–443.
11. Wolfe, J.M., K.R. Cave & S.L. Franzel. 1989. Guided search: an alternative to the feature integration model for visual search. *J. Exp. Psychol. Hum. Percept. Perform.* **15:** 419–433.
12. Desimone, R. 1998. Visual attention mediated by biased competition in extrastriate visual cortex. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **353:** 1245–1255.
13. Kaiser, D., N.N. Oosterhof & M.V. Peelen. 2016. The neural dynamics of attentional selection in natural scenes. *J. Neurosci.* **36:** 10522–10528.

14. Kastner, S., M.A. Pinsk, P. De Weerd, *et al.* 1999. Increased activity in human visual cortex during directed attention in the absence of visual stimulation. *Neuron* **22:** 751–761.
15. Luck, S.J., L. Chelazzi, S.A. Hillyard, *et al.* 1997. Neural mechanisms of spatial selective attention in areas V1, V2, and V4 of macaque visual cortex. *J. Neurophysiol.* **77:** 24–42.
16. Carrasco, M. 2011. Visual attention: the past 25 years. *Vision Res.* **51:** 1484–1525.
17. Posner, M.I., C.R. Snyder & B.J. Davidson. 1980. Attention and the detection of signals. *J. Exp. Psychol. Percept. Perform.* **109:** 160–174.
18. Dosher, B.A. & Z.L. Lu. 2000. Mechanisms of perceptual attention in precuing of location. *Vision Res.* **40:** 1269–1292.
19. Downing, C.J. 1988. Expectancy and visual-spatial attention: effects on perceptual quality. *J. Exp. Psychol. Hum. Percept. Perform.* **14:** 188–202.
20. Theeuwes, J. & E. Van der Burg. 2007. The role of spatial and nonspatial information in visual selection. *J. Exp. Psychol. Hum. Percept. Perform.* **33:** 1335–1351.
21. Theeuwes, J. 2013. Feature-based attention: it is all bottom-up priming. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **368:** 20130055.
22. Kok, P., J.F. Jehee & F.P. de Lange. 2012. Less is more: expectation sharpens representations in the primary visual cortex. *Neuron* **75:** 265–270.
23. Ling, S., T. Liu & M. Carrasco. 2009. How spatial and feature-based attention affect the gain and tuning of population responses. *Vision Res.* **49:** 1194–1204.
24. Wolfe, J.M., T.S. Horowitz, N. Kenner, *et al.* 2004. How fast can you change your mind? The speed of top-down guidance in visual search. *Vision Res.* **44:** 1411–1426.
25. Lamy, D.F. & A. Kristjansson. 2013. Is goal-directed attentional guidance just intertrial priming? A review. *J. Vis.* **13:** 14.
26. Folk, C.L., R.W. Remington & J.C. Johnston. 1992. Involuntary covert orienting is contingent on attentional control settings. *J. Exp. Psychol. Hum. Percept. Perform.* **18:** 1030–1044.
27. Chen, Y.C. & C. Spence. 2011. Crossmodal semantic priming by naturalistic sounds and spoken words enhances visual sensitivity. *J. Exp. Psychol. Hum. Percept. Perform.* **37:** 1554–1568.
28. Lupyan, G. & E.J. Ward. 2013. Language can boost otherwise unseen objects into visual awareness. *Proc. Natl. Acad. Sci. U.S.A.* **110:** 14196–14201.
29. Stein, T. & M.V. Peelen. 2015. Content-specific expectations enhance stimulus detectability by increasing perceptual sensitivity. *J. Exp. Psychol. Gen.* **144:** 1089–1104.
30. Evans, K.K., T.S. Horowitz & J.M. Wolfe. 2011. When categories collide: accumulation of information about multiple categories in rapid scene perception. *Psychol. Sci.* **22:** 739–746.
31. Stein, T. & M.V. Peelen. 2017. Object detection in natural scenes: independent effects of spatial and category-based attention. *Atten. Percept. Psychophys.* doi: 10.3758/s13414-017-1279-8.
32. Baldassi, S. & P. Verghese. 2005. Attention to locations and features: different top-down modulation of detector weights. *J. Vis.* **5:** 556–570.
33. Chelazzi, L., J. Duncan, E.K. Miller, *et al.* 1998. Responses of neurons in inferior temporal cortex during memory-guided visual search. *J. Neurophysiol.* **80:** 2918–2940.
34. Chelazzi, L., E.K. Miller, J. Duncan, *et al.* 1993. A neural basis for visual search in inferior temporal cortex. *Nature* **363:** 345–347.
