

Annual Review of Psychology

Turning Attention Inside Out: How Working Memory Serves Behavior

Freek van Ede¹ and Anna C. Nobre²

¹Institute for Brain and Behavior Amsterdam, and Department of Experimental and Applied Psychology, Vrije Universiteit Amsterdam, Amsterdam, Netherlands; email: freek.van.ede@vu.nl

²Departments of Experimental Psychology and Psychiatry, Oxford Centre for Human Brain Activity, and Wellcome Centre for Integrative Neuroimaging, University of Oxford, Oxford, United Kingdom; email: kia.nobre@psy.ox.ac.uk

ANNUAL
REVIEWS **CONNECT**

www.annualreviews.org

- Download figures
- Navigate cited references
- Keyword search
- Explore related articles
- Share via email or social media

Annu. Rev. Psychol. 2023. 74:137–65

First published as a Review in Advance on
August 12, 2022

The *Annual Review of Psychology* is online at
psych.annualreviews.org

<https://doi.org/10.1146/annurev-psych-021422-041757>

Copyright © 2023 by the author(s). This work is licensed under a Creative Commons Attribution 4.0 International License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited. See credit lines of images or other third-party material in this article for license information.



Keywords

working memory, selective attention, anticipation, expectation, vision, action

Abstract

Flexible behavior requires guidance not only by sensations that are available immediately but also by relevant mental contents carried forward through working memory. Therefore, selective-attention functions that modulate the contents of working memory to guide behavior (inside-out) are just as important as those operating on sensory signals to generate internal contents (outside-in). We review the burgeoning literature on selective attention in the inside-out direction and underscore its functional, flexible, and future-focused nature. We discuss in turn the purpose (why), targets (what), sources (when), and mechanisms (how) of selective attention inside working memory, using visual working memory as a model. We show how the study of internal selective attention brings new insights concerning the core cognitive processes of attention and working memory and how considering selective attention and working memory together paves the way for a rich and integrated understanding of how mind serves behavior.

Contents

INTRODUCTION	138
WHY: THE PURPOSE OF INTERNAL SELECTIVE ATTENTION	140
Selective Attention: From Outside-In to Inside-Out	140
Working Memory Operates in a Dynamic World and Serves the (Potential) Future	141
WHAT: THE TARGETS OF INTERNAL SELECTIVE ATTENTION	142
Object-Based Internal Selective Attention	142
Feature-Based Internal Selective Attention	143
Action Plans	144
Sensory-Motor Rules	146
WHEN: THE SOURCES OF INTERNAL SELECTIVE ATTENTION	146
External Cues	146
Internal States	147
Sensory-Driven Capture	148
Action	149
Multiple Sources of Internal Selective Attention	150
HOW: THE WORKINGS OF INTERNAL SELECTIVE ATTENTION	150
Multiple Stages of Internal Selective Attention	151
Manifold Mechanisms and Consequences of Internal Selective Attention	154
Spatial-Temporal Grounding of Internal Selective Attention	154
Sensorimotor Control over Internal Selective Attention	156
Cellular Mechanisms: Knowns and Unknowns	156
WHERE NEXT: THE FUTURE OF INTERNAL SELECTIVE ATTENTION ..	157

INTRODUCTION

At any given moment, human behavior is carved out of the external stimulation originating in the environment and of the internal traces in our memories. Contrary to our default understanding of memory as a repository for retrospective recollection, pioneering thinkers in our field have emphasized the fundamental prospective role of memories in guiding our perception and action (e.g., Dewey 1896, Helmholtz 1867). The richness of signals in the external environment and countless memories accumulated over various time scales offer boundless possibilities. Yet, our behavior requires focus. Even if we can envision and plan for several sequential (Tanji 2001) or potential (Cisek & Kalaska 2010) actions, our physiology prevents us from acting in multiple ways simultaneously. Thus, selecting the right information to focus perception and action is a major challenge embedded in our continual interactions with the environment.

Working memory plays a special role within this important confluence of external and internal signals. As far as we can piece together, the term was originally introduced by Miller et al. (1960) to denote a quick-access memory for the execution of plans. The term was also adopted in the seminal theoretical paper by Atkinson & Shiffrin (1968) to refer to the temporary short-term store interposed between early sensory registers and the permanent store of long-term memories. Later, the term was adopted by Baddeley & Hitch (1974) and has often been used as synonymous to their popularized multi-compartment model and its various subsequent refinements (Baddeley 2012). Here, we employ the term devoid of any particular theoretical baggage to mean the maintenance and manipulation of information over short periods of time to guide adaptive behavior. Like others

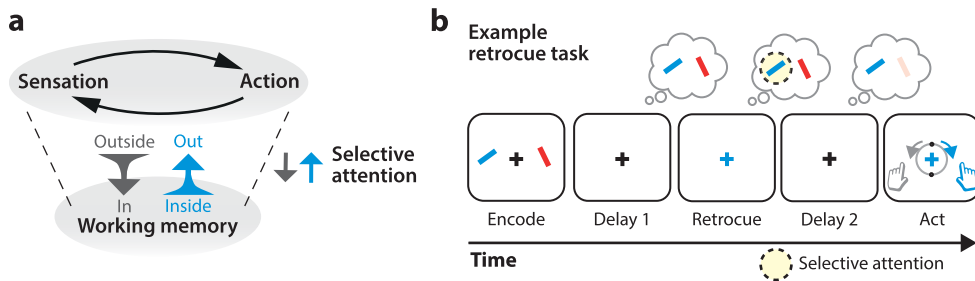


Figure 1

Attention: from outside-in to inside-out. (a) Working memory and selective attention link mind to behavior. In our model, working memory runs parallel to the continuous sensorimotor arc. Selective attention brings relevant sensory and motor information into working memory (outside-in), but it also helps select and prioritize relevant internal content for guiding ongoing and anticipated perception and action (inside-out). By helping to buffer relevant sensations for anticipated potential or sequential behavior—and by flexibly prioritizing contents across time—working memory and selective attention tremendously increase the flexibility of our behavioral repertoire. (b) Example retrocue task in which participants encode two visual objects before a color retrocue indicates which object from memory will (most likely) become relevant for guiding ensuing behavior. In this example, the right hand is used to reproduce the clockwise orientation of the cued (*blue*) object from working memory. Retrocues are about the past (memory content) but oriented to the future (task).

before us, we believe that working memory provides a vital bridge to facilitate ongoing behavior by guiding perception (e.g., Desimone & Duncan 1995, Olivers et al. 2011) and action (e.g., Cisek & Kalaska 2010, Fuster 1973) (**Figure 1a**).

In this review, we highlight the importance of selective attention in selecting and prioritizing the relevant contents within working memory. Although early models of working memory included control functions operating within (Atkinson & Shiffrin 1968) or upon (Baddeley & Hitch 1974) short-term memory, most subsequent research emphasized its limited capacity and fixed nature (e.g., Cowan 2001, Luck & Vogel 1997, Sperling 1960). About 20 years ago, the tide shifted. New experimental designs used cues that pointed toward the internal content that would likely be relevant for the upcoming decision, thus providing retrodictive information (Griffin & Nobre 2003, Landman et al. 2003). This allowed researchers to manipulate the likely relevance of internal contents within working memory (using experimental tasks like the one in **Figure 1b**), revealing pronounced modulation of performance. Studies using retrodictive cues (retrocues) complemented other lines of research suggestive of the ability to change the priority or accessibility among multiple coexisting internal representations in working memory (Garavan 1998, Gehring et al. 2003, Oberauer 2002) and breathed new life into this line of investigation. The study of selective attention directed at specific contents of working memory (internal selective attention, for short) has been gaining momentum since.

Next to revealing flexibility for attention-related modulation within working memory, this research field has enriched our understanding of the nature of working memory and selective attention themselves and of the control of adaptive behavior more generally. The increasingly established but still lively and formative nature of the field makes this a propitious moment to take stock of the first emerging principles and to highlight the foundational questions that come next. In what follows, we apply a forensic approach to reveal the why, what, when, and how of internal selective attention. In turn, we address the purpose of internal selective attention (why), its targets within working memory (what), the situations that trigger internal selective attention (when), and what is known about its psychological and neural mechanisms (how). We concentrate

on visual working memory, since this is the object of most research efforts, but we believe many of the lessons will generalize to other modalities and multisensory situations.