35. Tanaka, K. 1996. Inferotemporal cortex and object vision. *Annu. Rev. Neurosci.* **19:** 109–139.
36. Hopfinger, J.B., M.H. Buonocore & G.R. Mangun. 2000. The neural mechanisms of top-down attentional control. *Nat. Neurosci.* **3:** 284–291.
37. Muller, N.G. & A. Kleinschmidt. 2003. Dynamic interaction of object- and space-based attention in retinotopic visual areas. *J. Neurosci.* **23:** 9812–9816.
38. O'Connor, D.H., M.M. Fukui, M.A. Pinsk, *et al.* 2002. Attention modulates responses in the human lateral geniculate nucleus. *Nat. Neurosci.* **5:** 1203–1209.
39. Serences, J.T., S. Yantis, A. Culberson, *et al.* 2004. Preparatory activity in visual cortex indexes distractor suppression during covert spatial orienting. *J. Neurophysiol.* **92:** 3538–3545.
40. Chawla, D., G. Rees & K.J. Friston. 1999. The physiological basis of attentional modulation in extrastriate visual areas. *Nat. Neurosci.* **2:** 671–676.
41. Esterman, M. & S. Yantis. 2010. Perceptual expectation evokes category-selective cortical activity. *Cereb. Cortex* **20:** 1245–1253.
42. Giesbrecht, B., D.H. Weissman, M.G. Woldorff, *et al.* 2006. Pre-target activity in visual cortex predicts behavioral performance on spatial and feature attention tasks. *Brain Res.* **1080:** 63–72.
43. Harrison, S.A. & F. Tong. 2009. Decoding reveals the contents of visual working memory in early visual areas. *Nature* **458:** 632–635.
44. Kok, P., M.F. Failing & F.P. de Lange. 2014. Prior expectations evoke stimulus templates in the primary visual cortex. *J. Cogn. Neurosci.* **26:** 1546–1554.
45. Lepsien, J. & A.C. Nobre. 2007. Attentional modulation of object representations in working memory. *Cereb. Cortex* **17:** 2072–2083.
46. Peelen, M.V. & S. Kastner. 2011. A neural basis for real-world visual search in human occipitotemporal cortex. *Proc. Natl. Acad. Sci. U.S.A.* **108:** 12125–12130.
47. Puri, A.M., E. Wojciulik & C. Ranganath. 2009. Category expectation modulates baseline and stimulus-evoked activity in human inferotemporal cortex. *Brain Res.* **1301:** 89–99.
48. Ranganath, C., J. DeGutis & M. D'Esposito. 2004. Category-specific modulation of inferior temporal activity during working memory encoding and maintenance. *Brain Res. Cogn. Brain Res.* **20:** 37–45.
49. Serences, J.T., E.F. Ester, E.K. Vogel, *et al.* 2009. Stimulus-specific delay activity in human primary visual cortex. *Psychol. Sci.* **20:** 207–214.
50. Shibata, K., N. Yamagishi, N. Goda, *et al.* 2008. The effects of feature attention on prestimulus cortical activity in the human visual system. *Cereb. Cortex* **18:** 1664–1675.
51. Shulman, G.L., G. d'Avossa, A.P. Tansy, *et al.* 2002. Two attentional processes in the parietal lobe. *Cereb. Cortex* **12:** 1124–1131.

52. Soon, C.S., P. Namburi & M.W. Chee. 2013. Preparatory patterns of neural activity predict visual category search speed. *Neuroimage* **66:** 215–222.
53. Stokes, M., R. Thompson, A.C. Nobre, *et al.* 2009. Shape-specific preparatory activity mediates attention to targets in human visual cortex. *Proc. Natl. Acad. Sci U.S.A.* **106:** 19569–19574.
54. Wylie, G.R., D.C. Javitt & J.J. Foxe. 2006. Jumping the gun: is effective preparation contingent upon anticipatory activation in task-relevant neural circuitry? *Cereb. Cortex* **16:** 394–404.
55. Foxe, J.J. & A.C. Snyder. 2011. The role of alpha-band brain oscillations as a sensory suppression mechanism during selective attention. *Front. Psychol.* **2:** 154.
56. Fries, P. 2015. Rhythms for cognition: communication through coherence. *Neuron* **88:** 220–235.
57. Fries, P., J.H. Reynolds, A.E. Rorie, *et al.* 2001. Modulation of oscillatory neuronal synchronization by selective visual attention. *Science* **291:** 1560–1563.
58. Klimesch, W. 2012. Alpha-band oscillations, attention, and controlled access to stored information. *Trends Cogn. Sci.* **16:** 606–617.
59. Babiloni, C., C. Miniussi, F. Babiloni, *et al.* 2004. Sub-second "temporal attention" modulates alpha rhythms. A high-resolution EEG study. *Brain Res. Cogn. Brain Res.* **19:** 259–268.
60. Bastiaansen, M.C., K.B. Bocker, C.H. Brunia, *et al.* 2001. Event-related desynchronization during anticipatory attention for an upcoming stimulus: a comparative EEG/MEG study. *Clin. Neurophysiol.* **112:** 393–403.
61. Bastiaansen, M.C. & C.H. Brunia. 2001. Anticipatory attention: an event-related desynchronization approach. *Int. J. Psychophysiol.* **43:** 91–107.
62. Harris, J.B. 2005. Differential conditioning of alpha amplitude: a fresh look at an old phenomenon. *Clin. Neurophysiol.* **116:** 1433–1443.
63. Jensen, O. & A. Mazaheri. 2010. Shaping functional architecture by oscillatory alpha activity: gating by inhibition. *Front. Hum. Neurosci.* **4:** 186.
64. Klimesch, W., M. Doppelmayr, H. Russegger, *et al.* 1998. Induced alpha band power changes in the human EEG and attention. *Neurosci. Lett.* **244:** 73–76.
65. Klimesch, W., P. Sauseng & S. Hanslmayr. 2007. EEG alpha oscillations: the inhibition-timing hypothesis. *Brain Res. Rev.* **53:** 63–88.
66. Liu, Y., J. Bengson, H. Huang, *et al.* 2016. Top-down modulation of neural activity in anticipatory visual attention: control mechanisms revealed by simultaneous EEG–fMRI. *Cereb. Cortex* **26:** 517–529.
67. Rajagovindan, R. & M. Ding. 2011. From prestimulus alpha oscillation to visual-evoked response: an inverted-U function and its attentional modulation. *J. Cogn. Neurosci.* **23:** 1379–1394.
68. Samaha, J., T.C. Sprague & B.R. Postle. 2016. Decoding and reconstructing the focus of spatial attention from the topography of alpha-band oscillations. *J. Cogn. Neurosci.* **28:** 1090–1097.
69. Sauseng, P., W. Klimesch, W. Stadler, *et al.* 2005. A shift of visual spatial attention is selectively associated with human EEG alpha activity. *Eur. J. Neurosci.* **22:** 2917–2926.
70. Thut, G., A. Nietzel, S.A. Brandt, *et al.* 2006. Alpha-band electroencephalographic activity over occipital cortex indexes visuospatial attention bias and predicts visual target detection. *J. Neurosci.* **26:** 9494–9502.
71. Worden, M.S., J.J. Foxe, N. Wang, *et al.* 2000. Anticipatory biasing of visuospatial attention indexed by retinotopically specific alpha-band electroencephalography increases over occipital cortex. *J. Neurosci.* **20:** RC63.
72. Hummel, F., F. Andres, E. Altenmuller, *et al.* 2002. Inhibitory control of acquired motor programmes in the human brain. *Brain* **125:** 404–420.
73. Noonan, M.P., N. Adamian, A. Pike, *et al.* 2016. Distinct mechanisms for distractor suppression and target facilitation. *J. Neurosci.* **36:** 1797–1807.
74. Lange, J., R. Oostenveld & P. Fries. 2013. Reduced occipital alpha power indexes enhanced excitability rather than improved visual perception. *J. Neurosci.* **33:** 3212–3220.
75. Snyder, A.C. & J.J. Foxe. 2010. Anticipatory attentional suppression of visual features indexed by oscillatory alpha-band power increases: a high-density electrical mapping study. *J. Neurosci.* **30:** 4024–4032.
76. Mishkin, M., L.G. Ungerleider & K.A. Macko. 1983. Object vision and spatial vision: two cortical pathways. *Trends Neurosci.* **6:** 414–417.
77. Ungerleider, L.G. & M. Mishkin. 1982. "Two cortical visual systems." In *Analysis of Visual Behavior*. D.J. Ingle, M.A. Goodale & R.J.W. Mansfield, Eds.: 549–586. Cambridge, MA: The MIT Press.
78. Jokisch, D. & O. Jensen. 2007. Modulation of gamma and alpha activity during a working memory task engaging the dorsal or ventral stream. *J. Neurosci.* **27:** 3244–3251.