We build upon various other valuable reviews on (a) the comparison between external and internal attention (Chun et al. 2011), (b) different representational states in working memory (D’Esposito & Postle 2015, Nee & Jonides 2013, Olivers et al. 2011), (c) the functional interpretations of cueing benefits for working memory (Myers et al. 2017, Souza & Oberauer 2016), and (d) the functional and future-focused nature of working memory (Fuster & Bressler 2012, Heuer et al. 2020, Nobre & Stokes 2019, Olivers & Roelfsema 2020, van Ede 2020) and cognition more generally (Allport 1987, Cisek 2019, Engel et al. 2013).

The analysis casts working memory in a new light. We promote the importance of considering the pragmatic nature of working-memory contents (see Cisek 2019). Most studies to date have primarily considered the informational nature of working-memory contents, attempting to get at the perceptual qualities of internal states. These studies follow our natural curiosity about the phenomenology of working memory, which feels immediate and available through our mental experience. However, internal states are not merely descriptive. They evolved to be useful in guiding behavior. Accordingly, we position selective attention inside working memory as fundamentally functional, flexible, and future focused. We highlight empirical demonstrations of this “triple-F” perspective at various instances throughout this review. We also note that our proposed future-focused perspective on working memory echoes related ideas on the prospective functions of long-term memory to guide immediate (Nobre & Stokes 2019) or future (Schacter et al. 2007) behavior.

WHY: THE PURPOSE OF INTERNAL SELECTIVE ATTENTION

Selective attention consists of the processes for selecting and prioritizing the information that is relevant to our ongoing behavior (Nobre & Kastner 2014). It is at the heart of everything we do and is one of the most studied topics in psychology and cognitive neuroscience. It can apply equally well to prioritizing and selecting information derived from the sensory stream (external selective attention) and from internal memory contents (internal selective attention).

Selective Attention: From Outside-In to Inside-Out

Traditionally, the study of selective attention has been almost exclusively concerned with how we prioritize and select relevant signals and filter away the irrelevant signals from the sensory stream. Although our understanding is still incomplete, we have amassed volumes of knowledge about the psychological and neural mechanisms supporting external selective attention, and our ideas have become increasingly more refined and sophisticated (e.g., Fawcett et al. 2015, Nobre & Kastner 2014), thanks also to the continuous advancement of human neuroscience methods (Nobre & van Ede 2020). We can conceive of external selective attention as operating outside→in, by modulating the transformation of sensory signals (outside) into internal representations (in). In this kind of formulation, working memory is the end product of selective attention operating on the incoming sensory stream. Once a robust working-memory representation is formed, the work of attention has historically been considered to be done.

Critically, however, our exchanges with the world are far from being confined to direct sensorimotor dealings. Instead, they are deeply and pervasively shaped by experience. Memory in general, and working memory in particular, plays an essential role in shaping our perception and gating our actions. Indeed, one of the very purposes of working memory is to make available internal states for guiding behavior (**Figure 1a**).

We argue that selective attention is just as important inside working memory as toward sensory signals, though the aims may differ. Models of visual working memory differ in detail, but most agree that contents are highly limited and that features and attributes have already received considerable integration during the initial stages of sensory processing (for a review, see Brady et al. 2011). Therefore, the greater challenge is about selecting and prioritizing among a few internal representations for optimally guiding adaptive ongoing and anticipated behavior. Thus, we can conceive internal selective attention as acting inside→out, by selecting and prioritizing internal representations for guiding external behavior. This is the focus of our review.

Working Memory Operates in a Dynamic World and Serves the (Potential) Future

Selective attention inside working memory is useful because we are active beings in dynamic environments. From moment to moment, incoming information updates what is likely to happen next, our goal may change, and so on. Accordingly, different memoranda often become relevant at different moments, and selective attention can help us to select and prioritize relevant content flexibly. This may be particularly useful when working memory is recruited for dealing with the dynamic nature of the world, such as when planning for multiple potential (Cisek & Kalaska 2010) and sequential (Tanji 2001) courses of actions. In such cases, selective attention can prioritize the currently most relevant internal content for ongoing behavior and dynamically adjust priorities as the situation unfolds.

Imagine trying to reproduce a new rock-and-roll dance move, after your instructor has demonstrated how it is done. After paying close attention to the example, you are likely to use your working memory to remember the key steps to try yourself moments later. Critically, while reproducing the move, it is important not only to remember all constituent steps but also to select and prioritize the relevant steps at the right time. Only by carefully balancing priority among the steps in working memory will you be able to execute your move in the appropriate order, with flawless precision.

Our example stresses the pragmatic dimension of working-memory representations—their utility in guiding adaptive behavior. It illustrates how focusing on different contents at different moments is essential for orchestrating perception and action.

By taking an ecological perspective, we realize the most important purpose of working memory is not to reflect on the past but to bring relevant information from the past forward in order to prepare for the future (see also Fuster & Bressler 2012, Nobre & Stokes 2019, Olivers et al. 2011, van Ede 2020). An everyday example is that of driving by a road sign with directions. Here, working memory helps to carry past visual information forward to take the correct exit (action) in the near future—not to reflect on the aesthetic appeal of the road sign itself. We posit that its future-directed purpose and the associated role in gating behavior frame the core properties of selective attention inside working memory.

Importantly, working memory cannot just commit to a known, predetermined future but must also serve uncertain, potential futures. In dynamic contexts, the near future can take on multiple possibilities. Imagine you are playing a game of soccer and just gained possession of the ball. As you turn toward the goal, several team members disappear from sight. Some of them may become essential soon, prompting you to keep their whereabouts in working memory. Who will turn out to be relevant may depend on how the defendants move. From this pragmatic perspective (see also Cisek & Kalaska 2010), what we store in working memory may be tactfully stored not because we know it will become relevant (delayed action) but because we foresee that it may become relevant (potential action). In other words, a central purpose of working memory may be to help prepare

for potential futures (Nasrawi & van Ede 2022, van Ede et al. 2019b). As predictions change or uncertainties dissolve, selective attention selects and prioritizes the contents that are imminently relevant.

Viewing working-memory capacity limits from a functional perspective changes the narrative from that of a shortcoming in the cognitive ability of holding limited contents into that of a strength in the ability to support a rich repertoire of preparatory states to interface efficiently with multiple likely future states of the world. Internal selective attention, therefore, serves not merely to improve the qualities or accessibility of the memories themselves but also to enhance their ability to serve anticipated behavior.

WHAT: THE TARGETS OF INTERNAL SELECTIVE ATTENTION

After several decades, the field of external selective attention finally moved beyond identifying a fixed bottleneck and the singular type of target for selection and prioritization. Evidence gathered across methods and species clearly reveals a rich plurality of modulatory mechanisms operating on various types of representations throughout multiple stages of processing (Nobre & Kastner 2014).

Research on internal selective attention is less mature. Nevertheless, the findings to date indicate a similar plurality of targets, sources, and mechanisms. Trying to pinpoint the definitive units for internal selection and prioritization is likely to be futile. The functional perspective naturally accommodates the notion that different aspects of internal contents may be useful for guiding behavior in different contexts.

Understanding the units that support internal selective attention can be informative beyond merely commenting on the plurality of selective attention mechanisms. Revealing that a level of representation is available for modulation provides indirect confirmation that this type of information is preserved within working memory.

Object-Based Internal Selective Attention

Some prominent models of working memory consider bound objects to be the primary unit of representation within working memory (e.g., Cowan 2010, Luck & Vogel 1997). When one considers the contents of working memory to be a product of sensory processing, this is intuitive, because increased integration of features and attributes results in object-level representations at higher levels of the sensory hierarchies (e.g., Maunsell & Newsome 1987), which can undergo further contextualization (e.g., Eichenbaum et al. 2007). Objects are also considered the natural units for actions (e.g., Goodale et al. 2004).

Accordingly, most internal selective attention studies have manipulated selection and prioritization at the object level (see **Figure 1b** for an example retrocue task). The first retrocuing studies used spatial cues—presented during the working-memory delay—to indicate objects that would be most relevant for subsequent performance (Griffin & Nobre 2003, Landman et al. 2003). Dozens of subsequent studies have replicated the benefits of retrocues operating at the object level. Spatial cues to signal a relevant object are convenient but are not the only way to direct internal selective attention to memorized objects. Studies have also successfully indicated the relevance of objects through, for example, color (Heuer & Schubö 2016, Pertzov et al. 2013, Poch et al. 2017, van Ede et al. 2019a), shape (Kuo et al. 2009, Panichello & Buschman 2021, van Ede et al. 2019a), category (Backer et al. 2020, Lepsien & Nobre 2007), serial position (Harrison & Tong 2009, Heuer & Rolfs 2021a), temporal interval (van Ede et al. 2017, Zokaei et al. 2019), order (de Vries et al. 2017), and value (Atkinson et al. 2018, Gong & Li 2014).