79. Knakker, B., B. Weiss & Z. Vidnyanszky. 2014. Object-based attentional selection modulates anticipatory alpha oscillations. *Front. Hum. Neurosci.* **8:** 1048.
80. Romei, V., J. Gross & G. Thut. 2010. On the role of prestimulus alpha rhythms over occipito-parietal areas in visual input regulation: correlation or causation? *J. Neurosci.* **30:** 8692–8697.
81. Reeder, R.R., F. Perini & M.V. Peelen. 2015. Preparatory activity in posterior temporal cortex causally contributes to object detection in scenes. *J. Cogn. Neurosci.* **27:** 2117–2125.
82. Bichot, N.P., A.F. Rossi & R. Desimone. 2005. Parallel and serial neural mechanisms for visual search in macaque area V4. *Science* **308:** 529–534.
83. Wolfe, J.M. 1994. Guided Search 2.0. A revised model of visual search. *Psychon. Bull. Rev.* **1:** 202–238.
84. Becker, S.I., C.L. Folk & R.W. Remington. 2010. The role of relational information in contingent capture. *J. Exp. Psychol. Hum. Percept. Perform.* **36:** 1460–1476.
85. Becker, S.I., C.L. Folk & R.W. Remington. 2013. Attentional capture does not depend on feature similarity, but on target–nontarget relations. *Psychol. Sci.* **24:** 634–647.
86. Duncan, J. & G.W. Humphreys. 1989. Visual search and stimulus similarity. *Psychol. Rev.* **96:** 433–458.
87. Navalpakkam, V. & L. Itti. 2007. Search goal tunes visual features optimally. *Neuron* **53:** 605–617.
88. Scolari, M. & J.T. Serences. 2009. Adaptive allocation of attentional gain. *J. Neurosci.* **29:** 11933–11942.

89. van Driel, J., E. Gunseli, M. Meeter, *et al.* 2016. Local and interregional alpha oscillatory dynamics are sensitive to different levels of working memory-guided visual search. *J. Vis.* **16:** 709.
90. Treisman, A. 1986. Properties, parts and objects. In *Handbook of Perception and Human Performance*. K. Boff, L. Kaufman & J. Thomas, Eds.:1–70 New York: Wiley.
91. Wolfe, J.M. 1998. "Visual seach." In *Attention*. H. Pashler, Ed.: 13–74. Hove, East Sussex: Psychology Press Ltd.
92. Logothetis, N.K., J. Pauls & T. Poggio. 1995. Shape representation in the inferior temporal cortex of monkeys. *Curr. Biol.* **5:** 552–563.
93. Frank, S.M., E.A. Reavis, P.U. Tse, *et al.* 2014. Neural mechanisms of feature conjunction learning: enduring changes in occipital cortex after a week of training. *Hum. Brain Mapp.* **35:** 1201–1211.
94. Reeder, R.R., T. Stein & M.V. Peelen. 2016. Perceptual expertise improves category detection in natural scenes. *Psychon. Bull. Rev.* **23:** 172–179.
95. Li, F.F., R. VanRullen, C. Koch, *et al.* 2002. Rapid natural scene categorization in the near absence of attention. *Proc. Natl. Acad. Sci. U.S.A.* **99:** 9596–9601.
96. Thorpe, S., D. Fize & C. Marlot. 1996. Speed of processing in the human visual system. *Nature* **381:** 520–522.
97. Gauthier, I. & N.K. Logothetis. 2000. Is face recognition not so unique after all? *Cogn. Neuropsychol.* **17:** 125–142.
98. McGugin, R.W., J.C. Gatenby, J.C. Gore, *et al.* 2012. High-resolution imaging of expertise reveals reliable object selectivity in the fusiform face area related to perceptual performance. *Proc. Natl. Acad. Sci. U.S.A.* **109:** 17063–17068.
99. Reeder, R.R. & M.V. Peelen. 2013. The contents of the search template for category-level search in natural scenes. *J. Vis.* **13:** 13.
100. Maxfield, J.T. & G.J. Zelinsky. 2012. Searching through the hierarchy: how level of target categorization affects visual search. *Vis. Cogn.* **20:** 1153–1163.
101. Schmidt, J. & G.J. Zelinsky. 2009. Search guidance is proportional to the categorical specificity of a target cue. *Q. J. Exp. Psychol. (Hove)* **62:** 1904–1914.
102. Vickery, T.J., L.W. King & Y. Jiang. 2005. Setting up the target template in visual search. *J. Vis.* **5:** 81–92.
103. Wu, R., G. Scerif, R.N. Aslin, *et al.* 2013. Searching for something familiar or novel: top-down attentional selection of specific items or object categories. *J. Cogn. Neurosci.* **25:** 719–729.
104. Peelen, M.V. & S. Kastner. 2014. Attention in the real world: toward understanding its neural basis. *Trends Cogn. Sci.* **18:** 242–250.
105. Tanaka, K. 2003. Columns for complex visual object features in the inferotemporal cortex: clustering of cells with similar but slightly different stimulus selectivities. *Cereb. Cortex* **13:** 90–99.
106. Arcaro, M.J., S.A. McMains, B.D. Singer, *et al.* 2009. Retinotopic organization of human ventral visual cortex. *J. Neurosci.* **29:** 10638–10652.
107. Brewer, A.A., J. Liu, A.R. Wade, *et al.* 2005. Visual field maps and stimulus selectivity in human ventral occipital cortex. *Nat. Neurosci.* **8:** 1102–1109.
108. Golomb, J.D. & N. Kanwisher. 2012. Higher level visual cortex represents retinotopic, not spatiotopic, object location. *Cereb. Cortex* **22:** 2794–2810.
109. Wandell, B.A. & J. Winawer. 2011. Imaging retinotopic maps in the human brain. *Vision Res.* **51:** 718–737.
110. Daffron, J.L. & G. Davis. 2016. Target templates specify visual, not semantic, features to guide search: a marked asymmetry between seeking and ignoring. *Atten. Percept. Psychophys.* **78:** 2049–2065.
111. de Groot, F., F. Huettig & C.N.L. Olivers. 2016. When meaning matters: the temporal dynamics of semantic influences on visual attention. *J. Exp. Psychol. Hum. Percept. Perform.* **42:** 180–196.
112. Hickey, C., D. Kaiser & M.V. Peelen. 2015. Reward guides attention to object categories in real-world scenes. *J. Exp. Psychol. Gen.* **144:** 264–273.
113. Moores, E., L. Laiti & L. Chelazzi. 2003. Associative knowledge controls deployment of visual selective attention. *Nat. Neurosci.* **6:** 182–189.
114. Reeder, R.R., W. van Zoest & M.V. Peelen. 2015. Involuntary attentional capture by task-irrelevant objects that match the search template for category detection in natural scenes. *Atten. Percept. Psychophys.* **77:** 1070–1080.
115. Seidl-Rathkopf, K.N., N.B. Turk-Browne & S. Kastner. 2015. Automatic guidance of attention during real-world visual search. *Atten. Percept. Psychophys.* **77:** 1881–1895.
116. Wyble, B., C. Folk & M.C. Potter. 2013. Contingent attentional capture by conceptually relevant images. *J. Exp. Psychol. Hum. Percept. Perform.* **39:** 861–871.
117. Awh, E. & J. Jonides. 2001. Overlapping mechanisms of attention and spatial working memory. *Trends Cogn. Sci.* **5:** 119–126.
118. Gazzaley, A. & A.C. Nobre. 2012. Top-down modulation: bridging selective attention and working memory. *Trends Cogn. Sci.* **16:** 129–135.
119. Cowan, N. 1998. *Attention and Memory: An Integrated Framework*. New York: Oford University Press.
120. Stokes, M.G. 2011. Top-down visual activity underlying VSTM and preparatory attention. *Neuropsychologia* **49:** 1425–1427.
121. Fuster, J.M., R.H. Bauer & J.P. Jervey. 1981. Effects of cooling inferotemporal cortex on performance of visual memory tasks. *Exp. Neurol.* **71:** 398–409.
122. Fuster, J.M. & J.P. Jervey. 1981. Inferotemporal neurons distinguish and retain behaviorally relevant features of visual stimuli. *Science* **212:** 952–955.
123. Fuster, J.M. & J.P. Jervey. 1982. Neuronal firing in the inferotemporal cortex of the monkey in a visual memory task. *J. Neurosci.* **2:** 361–375.
124. Vogels, R. & G.A. Orban. 1994. Activity of inferior temporal neurons during orientation discrimination with successively presented gratings. *J. Neurophysiol.* **71:** 1428–1451.
125. Fuster, J.M. 1990. Inferotemporal units in selective visual attention and short-term memory. *J. Neurophysiol.* **64:** 681–697.
126. Colombo, M. & C.G. Gross. 1994. Responses of inferior temporal cortex and hippocampal neurons during delayed matching to sample in monkeys (*Macaca fascicularis*). *Behav. Neurosci.* **108:** 443–455.