Object-based internal selective attention has also been observed in other sensory modalities, including in audition (Backer & Alain 2012, Fan et al. 2021) and touch (Katus et al. 2017, Spitzer &

Blankenburg 2011). Studies across different modalities highlight the generality of internal selective attention, but they also raise interesting questions about the different challenges for internal selective attention in different modalities. In many cases, visual sensory stimulation changes slowly in the environment. We keep things in working memory as we turn away from objects that still remain in the environment and that we can resample by orienting back toward them (Ballard et al. 1997, Draschkow et al. 2021, Tatler & Land 2011). Stimulation in other modalities can be more transient. For example, auditory objects, such as a bird call, can be fleeting, and working memory is therefore required for preserving the sound in mind. Whether and how the salient differences between the modalities affect the mechanisms for internal selective attention remain interesting questions deserving exploration.

Disentangling object-based selective attention from selective attention to the spatial locations or constituent features of objects is not straightforward, given that these types of information are necessarily bundled in their co-occurrence. A hallmark signature of external object-based selective attention is that selecting and prioritizing one feature in an object leads to a similar selection and prioritization of another feature shared by the object, independent of spatial proximity (Egley et al. 1994). Studies dissecting the object-based consequences of internal selective attention have confirmed the co-modulation of features shared by the same object in working memory but not of equidistant features belonging to another object (Lin et al. 2021a, Peters et al. 2015).

Object-based internal selective attention is thus a common experience and has appropriately served as the workhorse for laboratory studies. Given the primacy of object-level representations in some models of working memory, an important question also arises about whether objects are the only type of representation that can support internal selective attention.

Feature-Based Internal Selective Attention

By now, multiple laboratories have confirmed the benefits of directing attention selectively to feature dimensions that cut across object representations in working memory. These results challenge models proposing feature-integrated objects as the sole unit of representation in working memory.

Brain imaging studies using multivariate pattern analyses indicated that it is possible to prioritize visual processing of different features of objects in working memory depending on the anticipated task (Serences et al. 2009). Building on this work, retrocue tasks made it possible to manipulate selective attention to specific feature dimensions during working-memory maintenance, ruling out contributions from differential feature extraction during initial encoding.

For example, in one of our studies (Niklaus et al. 2017), participants viewed an array of colored oriented arrows and had to reproduce either the color or the angle of one of the arrows when probed after a working-memory delay. Informative retrocues indicated which feature dimension was likely to be probed for subsequent report (with 75% validity) within any arrow in memory. Errors in reporting either the color or the angle were reduced in trials with valid retrocues, consistent with a selective up-regulation of the relevant visual feature among all memoranda. Similar results were reported by Kalogeropoulou et al. (2017), Park et al. (2017), and Ye et al. (2016). Complementing this work, feature-based prioritization in working memory has also been reported in the absence of explicit feature cues, for example, when anticipating specific distractors (Boettcher et al. 2020, Lee & Geng 2019) or planning specific actions (Heuer & Schubö 2017).

At least one study to date has directly compared the consequences of internal selective attention by retrocues toward objects and toward feature dimensions (Hajonides et al. 2020). The results confirmed robust benefits of both retrocue types on performance. Performance benefits for both cue types correlated, though the effects were larger for selective attention at the object level. This

is consistent with a related study by Lin et al. (2021a), who used joint object and feature retrocues and included invalid-cue trials in which the other feature dimension of the same object or the same feature dimension of the other object could become probed. The results showed that retrocuing features was advantageous, since the errors were smaller after cues correctly predicting the object and the feature compared to both types of invalid cues. However, retrocuing at the object level was more advantageous, since switching to the other feature dimension in the same object was less costly than switching to the same dimension of the other object.

A different experimental approach has also demonstrated preserved feature-level information in working memory. Kong & Fournie (2019) introduced a working memory–update task. In this task, participants encode a visual array into working memory. During the delay, they are prompted to select an element and update its location. Finally, they compare the updated memory array with a presented probe display. Participants searched and updated information in the memorized array faster when prompted to update targets defined by individual features rather than targets defined by a conjunction of features. This shows that feature-level information in working memory remains present and can sometimes guide selection more effectively than object-level representations with integrated features.

Taken together, the results of studies investigating object-based and feature-based selective attention in working memory demonstrate plainly that both types of information are available for selection and prioritization (see also Brady et al. 2011). From a functional perspective, this is a comfortable conclusion, as it follows that what type of information is prioritized may depend simply on what is most useful for the task.

Action Plans

In line with the intuitive phenomenological stance, the study of internal selective attention has predominantly focused on the modulation of sensory representations, which carry the informational content of the signals from the environment. However, the pragmatic representations used to guide our actions are equally important.

In everyday life, selecting informational content and pragmatic guiding of action are intrinsically connected. Indeed, this linking may be the defining purpose of working memory (**Figure 1a**). The laboratory, however, has largely uncoupled the two sides of the perception–action cycle. Conventionally, studies on sensory working memory have considered the retention of sensory attributes in isolation from prospective actions, whereas studies on action planning have considered actions to specific target locations (e.g., eye or arm movements to particular points in space) that do not require guidance by detailed sensory representations from working memory (van Ede 2020).

From a functional, ecological perspective, this artificial polarization is unhelpful. To reconnect perception and action within working memory, we recently developed an experimental task in which sensory objects were linked to prospective actions (van Ede et al. 2019b). We found that selection of pragmatic representations (action plan) within working memory does not require prior selection of the relevant informational content (visual object). Participants viewed two tilted bars (as in **Figure 1b**), one on each side of visual fixation, each associated with a distinct response hand as a function of its orientation. After a working-memory delay, a cue indicated which bar should be selected to reproduce its orientation. We measured markers of brain activity related to the selection of the spatial location of the relevant object and to the selection of the motor plan to reproduce the memorized tilt with the left or right hand. (We could track these independently because we manipulated object location and response hand independently.) If the primary or only information maintained during a visual working-memory task is the sensory, visual content,

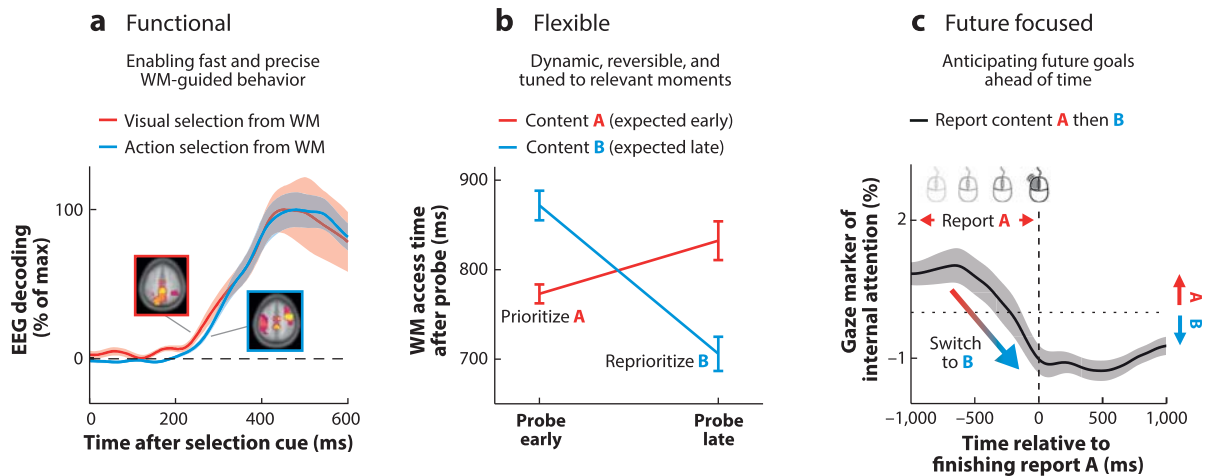


Figure 2

Selective attention inside working memory (WM) is functional, flexible, and future focused. (a) Empirical result highlighting the functional nature of internal selective attention. Participants held two visual objects in mind that were associated with two distinct manual actions. After a selection cue, electroencephalogram (EEG) decoding shows parallel selection of the relevant action plan (blue) and object location (red). Panel adapted from van Ede et al. (2019b). (b) Empirical result highlighting the flexible nature of internal selective attention. Participants held two visual objects in mind. One was more likely to be probed early (after a 1,250 ms delay) and the other to be probed late (after a 2,500 ms delay). Working-memory access times (from probe to response onset) revealed flexible and reversible object prioritization that changed with elapsed time in the absence of any explicit cues. Unattended content B was accessed more slowly at the early interval but became more accessible (attended) at the later interval, when it was anticipated. Panel adapted from van Ede et al. (2017). (c) Empirical result highlighting the future-focused nature of internal selective attention. Participants held two visual objects in mind that they had to report in sequence (A, then B). A microsaccadic gaze marker of internal selective attention revealed how participants looked ahead to memory content B (that would become needed for the next report) before completing the preceding report of object A. Figure adapted from van Ede et al. (2021).

participants would first have to select the relevant object when prompted to respond, and only then formulate the appropriate action plan. In stark contrast, we observed that markers of visual-spatial and motor-plan selection occurred concurrently (**Figure 2a**). Our results made clear that working memory is not just about sensory, content-related representations. When possible, pragmatic representations are also encoded and maintained, ready for guiding performance (see also Boettcher et al. 2021, Nasrawi & van Ede 2022, Schneider et al. 2017). Indeed, as a temporally extended bridge between sensations and actions, working memory provides the ideal medium for preparing and maintaining potential actions ahead of behavioral implementation.