127. Miller, E.K., L. Li & R. Desimone. 1993. Activity of neurons in anterior inferior temporal cortex during a short-term memory task. *J. Neurosci.* **13:** 1460–1478.
128. Miyashita, Y. & H.S. Chang. 1988. Neuronal correlate of pictorial short-term memory in the primate temporal cortex. *Nature* **331:** 68–70.
129. Buffery, A.W. 1967. Learning and memory in baboons with bilateral lesions of frontal or inferotemporal cortex. *Nature* **214:** 1054–1056.
130. Kovner, R. & J.S. Stamm. 1972. Disruption of short-term visual memory by electrical stimulation of inferotemporal cortex in the monkey. *J. Comp. Physiol. Psychol.* **81:** 163–172.
131. Stepien, L.S., J.P. Cordeau & T. Rasmussen. 1960. The effect of temporal lobe and hippocampal lesions on auditory and visual recent memory in monkeys. *Brain* **83:** 470–489.
132. Wilson, M., H.M. Kaufman, R.E. Zieler, *et al.* 1972. Visual identification and memory in monkeys with circumscribed inferotemporal lesions. *J. Comp. Physiol. Psychol.* **78:** 173–183.
133. Fuster, J.M., R.H. Bauer & J.P. Jervey. 1985. Functional interactions between inferotemporal and prefrontal cortex in a cognitive task. *Brain Res.* **330:** 299–307.
134. Ester, E.F., J.T. Serences & E. Awh. 2009. Spatially global representations in human primary visual cortex during working memory maintenance. *J. Neurosci.* **29:** 15258–15265.
135. van de Ven, V. & A.T. Sack. 2013. Transcranial magnetic stimulation of visual cortex in memory: cortical state, interference and reactivation of visual content in memory. *Behav. Brain Res.* **236:** 67–77.
136. Zokaei, N., S. Manohar, M. Husain, *et al.* 2014. Causal evidence for a privileged working memory state in early visual cortex. *J. Neurosci.* **34:** 158–162.
137. Soto, D., D. Llewelyn & J. Silvanto. 2012. Distinct causal mechanisms of attentional guidance by working memory and repetition priming in early visual cortex. *J. Neurosci.* **32:** 3447–3452.
138. Baddeley, A. 2000. The episodic buffer: a new component of working memory? *Trends Cogn. Sci.* **4:** 417–423.
139. Cowan, N. 1988. Evolving conceptions of memory storage, selective attention, and their mutual constraints within the human information-processing system. *Psychol. Bull.* **104:** 163–191.
140. Atkinson, R.C. & R.M. Shiffrin. 1971. *The Control Processes of Short-Term Memory*. Stanford: Stanford University.
141. Baddeley, A.D. & G. Hitch. 1974. Working memory. *Psychol. Learn. Motiv.* **8:** 47–89.
142. Engle, R.W. & M.J. Kane. 2003. Executive attention, working memory capacity, and a two-factor theory of cognitive control. *Psychol. Learn. Motiv.* **44:** 145–199.
143. Downing, P.E. 2000. Interactions between visual working memory and selective attention. *Psychol. Sci.* **11:** 467–473.
144. Olivers, C.N., F. Meijer & J. Theeuwes. 2006. Feature-based memory-driven attentional capture: visual working memory content affects visual attention. *J. Exp. Psychol. Hum. Percept. Perform.* **32:** 1243–1265.
145. Soto, D., D. Heinke, G.W. Humphreys, *et al.* 2005. Early, involuntary top-down guidance of attention from working memory. *J. Exp. Psychol. Hum. Percept. Perform.* **31:** 248–261.
146. Soto, D., J. Hodsoll, P. Rotshtein, *et al.* 2008. Automatic guidance of attention from working memory. *Trends Cogn. Sci.* **12:** 342–348.
147. Houtkamp, R. & P.R. Roelfsema. 2006. The effect of items in working memory on the deployment of attention and the eyes during visual search. *J. Exp. Psychol. Hum. Percept. Perform.* **32:** 423–442.
148. Peters, J.C., R. Goebel & P.R. Roelfsema. 2009. Remembered but unused: the accessory items in working memory that do not guide attention. *J. Cogn. Neurosci.* **21:** 1081–1091.
149. Woodman, G.F. & S.J. Luck. 2007. Do the contents of visual working memory automatically influence attentional selection during visual search? *J. Exp. Psychol. Hum. Percept. Perform.* **33:** 363–377.
150. Downing, P. & C. Dodds. 2004. Competition in visual working memory for control of search. *Vis. Cogn.* **11:** 689–703.