Within the functional perspective, the response is not a termination point. Instead, action and perception coexist in a mutually informative cycle (Cisek & Kalaska 2010, Dewey 1896, Hommel et al. 1994), and are each supported by working memory (**Figure 1a**). Furthermore, action goals often, if not always, take precedence and determine what informational contents are relevant. We propose, therefore, that informational, sensory representations and pragmatic, motor representations work together within working memory to support behavior that is both efficient (action ready) and precise (informed by sensory representations).

Action-ready representations can make the difference between winning and losing in a game of sport. Imagine trying to gain possession of the ball close to the opposition's goal. While focused on the ball, you may hold the current whereabouts of the keeper in working memory so that, if you obtain the ball, you know where to shoot. Working memory thereby saves precious time, which would otherwise be required for carefully scanning the visual scene once you obtain the

ball. Moreover, by having not only the visual representation but also the associated action ready, you are in the ideal position to catch the keeper off guard and score. Planning multiple potential actions is useful because you may not gain possession of the ball. In this case, you may need to attend another working-memory representation that serves an alternative course of action, such as to go into defense mode. Thus, by keeping sensory representations in memory that serve multiple potential future courses of action, working memory prepares us for volatile states of the world around us.

Sensory-Motor Rules

In addition to representations of sensory contents and action plans, there are pragmatic representations that specify the rules linking these together. In different contexts, different rule representations may prevail. For example, when alone at your workplace you may reach for the remembered location of your comic book to pick it up and enjoy a moment of rest. When your boss is walking by, you may reach to shove it off the desk instead. To date, not many studies have looked specifically at how we selectively attend to internal task rules, as far as we know. Some studies have started looking at the nature of task-rule representations, suggesting that encoding a rule may involve a declarative representation that is available to awareness, which is transformed through learning into an automatic, procedural representation for guiding behavior (Brass et al. 2017, Oberauer 2010). Internal selective attention has been proposed to play a role in transforming task rules into their procedural, action-ready state (González-García et al. 2020; see also Kikumoto & Mayr 2020).

It is worth noting that this distinction between declarative and procedural representations (Cohen & Squire 1980) in theory is also applicable to sensory and motor representations in working memory. Sensory contents or motor plans may be describable and available to awareness or may be maintained in brain states that are unavailable to awareness but that can nevertheless impact behavior.

WHEN: THE SOURCES OF INTERNAL SELECTIVE ATTENTION

The study of internal selective attention was reenergized by introducing retrodictive cues into working-memory tasks (Griffin & Nobre 2003, Landman et al. 2003). Retrocues have proven to be an effective tool for identifying the mechanisms that control internal selective attention and for dissecting the resulting consequences on performance and brain activity. At the same time, we rarely encounter such obvious and explicit prompts for directing internal selective attention during natural behavior. In this section, we consider when internal selective attention may be triggered. We propose four separate triggering sources.

External Cues

The bulk of research on internal selective attention makes use of the versatile retrocues. Retrocues can be retrospectively predictive (e.g., Griffin & Nobre 2003, Landman et al. 2003) or deterministically instructive (e.g., Nobre et al. 2004, van Ede et al. 2021) of the contents to be selected. As we have seen, they can indicate various aspects of objects (e.g., location, feature, order, timing, category, or reward value), they can indicate feature dimensions shared across objects, or they can indicate actions and task rules. The timing of retrocues can be adjusted to examine the consequences of internal selective attention at different life times of internal representations (e.g., Astle et al. 2012, Sligte et al. 2008) and to study how long internal selection takes to unfold (e.g., Schneider et al. 2016, van Moorselaar et al. 2015b).

Most researchers consider retrocues to prompt voluntary shifts of internal selective attention based on expectations or instructions serving task goals. The voluntary nature of retrocueing is

suggested by studies showing their diminished efficacy in dual-task situations (Janczyk & Berryhill 2014, Lin et al. 2021b), though sustained attention on contents may not be required after retrocues (Myers et al. 2017, Rerko et al. 2014). We consider the mechanisms through which retrocues may influence performance in the section titled *How: The Workings of Internal Selective Attention*. At this point, it is just worth noting that, although the term “retro” emphasizes the retrospective nature of the relevant sensory informational content, the cues are equally prospective in selecting pragmatic representations to guide future action.

Retrocues are not the only type of cues shown to change performance related to working-memory contents in a selective way. Refresh cues instruct individuals to briefly think of a previously experienced stimulus. They have been proposed to trigger an elemental executive process of refreshing representations, considered to be essential to their maintenance (see Johnson 1992; for a review, see Camos et al. 2018). Unlike retrocues, refresh cues need not be predictive of the relevance of the cued object to facilitate performance (Souza et al. 2015). Similarly, benefits to working-memory performance have been observed after nonpredictive cues that prompt selection of working-memory content for performing a secondary task (Zokaei et al. 2014). Although the mechanisms tapped by such findings remain underspecified, there are indications that they may invoke additional or different mechanisms of selection and prioritization compared to retrocues. For example, the benefits of refresh cues remain observable even after successive cues refreshing alternative contents (Souza et al. 2015).

Internal States

External cues are the dominant sources for orienting selective attention in the laboratory, but they are rare in everyday situations. In most ordinary cases, we orient our attention within dynamically unfolding contexts based on internally generated goals and expectations informed by learning. For example, in our earlier example of practicing our new rock-and-roll dance move, what helps us execute our move by prioritizing the right elements at the right time is our own internal knowledge of their temporal ordering in a learned sequence (this is not to say that we do not also rely on external cues to fine-tune our actions).

Studies investigating how changing internal states affect working-memory performance may not only bring us a step closer to internal selective attention in natural behavior but also reveal important properties that distinguish internal selective attention from its external counterpart.

In our first study of this kind (van Ede et al. 2017), participants viewed two colored oriented bars and were prompted to report the orientation of one of them after either a shorter (1,250 ms) or longer (2,500 ms) working-memory interval. The likelihood that a given color bar would be probed varied systematically with the interval; one color was more likely to be probed early (80%) and the other to be probed late (80%). The improvements in both decision times (**Figure 2b**) and accuracy of responses tracked the probabilities without any explicit cue indicating the passage of time or the change of object likelihood over time (van Ede et al. 2017). Similar dynamics of prioritization were reported by Zokaei et al. (2019).

Intriguingly, these studies revealed the highly flexible and reversible nature of internal selective attention (see **Figure 2b**). They showed that contents can be dynamically placed in and out of the internal focus without significant deterioration of information. Even contents that were unattended at first could become selected and prioritized subsequently as internal expectations changed to favor their likely relevance (van Ede et al. 2017, Zokaei et al. 2019). Related studies using successive cues and retrieval probes have reached similar conclusions (Christophel et al. 2018, de Vries et al. 2018, Lewis-Peacock et al. 2012, Myers et al. 2018, Rerko & Oberauer 2013, van Ede et al. 2021, van Moorselaar et al. 2015c). Importantly, and in contrast to what is observed in

external attention, selectively prioritizing content A in working memory does not always imply that content B will be dropped, forgotten, or impoverished. The strong implication is that when content B may still become useful in the future, it can be retained in a temporarily unattended state and still be reprioritized later. This flexibility and reversibility are some of the hallmarks of internal selective attention.

Central to these dynamic working-memory studies is the construct of internal priority switching (de Vries et al. 2018, Muhle-Karbe et al. 2021, van Ede et al. 2017), that is, disengaging priority from one content to prioritize another. In a recent study (van Ede et al. 2021), we asked how the brain juggles such internal priorities across time during sequential memory-guided behavior. Strikingly, we found that internal priority switched to the next-relevant memory contents even before behavioral guidance by the preceding content was finished (**Figure 2c**). In other words, while guiding behavior by memory content A, the brain already starts to look ahead to memory content B needed to guide behavior next. The observation speaks to the future-focused nature of internal selective attention and has a parallel in the looking-ahead behavior (Pelz & Canosa 2001) commonly reported in tasks guided by external vision.

Sensory-Driven Capture

The literature on external selective attention makes a fundamental distinction between goal-driven and stimulus-driven sources of focus (James 1890, Jonides 1981, Posner & Cohen 1984). In contrast, to date, studies of internal selective attention have mostly considered goal-driven shifts prompted by external cues or internal states. Yet, involuntary capture of contents in working memory according to sensory stimuli is conceivable. To retrodict the relevant working-memory content, retrocues often share a feature (e.g., color) of the relevant memorandum. It is possible that processing of the sensory properties of the retrocues interacts with sensory aspects of working-memory representations. Matching sensory stimulation could, for example, trigger an involuntary shift of selective attention to matching contents within working memory.

According to this scenario, feature-matching retrocues can, in principle, guide internal selective attention through two separate routes: voluntary goal-driven shifts based on cue informativeness, and involuntary stimulus-driven shifts based on the sensory matching of features between the cue and a specific memory content. To test for and dissect the contribution of goal-driven versus sensory-driven internal selective attention in working memory, we recently developed the anti-retrocue task (van Ede et al. 2020). In typical retrocue tasks, the informativeness and sensory-matching dimensions of the cue are congruent (e.g., red retrocue predicts the red object will be relevant and shares the color red with the object). In our anti-retrocue task, we separated these dimensions. Cues sharing a feature with one of the working-memory objects (e.g., red) now indicated that the other (e.g., blue) object was relevant and would become probed. Informativeness and sensory matching of cues varied orthogonally. Our results showed that both routes exist for internal selective attention. Furthermore, the pattern of behavioral results revealed a double dissociation in the pattern of benefits. The informative aspect of retrocues substantially decreased decision times but had only a modest effect on the precision (accuracy) of the orientation report. In contrast, feature-matching cues substantially improved the accuracy of reports but had little impact on decision times (van Ede et al. 2020). The results suggest that different sources of internal selective attention (goal driven and stimulus driven) can deliver benefits by changing the settings related to the quality of information represented or the pragmatic action-readiness of these representations.

The unveiled sensory-driven capture of internal contents may be the equivalent, but in reverse, of the selective capture of external sensory signals that match the content in working memory [reviewed by Kiyonaga & Egner (2013), Olivers et al. (2011), and Soto & Humphreys (2007)]. Just

like working-memory contents may automatically draw attention to matching sensory stimuli in the world, sensory stimuli may automatically draw attention to matching contents in working memory. At least one study to date suggests that sensory-driven capture of internal selective attention may provide a powerful tool for experimentally manipulating working memory, for example, for manipulating serial rehearsal dynamics (Li et al. 2021).

The recency effect—the improved performance for the last encoded memory content—has also been interpreted as representing a type of sensory-based attentional focus operating within working memory (McElree & Doshier 1989, Niklaus et al. 2019). The properties of the behavioral advantages conferred through encoding recency differ from those conferred through voluntary orienting by retrocues. For example, final objects are particularly vulnerable to interference from irrelevant visual distraction (Hu et al. 2014), whereas informative retrocues help protect contents from visual interference (Makovski et al. 2008, van Moorselaar et al. 2015a). A recent study directly comparing last-object prioritization and retrocue benefits confirmed the additive and independent nature of the effects (Niklaus et al. 2019). The results reinforce the proposition that different mechanisms may selectively facilitate performance in working memory.

Action

Returning to our perspective on working memory, serving behavior is of the essence. This invites the natural question of whether intended actions can, in themselves, trigger selection and prioritization of working-memory contents. Actions are not prepared in the void but are informed by and tethered to informational content, both from the environment and from working memory. Prioritization of sensory contents as a function of action plans is therefore an intuitive and adaptive process from a functional perspective (Allport 1987, Cisek & Kalaska 2010, Deubel & Schneider 1996, Kowler et al. 1995).

Action-related sources of attention are widely acknowledged to modulate the processing of external sensory signals. The organization of selective attention by intended action is at the core of major theoretical frameworks, such as the premotor theory of attention (Rizzolatti et al. 1987). A vast and sophisticated literature attests to the strong and automatic modulation of sensory processing for the targets of saccades (Deubel & Schneider 1996, Kowler et al. 1995) and hand movements (Baldauf & Deubel 2010), and it may apply concurrently to multiple targets when a sequence of actions is planned (Baldauf & Deubel 2010).

A mounting number of studies has begun to highlight the similarly important role of action planning in directing internal selective attention (Heuer et al. 2020). Studies prompting an action or action plan during the working-memory delay show performance benefits for memory contents congruent with the action location. These effects occur despite the fact that motor cues are not predictive for the memory task. Facilitation has been reported for both eye (Hanning et al. 2016, Ohl & Rolfs 2017) and hand (Hanning & Deubel 2018, Heuer & Schubö 2017) movements. Saccade preparation facilitates memory performance for memoranda at the same location even if these memoranda have been effectively masked, suggesting the effects hold for stable, consolidated working-memory representations and not only for fragile or iconic representations (Ohl & Rolfs 2018). Benefits are also observed if actions are only prepared and not executed (Heuer & Schubö 2017, Ohl & Rolfs 2017).

Studies manipulating different action prompts provide interesting insights. For example, in a study directing eye and hand movements to distinct locations, memory performance improved at both locations, without any trade-off in the effect sizes (Hanning & Deubel 2018). These tandem foci of attention argue against strict proposals for one unitary focus of attention within working memory. In another revealing study, Heuer & Schubö (2017) showed that feature representations were prioritized according to their pragmatic utility for the action to be delivered. When

memorizing colored objects of different sizes, memory was better for size when planning a grasping action, and it was better for color when planning a pointing action.

In principle, action-driven internal selective attention can include voluntary or involuntary mechanisms. Studies exploring the factors affecting motor-driven internal selective attention have argued for a contribution of involuntary effects. For example, Ohl & Rolfs (2017) reported better memory for action-congruent objects even when the action-congruent memory object was substantially less likely to be probed. At the same time, it is important to appreciate that in everyday life, planning an action toward a location is often accompanied by attending to the contents, external and internal, associated with the same location. Both voluntary and involuntary consequences of action planning are likely to come together to guide goal-directed behavior.

Multiple Sources of Internal Selective Attention

Since retrocues reignited the study of internal selective attention, our appreciation has grown for the multiple situations that lead to selection and prioritization of internal contents. Voluntary and involuntary orienting can be driven by cues, internal states, sensory stimuli, and intended action. Although these sources of internal selective attention tend to be studied in isolation in the laboratory, in our everyday life they work together and probably interact in interesting ways we are yet to uncover.

Studying multiple sources of internal selective attention together will be important not only for approximating real-world cognition but also for addressing pivotal theoretical questions. For example, theoretical proposals that posit or assume a single focus of attention would require different sources to compete if they highlight different contents.

The few studies considering multiple potential sources of internal selective attention are beginning to paint a rich picture that suggests that multiple sources of selective attention can work in tandem to affect performance concurrently. As we described above, our own study comparing working-memory modulation by the voluntary orienting based on retrocue informativeness and by the involuntary sensory-driven capture by feature matching revealed dissociable benefits on access to representations and their informational fidelity (van Ede et al. 2020). Moreover, a continuous gaze marker of internal selective attention showed more transient sensory-driven influences and longer-lasting goal-driven influences. Niklaus et al. (2019) similarly showed that the effects of retrocues were independent of last-object prioritization. A similar theme of dissociable effects emerges when comparing internal selective attention based on task relevance and on action planning (Ohl & Rolfs 2017). Comparing patterns across studies also suggests multiple mechanisms. For example, whereas retrocue benefits vary considerably according to memory load (Asthle et al. 2012, Nobre et al. 2008, Sligte et al. 2008, Souza et al. 2014), this appears not to be the case for the benefits of saccade preparation at congruent locations (Ohl & Rolfs 2020). Thus, internal selective attention comes in many flavors, mediated by multiple sources, and with manifold consequences for cognition and behavior, as we turn to next.

HOW: THE WORKINGS OF INTERNAL SELECTIVE ATTENTION

Having considered the ecological advantage of focusing on mental contents that are relevant to guide possible future behavior (why), shown how different types of content may be useful for different purposes (what), and described various situations that prompt internal selective attention (when), we finally arrive at the question: How does the brain select and prioritize among the contents in working memory? In this section, we sketch some of the mechanisms being discovered and principles emerging.