151. Olivers, C.N., J. Peters, R. Houtkamp, *et al.* 2011. Different states in visual working memory: when it guides attention and when it does not. *Trends Cogn. Sci.* **15:** 327–334.
152. Houtkamp, R. & P.R. Roelfsema. 2009. Matching of visual input to only one item at any one time. *Psychol. Res.* **73:** 317–326.
153. LaRocque, J.J., A.C. Riggall, S.M. Emrich, *et al.* 2017. Within-category decoding of information in different attentional states in short-term memory. *Cereb. Cortex* [Epub ahead of print].
154. Lewis-Peacock, J.A., A.T. Drysdale, K. Oberauer, *et al.* 2012. Neural evidence for a distinction between short-term memory and the focus of attention. *J. Cogn. Neurosci.* **24:** 61–79.
155. Serences, J.T. 2016. Neural mechanisms of information storage in visual short-term memory. *Vision Res.* **128:** 53–67.
156. Stokes, M.G. 2015. 'Activity-silent' working memory in prefrontal cortex: a dynamic coding framework. *Trends Cogn. Sci.* **19:** 394–405.
157. Sugase-Miyamoto, Y., Z. Liu, M.C. Wiener, *et al.* 2008. Short-term memory trace in rapidly adapting synapses of inferior temporal cortex. *PLoS Comput. Biol.* **4:** e1000073.
158. Albers, A.M., P. Kok, I. Toni, *et al.* 2013. Shared representations for working memory and mental imagery in early visual cortex. *Curr. Biol.* **23:** 1427–1431.
159. Christophel, T.B., R.M. Cichy, M.N. Hebart, *et al.* 2015. Parietal and early visual cortices encode working memory content across mental transformations. *Neuroimage* **106:** 198–206.
160. Cichy, R.M., J. Heinzle & J.D. Haynes. 2012. Imagery and perception share cortical representations of content and location. *Cereb. Cortex* **22:** 372–380.
161. Johnson, M.R. & M.K. Johnson. 2014. Decoding individual natural scene representations during perception and imagery. *Front. Hum. Neurosci.* **8:** 59.
162. Lee, S.H., D.J. Kravitz & C.I. Baker. 2012. Disentangling visual imagery and perception of real-world objects. *Neuroimage* **59:** 4064–4073.
163. Naselaris, T., C.A. Olman, D.E. Stansbury, *et al.* 2015. A voxel-wise encoding model for early visual areas decodes mental images of remembered scenes. *Neuroimage* **105:** 215–228.

164. Pearson, J., T. Naselaris, E.A. Holmes, *et al.* 2015. Mental imagery: functional mechanisms and clinical applications. *Trends Cogn Sci.* **19:** 590–602.
165. Reddy, L., N. Tsuchiya & T. Serre. 2010. Reading the mind's eye: decoding category information during mental imagery. *Neuroimage* **50:** 818–825.
166. Stokes, M., R. Thompson, R. Cusack, *et al.* 2009. Top-down activation of shape-specific population codes in visual cortex during mental imagery. *J. Neurosci.* **29:** 1565–1572.
167. Tong, F. 2013. Imagery and visual working memory: one and the same? *Trends Cogn. Sci.* **17:** 489–490.
168. Keogh, R. & J. Pearson. 2011. Mental imagery and visual working memory. *PLoS One* **6:** e29221.
169. Keogh, R. & J. Pearson. 2014. The sensory strength of voluntary visual imagery predicts visual working memory capacity. *J. Vis.* **14**. doi: 10.1167/14.12.7.
170. Pylyshyn, Z. 2003. Return of the mental image: are there really pictures in the brain? *Trends Cogn. Sci.* **7:** 113–118.
171. Muller, H.J., B. Reimann & J. Krummenacher. 2003. Visual search for singleton feature targets across dimensions: stimulus- and expectancy-driven effects in dimensional weighting. *J. Exp. Psychol. Hum. Percept. Perform.* **29:** 1021–1035.
172. Summerfield, C. & T. Egner. 2009. Expectation (and attention) in visual cognition. *Trends Cogn. Sci.* **13:** 403–409.
173. Summerfield, C. & F.P. de Lange. 2014. Expectation in perceptual decision making: neural and computational mechanisms. *Nat. Rev. Neurosci.* **15:** 745–756.
174. Bell, A.H., C. Summerfield, E.L. Morin, *et al.* 2016. Encoding of stimulus probability in macaque inferior temporal cortex. *Curr. Biol.* **26:** 2280–2290.