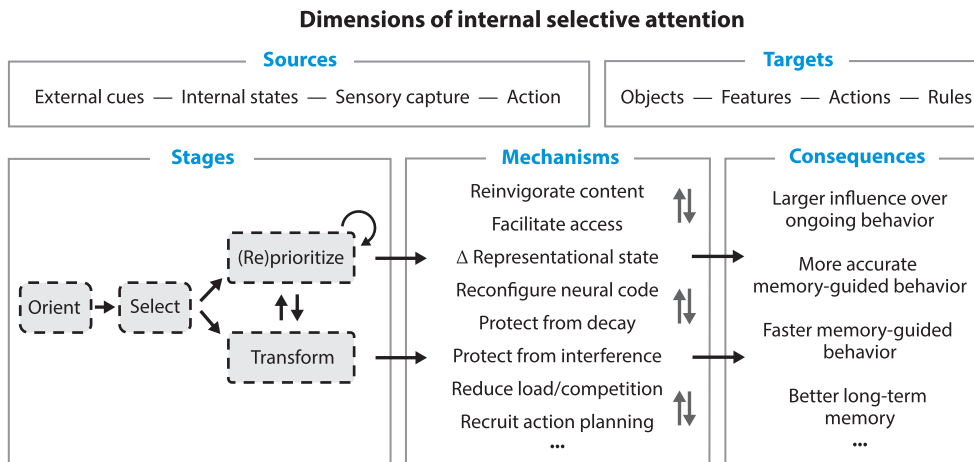


Figure 3

Sources, targets, stages, mechanisms, and consequences of internal selective attention. As discussed throughout the review, internal selective attention can be driven by multiple sources (when), can act on various representational targets (what), and can be mediated by multiple stages and mechanisms to yield various consequences (how). Note that this overview is not intended to be exhaustive, nor are the listed mechanisms mutually exclusive. Instead, the various mechanisms are likely to be interdependent and reinforce each other (as indicated by the vertical arrows).

Knowledge of the control and modulatory mechanisms in external selective attention has advanced through decades of investigations across species, including recordings at the single-cell level, imaging of neural systems, fractionating of behavioral markers, and computational modeling. In comparison, the study of internal selective attention is nascent. For example, the first study in nonhuman primates was published only recently (Panichello & Buschman 2021), opening the investigation of detailed neurobiological mechanisms (see van Ede & Nobre 2021). Without question, the knowledge we have gained from and the tools we have developed for investigating external selective attention offer a head start for exploring its internal counterpart. However, it is important to avoid the hasty assumption that selective attention works in the same way whether directed externally or internally.

The other important trap to avoid is that of looking for the unitary mechanism for internal selective attention. A number of studies to date have focused on identifying the key mechanism or arbitrating among contenders. Many possibilities have been suggested, including, for example, reinvigorating relevant internal content, facilitating retrieval or access, placing contents in a privileged state, reconfiguring neural codes, protecting from decay, protecting from interference, reducing memory load and competition, and recruiting action planning for attended content (**Figure 3**). As the previous sections of this review emphasize, internal selective attention can target multiple types of internal representations and be prompted by various situations. The patterns of behavioral benefits can differ depending on the targets and sources of internal selective attention and are likely to differ depending on task demands. Getting to the big picture and abstracting the operational principles of internal selective attention will necessarily require embracing the plurality of mechanisms by which internal contents are modulated to serve future behavior.

Multiple Stages of Internal Selective Attention

Following from the observation that internal selective attention can act on different types of internal contents and be driven by various sources is the inference that internal selective attention

can modulate multiple stages of processing and thereby have manifold consequences for cognition and behavior (see **Figure 3** for an overview). These stages and consequences of modulation need not be mutually exclusive, nor need we assume that internal selective attention always follows a defined modulatory pathway toward a single consequence.

Internal selective attention serves as an umbrella term for the set of mechanisms modulating internal contents during multiple stages of processing. As a starting point, we propose differentiating among the following four stages: orienting, selecting, prioritizing (and reprioritizing), and transforming. As our knowledge grows, it may be possible to define stages more accurately, add additional stages (such as gradual sampling and making decisions; van Ede & Nobre 2022), and redraw boundaries. Sometimes there is a tendency to equate internal selective attention just with selection, but this can blind the research enterprise to interesting possibilities. For example, orienting need not imply selection—just like orienting yourself to inspect a product in the supermarket is not equivalent to selecting it and placing it in your cart. Similarly, selection need not imply prioritization and may sometimes trigger a transformation of the attended memory content instead, whereby there is a change in its neural coding and representational state.

Orienting toward selective contents in working memory was the first aspect investigated by retrocue studies. These compared the brain processes triggered by predictive cues appearing before the stimulus array (precues) and those triggered by retrodictive cues appearing during the working-memory interval (retrocues) (Griffin & Nobre 2003, Nobre et al. 2004). These early studies revealed substantial overlap between the neural systems and dynamics for orienting attention in the external and internal landscapes. Orienting attention to locations within working memory engaged the same dorsal frontal-parietal network involved in controlling external spatial attention (Nobre et al. 2004; see also Nobre & Mesulam 2014). Subsequent studies of internal selective attention also found engagement of these large-scale frontal parietal networks (Nee & Jonides 2008, Wallis et al. 2015). Recordings of event-related potentials showed that spatial retrocues trigger similar potentials to spatial precues (Griffin & Nobre 2003).

Unlike orienting in external selective attention, orienting within working memory occurs in the context of preexisting contents that are directly available for selection. Accordingly, brain imaging and neurophysiology studies further showed engagement of additional brain areas and processes related to the selection of contents, with recruitment of medial and lateral prefrontal areas as well as the basal ganglia (Chatham & Badre 2015, Nelissen et al. 2013, Nobre et al. 2004). Magnetoencephalography recordings showed that the engagement of the frontal cingulo-opercular followed that of the frontal parietal network (Wallis et al. 2015), suggesting an operation downstream to orienting, such as selection or output gating (Chatham & Badre 2015). Functional magnetic resonance studies examining functional connectivity reinforce the finding that frontal areas contribute to the selection of sensory contents during internal selective attention (Kuo et al. 2014, Nelissen et al. 2013).

Prioritization of selected contents in working memory has been visualized by several brain imaging and neurophysiology studies, though it has been challenging to separate changes in neural activity related to prioritization of working-memory content from the anticipation of probe stimuli sharing similar attributes (see Lepsien & Nobre 2007). Nevertheless, clear modulation of brain activity related to internal prioritization has been observed in numerous well-controlled studies that rule out contributions of probe anticipation. Using fMRI, one example is the retinotopic modulation in visual areas triggered by shape retrocues corresponding to the memorized location of an object that would be probed centrally (Kuo et al. 2014). Using univariate analyses, brain imaging studies have shown increases in visual activity levels related to retinotopic locations (Kuo et al. 2014, Sligte et al. 2009) and functional specialization (Lepsien & Nobre 2007) by spatial and object-based internal selective attention, respectively. Going further, multivariate analyses

have shown enhancement of the sensory information defining the attended content in working memory (Harrison & Tong 2009, Lewis-Peacock et al. 2012, Serences et al. 2009). Bolstering findings from the behavioral literature (Murray et al. 2013), internal selective attention toward visual objects in working memory has been found to restore previously unresolvable activation patterns (Lewis-Peacock et al. 2012, Sprague et al. 2016).

A common observation is that patterns of brain activity related to currently unattended contents are harder to decode (Lewis-Peacock et al. 2012, Sprague et al. 2016) even when the content may still become relevant for later use. These differences in decodability of attended versus unattended memoranda have reinforced the view that internal content can exist in different formats, such as in the settings of synaptic weights modified by short-term plasticity (silent) or through continued firing during the delay period (active) (Stokes 2015). In addition to strengthening activity patterns, internal selective attention may therefore also change the representational states of memoranda (Muhle-Karbe et al. 2021, Olivers et al. 2011) and/or the brain areas recruited for attended versus unattended contents (Christophel et al. 2018).

In human neurophysiology studies, spatially specific modulation of contralateral delay activity (Katus et al. 2017, Kuo et al. 2012) and alpha-band activity (de Vries et al. 2017, Poch et al. 2017, van Ede et al. 2017, Wallis et al. 2015, Wolff et al. 2017) has been noted in numerous spatial retrocue studies even when the anticipated probe was presented centrally. Neurophysiological studies have also supported the possible maintenance of working-memory content in different representational states. Researchers have borrowed the approach from sonar technology to probe (or “ping”) the pattern of information latent in the synaptic connection strengths in visual areas by using a salient arbitrary visual stimulus (Wolff et al. 2017) or a transcranial magnetic stimulation pulse (Rose et al. 2016). By analyzing the resulting activation pattern, these studies have shown that it is possible to read out the content associated with currently unattended stimuli that remain potentially relevant for task performance.

Although human imaging and neurophysiology studies so far demonstrate prioritization in working memory, they say little about how prioritization occurs. With more granular methods, it will be interesting to explore how contents are prioritized. Many putative mechanisms could contribute—e.g., reinvigorating relevant content, weakening competition from other content, placing contents in different representational states, and so on (**Figure 3**).

Interestingly, within working memory, prioritization of information is much more flexible than during external selective attention. Contents can come in and out of focus without significant erosion in their quality or accessibility. In external selective attention, focusing on some sensory signals degrades the processing of other, competing signals (Carrasco 2011, Desimone & Duncan 1995). In contrast, it is possible to change the focus among contents in working memory flexibly (**Figure 2b,c**) (Christophel et al. 2018; de Vries et al. 2018; Lewis-Peacock et al. 2012; Myers et al. 2018; Rerko & Oberauer 2013; van Ede et al. 2017, 2021; van Moorselaar et al. 2015c; Zokaei et al. 2019) and to do so without trade-offs in the information that remains accessible for contents in or out of focus (Myers et al. 2018). One simple reason for this striking difference lies in the nature of the domain in which external and internal selective attention operate. The competition among external stimuli is fierce, and sensory signals must vie for coding within neuronal receptive fields (Desimone & Duncan 1995). Within working memory the competition is much reduced, having been weeded out through the sensory processing, and the content represented is much better integrated. Therefore, internal selective attention can involve not only prioritization but also the flexible reprioritization of content.

Beyond prioritization and reprioritization, researchers have also suggested the importance of transforming relevant content into pragmatic representations to guide action according to the upcoming task (González-García et al. 2020, Myers et al. 2018, van Ede et al. 2019b). Recent cellular

recordings in primates have confirmed the transformation of relevant information in working-memory content, by shifting population-level neuronal codes of attended memory content into a task-oriented format that abstracts away from nonrelevant attributes, such as spatial location (Panichello & Buschman 2021). Thus, internal selective attention is not just about selecting and prioritizing but also about transforming contents for guiding action.

Manifold Mechanisms and Consequences of Internal Selective Attention

Modulation of different content at different stages for different reasons naturally allows for many possible mechanisms and consequences of internal selective attention (see **Figure 3** for a non-exhaustive overview). It may therefore be more sensible to stop asking what single mechanism explains internal selection attention and start asking about the conditions that enable different mechanisms to operate and the ways in which different mechanisms interact.

As we noted above, internal selective attention sometimes predominantly improves response speeds, while other times it predominantly enhances accuracy (van Ede et al. 2020). Ultimately, the behavioral consequences may reflect an amalgam of modulatory influences, depending on the sources of information available to orient attention as well as the sensory properties of the encoded materials and the anticipated task demands.

Finally, it is interesting to note a relative lacuna in studies investigating the consequences of internal selective attention, regarding its role in facilitating the formation of effective long-term memories. Our interface with the external environment serves not only to direct behavior in the here and now but also to learn about events that, through our long-term memories, may come to guide our perception, cognition, and behavior in the future (Nobre & Stokes 2019). According to most memory models, maintenance of information in working memory is a precursor to the formation of long-term memory (e.g., Atkinson & Shiffrin 1968, Baddeley 2012, Johnson 1992), even if the two time spans of memory may come to differ in their representational states and distribution within brain systems. Therefore, understanding whether and how internal selective attention improves long-term memory performance will be fundamental. It is easy to imagine the important ramifications for understanding how to improve learning and memory in education, as a function of ageing, and so on. Studies beginning to explore this question using refresh cues (Bartsch et al. 2018) and retrocues (Fan & Turk-Browne 2013, Strunk et al. 2019) suggest that this will be a highly fruitful area for investigation.

Spatial-Temporal Grounding of Internal Selective Attention

Although it may be naïve to propose a singular mechanism for internal selective attention, general properties may emerge. Below, we highlight consistent observations that point to possible guiding principles.

A common observation in studies of visual working memory is the important role space plays in maintaining and modulating internal representations. Visual working memory maintains a spatial mapping of objects encoded from the external environment even when location is not required or directly relevant to the task (e.g., Kuo et al. 2009, Schneegans & Bays 2017, van Ede et al. 2019a). These observations have led researchers to propose that space provides an important scaffolding for working-memory representations.

The study of internal selective attention reinforces the notion that the retention of spatial information is not gratuitous but instead serves a functional role. Preserving a spatial mapping allows for orienting, selecting, and prioritizing contents in working memory according to their unique memorized location, even when cues or other sources of attention are not themselves spatial. Thus, space can serve as a potent medium for internal selective attention by capitalizing

on the rich spatial organization within sensory and higher-order brain areas (Groen et al. 2022). By anchoring memory contents to distinct anatomical locations within spatiotopic maps, modulation of internal representations is greatly facilitated. Once the relevant contents have been selected, prioritized, and transformed into pragmatic representations, spatial information may eventually be dropped if no longer relevant for task performance (Panichello & Buschman 2021).

Although many researchers agree on the important role of spatial frames in supporting working memory and internal selective attention, there has been relatively little consideration of how different types of spatial scaffolding may contribute. The study of spatial maps in navigation (Burgess 2006) and in sensorimotor systems (Andersen et al. 1997) has taught us about the existence of multiple spatial frames, both allocentric and egocentric. Yet, studies of visual working memory have predominantly used static, two-dimensional visual displays with which participants interact in a fixed, seated position. These highly artificial conditions used for maximizing experimental control do not capture the richness of spatial frames relevant for our everyday behavior.

In its natural habitat—the mind of observers moving through dynamic environments—the potential role of space in supporting working memory and internal selective attention becomes considerably richer. Imagine turning toward the goal during a game of soccer. As you turn, relevant information disappears from sight not because the information magically vanishes in front of you, as in conventional laboratory tasks of visual working memory, but because you move away. In such situations, multiple spatial frames can potentially serve the retention and selection of sensory information in working memory. For example, after turning, you may remember where relevant team members are located in the world relative to your own position, which is critical for passing the ball. However, you may additionally remember where two team members are relative to each other, which may prove useful for selecting and prioritizing one memorized team member over another as the game develops.

In a recent study by Draschkow et al. (2022), we investigated how different spatial frames support working memory in immersive, dynamic contexts using virtual reality combined with eye tracking. Participants viewed tilted color bars projected on a virtual wall to the left and to the right of a visual fixation marker. In the critical condition, the stimuli disappeared because participants themselves turned 90° to the left or to the right. By measuring systematic spatial biases in gaze (van Ede et al. 2019a), we found that multiple spatial frames supported working-memory performance: the positions of encoded memory objects relative to one another and relative to the observer (as in our soccer example above). This discovery illustrates how studying working memory in more natural settings (see also Ballard et al. 1997, Draschkow et al. 2021, Tatler & Land 2011) can open new questions and add important insights.

Like space, time is an essential dimension for scaffolding cognition and making sense of experience. For example, in studies involving encoding of multiple objects appearing sequentially, working-memory performance for detecting a color change was significantly impaired if either the spatial or temporal configuration was removed at testing (Heuer & Rolfs 2021b). Thus, even though neither locations nor intervals were required for the task (color judgement), both attributes were incidentally encoded and guided performance.

When considering working memory outside of the visual domain, we note that spatial location is not always available for differentiating stimuli. For example, working memory can exist for inherently nonspatial representations, such as words, task rules, or thoughts. Space cannot therefore be the only medium for maintaining internal representations and for supporting internal selective attention. In such cases, temporal features may play an even more important role. Yet, given that our understanding of how temporal information is stored and used by the brain remains fragmentary, it is still challenging to conceive how time can support working memory and internal selective attention. In some cases, the brain may also impose spatial structures onto nonspatially

organized stimuli. For example, some studies suggest that participants project serially presented contents onto different locations in mental representations (e.g., Rasoulzadeh et al. 2021), which can facilitate working-memory performance and internal selective attention. It will be interesting to test whether these intriguing findings generalize beyond specific task strategies and point to a more general process.

Sensorimotor Control over Internal Selective Attention

The spatial-temporal grounding of visual working memory and internal selective attention is consistent with the overarching framework of sensory recruitment: the recruitment of sensory areas for maintaining and modulating informational content in mind (Harrison & Tong 2009, Serences et al. 2009, Sreenivasan et al. 2014).