175. Deubel, H. & W.X. Schneider. 1996. Saccade target selection and object recognition: evidence for a common attentional mechanism. *Vision Res.* **36:** 1827–1837.
176. Moore, T., K.M. Armstrong & M. Fallah. 2003. Visuomotor origins of covert spatial attention. *Neuron* **40:** 671–683.
177. Rizzolatti, G., L. Riggio, I. Dascola, *et al.* 1987. Reorienting attention across the horizontal and vertical meridians: evidence in favor of a premotor theory of attention. *Neuropsychologia* **25:** 31–40.
178. Treisman, A.M. & G. Gelade. 1980. A feature-integration theory of attention. *Cogn. Psychol.* **12:** 97–136.
179. Corbetta, M. & G.L. Shulman. 2002. Control of goal-directed and stimulus-driven attention in the brain. *Nat. Rev. Neurosci.* **3:** 201–215.
180. Miller, E.K. & T.J. Buschman. 2013. Cortical circuits for the control of attention. *Curr. Opin. Neurobiol.* **23:** 216–222.
181. Pessoa, L., S. Kastner & L.G. Ungerleider. 2003. Neuroimaging studies of attention: from modulation of sensory processing to top-down control. *J. Neurosci.* **23:** 3990–3998.
182. Petersen, S.E. & M.I. Posner. 2012. The attention system of the human brain: 20 years after. *Annu. Rev. Neurosci.* **35:** 73–89.
183. Scolari, M., K.N. Seidl-Rathkopf & S. Kastner. 2015. Functions of the human frontoparietal attention network: evidence from neuroimaging. *Curr. Opin. Behav. Sci.* **1:** 32–39.
184. Egner, T., J.M. Monti, E.H. Trittschuh, *et al.* 2008. Neural integration of top-down spatial and feature-based information in visual search. *J. Neurosci.* **28:** 6141–6151.
185. Giesbrecht, B., M.G. Woldorff, A.W. Song, *et al.* 2003. Neural mechanisms of top-down control during spatial and feature attention. *Neuroimage* **19:** 496–512.
186. Liu, T., S.D. Slotnick, J.T. Serences, *et al.* 2003. Cortical mechanisms of feature-based attentional control. *Cereb. Cortex* **13:** 1334–1343.
187. Slagter, H.A., B. Giesbrecht, A. Kok, *et al.* 2007. fMRI evidence for both generalized and specialized components of attentional control. *Brain Res.* **1177:** 90–102.
188. Wojciulik, E. & N. Kanwisher. 1999. The generality of parietal involvement in visual attention. *Neuron* **23:** 747–764.
189. Buschman, T.J., E.L. Denovellis, C. Diogo, *et al.* 2012. Synchronous oscillatory neural ensembles for rules in the prefrontal cortex. *Neuron* **76:** 838–846.
190. Miller, E.K., C.A. Erickson & R. Desimone. 1996. Neural mechanisms of visual working memory in prefrontal cortex of the macaque. *J. Neurosci.* **16:** 5154–5167.
191. Rao, S.C., G. Rainer & E.K. Miller. 1997. Integration of what and where in the primate prefrontal cortex. *Science* **276:** 821–824.
192. Baldauf, D. & R. Desimone. 2014. Neural mechanisms of object-based attention. *Science* **344:** 424–427.
193. Zanto, T.P., M.T. Rubens, A. Thangavel, *et al.* 2011. Causal role of the prefrontal cortex in top-down modulation of visual processing and working memory. *Nat. Neurosci.* **14:** 656–661.
194. Todd, J.J. & R. Marois. 2004. Capacity limit of visual short-term memory in human posterior parietal cortex. *Nature* **428:** 751–754.
195. Lavie, N. 1995. Perceptual load as a necessary condition for selective attention. *J. Exp. Psychol. Hum. Percept. Perform.* **21:** 451–468.
196. Zhang, W. & S.J. Luck. 2009. Feature-based attention modulates feedforward visual processing. *Nat. Neurosci.* **12:** 24–25.
197. Wolfe, J.M., M.L. Vo, K.K. Evans, *et al.* 2011. Visual search in scenes involves selective and nonselective pathways. *Trends Cogn. Sci.* **15:** 77–84.
198. Oliva, A. & A. Torralba. 2006. Building the gist of a scene: the role of global image features in recognition. *Prog. Brain Res.* **155:** 23–36.
199. Le-Hoa, Vo M. & J.M. Wolfe. 2015. The role of memory for visual search in scenes. *Ann. N.Y. Acad. Sci.* **1339:** 72–81.