At the same time, the spatial-temporal grounding in working memory suggests a strong link to action systems. Motor areas are increasingly implicated in driving active sensing of relevant sensory information (Schroeder et al. 2010). Visual sampling occurring through eye movements is a prime example. Ample evidence points to the causal involvement of the oculomotor system in covert shifts of spatial attention, even in the absence of concurrent large eye movements (Krauzlis et al. 2013, Moore et al. 2003). Although labeled “covert,” these shifts of attention are nonetheless accompanied by directional biases in small eye movements commonly referred to as microsaccades [as reviewed by Corneil & Munoz (2014)].

The puzzling question that follows is whether sensorimotor systems and motor-driven active sampling also apply when sampling information within the spatial landscape of the mind. Do the motor-related mechanisms that facilitate foraging of information in the external environment also apply to our internal vision? For example, if internal selective attention recycles or adapts sensorimotor mechanisms used for external selective attention, microsaccadic biases may be detectable even when shifting the internal focus of attention.

Following this interesting trail, we recently uncovered robust directional biases in microsaccades when participants directed selective attention to the locations of objects maintained in working memory (Liu et al. 2022, van Ede et al. 2019a). The gaze biases occurred even though we never asked about memorized object location, strengthening the idea that space helps scaffold visual working memory. Our results (like those of others before us; e.g., Spivey & Geng 2001) suggest that the mechanisms for internal spatial orienting build on and adapt mechanisms for external spatial orienting, which in turn build on and adapt mechanisms for controlling overt action. These results urge a promotion of the sensory-recruitment view of working memory into a sensory-motor-recruitment view of working memory (see also D’Esposito & Postle 2015). They also champion the importance of evolutionary perspectives to understand the organization of cognition more generally (Cisek 2019).

Cellular Mechanisms: Knowns and Unknowns

Compared to the progress in behavioral, brain imaging, and magneto/electro-encephalography studies of internal selective attention, little is known about the cellular mechanisms. Cellular recording studies of external selective attention date back half a century (e.g., Goldberg & Wurtz 1972). In contrast, at the time of writing, only one published study has investigated the cellular mechanisms of internal selective attention (Panichello & Buschman 2021). Several relevant insights arose from those observations. For example, comparing internal and external selective attention showed similar coding in lateral prefrontal cortex and a similar time course for prefrontal signals related to internal and external shifts. Coding in other recording areas was more dissimilar for internal versus external attention. Significantly, the study provided direct evidence for the

neural transformation of attended working-memory contents. In Panichello & Buschman's (2021) task requiring a color-based response, attended representations became abstracted from the spatial information as location became irrelevant. The latter finding corroborates proposals based on the human experimental literature (Myers et al. 2017) that attended representations change to become pragmatically useful to guide behavior within the particular task.

Future studies targeting cellular mechanisms in animal models will be critical for progressing the mechanistic understanding and ultimately the theoretical principles of internal selective attention. As additional invasive studies develop, it is essential not to forget the richness of the phenomenon under investigation. As we have reviewed (**Figure 3**; see also the **Summary Points** section below), multiple types of targets can be influenced along multiple stages of processing by multiple sources, with different consequences for cognition and behavior depending on the task demands.

WHERE NEXT: THE FUTURE OF INTERNAL SELECTIVE ATTENTION

We have promoted the view that reflecting back in working memory is most useful for planning forward. We end by applying the same approach, focusing on what we have learned about internal selective attention to look ahead at the exciting and important new research questions and applications.

The study of internal selective attention has come a long way over a short period. The rich and well-established research fields of working memory and of external selective attention provided a great launchpad of relevant mechanistic insights, theoretical approaches, and methodological tools. Sometimes, however, the comfort of apparent similarities can mask important differences. Moving ahead, it will be pivotal to keep scratching beneath the surface to uncover the unique ways in which we juggle the contents in our mindscape to navigate our experience.

Situating the research in more natural immersive environments holds great promise. With improving virtual-reality methods, we can gain a more relevant understanding of how we interact with mental contents selectively and adaptively in our daily lives. As initial studies demonstrate, properties we extract from highly controlled laboratory tasks do not always transfer simplistically to dynamic immersive situations (Draschkow et al. 2022). Utilizing richer behavioral methods will also add layers to our understanding. Activity in the brain can be read out not only from single button presses but also from involuntary gaze shifts, eye movements, pupil dilation, reaching trajectories, postural alignment, and more. As research using gaze shifts (van Ede et al. 2019a, 2020, 2021) and pupil changes (Zokaei et al. 2019) has started to show, continuous measures of behaviors can help us read out the contents in our minds in real time, which should help us chart the dynamics of and interrelations among the varieties of internal selective attention.

A natural next step is to translate the study of internal selective attention into settings where it is likely to make a significant difference to our development and well-being. If attending to contents in working memory proves to have a significant impact on subsequent memory (Bartsch et al. 2018, Fan & Turk-Browne 2013, Strunk et al. 2019), it could become a vital skill for learning. It would be highly relevant for children's educational settings and play an important role in buttressing adaptive cognition during development (Shimi et al. 2014) as well as during healthy ageing (Mok et al. 2016) and in ageing-related disorders (Newsome et al. 2015). It will also be worthwhile to investigate the role internal selective attention may play in reinforcing pathological emotional biases associated with mood disorders and to explore its ability to act as a platform for redressing these.

Taking a step in a more fundamental direction, we should build on findings and methods developed within internal selective attention in working memory to study how we select and prioritize contents from the boundless pool of long-term memories stored over various time scales in

our brains. Our continual everyday acts of voluntary retrieval, as well as the occasional retrieved associations we enjoy, are clear acts of selective attention. Though theoretical models have highlighted the close relation between long-term memory and attention (Cabeza et al. 2008, Chun et al. 2011, Johnson 1992), we have little understanding of how the processes of orienting, selecting, (re)prioritizing, and transforming relevant contents in long-term memory unfold. The study of internal selective attention in working memory thus opens the door to exploring the deeper fundamental questions about our flexible and adaptive utilization of memories.

A final challenge will be to bring the fields of external and internal selective attention together. In our real-life routines, sensory and memory signals are coordinated and integrated most of the time. How the brain co-organizes representations from external stimulation and from active internal contents is a fascinating mystery (Rademaker et al. 2019). Understanding how we shift attention between the external environment and internal representations goes one step further (Verschooren & Egner 2022, Weber et al. 1986). Only by jointly considering internal and external information—and their appropriately timed selection, prioritization, and transformation—will we be able to understand how cognition enables and facilitates flexible and adaptive goal-directed behavior.

SUMMARY POINTS

1. Adaptive flexible behavior combines both external sensory signals and internal contents in working memory.
2. Selective attention works in two directions: modulating sensory stimulation to build internal contents (outside-in) or modulating internal contents to guide adaptive behavior (inside-out).
3. Internal selective attention is functional, flexible, and future focused. To guide adaptive behavior, different sources of modulation (external cues, internal states, sensory capture, intended action) can target multiple types of representations (objects, features, actions, rules) along separate processing stages [orienting, selecting, (re)prioritizing, transforming] through various mechanisms and with manifold benefits to performance.
4. Rather than emphasizing the informational capacity limits of working memory, it is useful to consider its pragmatic utility in enabling behavioral flexibility by preparing for multiple potential and sequential courses of action.
5. Relative to the study of external selective attention, the study of internal selective attention is still in its infancy. Research ahead holds enormous promise for clinical and societal applications as well as for reaching greater depth of understanding of how working memory links mind to behavior.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS

This work was supported by an ERC Starting Grant from the European Research Council (MENTICIPATION, 850636) to F.v.E., a Wellcome Trust Senior Investigator Award

(104571/Z/14/Z) and a James S. McDonnell Foundation Understanding Human Cognition Collaborative Award (220020448) to A.C.N, and by the NIHR Oxford Health Biomedical Research Centre. The Wellcome Centre for Integrative Neuroimaging is supported by core funding from the Wellcome Trust (203139/Z/16/Z). We also wish to thank the members of the Proactive Brain Lab in Amsterdam and the Brain & Cognition Lab in Oxford for all the collaborative research and enriching exchanges that have shaped this review. Special thanks go to Daniela Gresch, Sage Boettcher, Rose Nasrawi, and Baiwei Liu for their careful reading of and input into earlier drafts of the manuscript.

LITERATURE CITED

- Allport A. 1987. Selection for action: some behavioral and neurophysiological considerations of attention and action. In *Perspectives on Perception and Action*, ed. H Heuer, A Sanders, pp. 395–419. London: Routledge
- Andersen RA, Snyder LH, Bradley DC, Xing J. 1997. Multimodal representation of space in the posterior parietal cortex and its use in planning movements. *Annu. Rev. Neurosci.* 20:303–30
- Astle DE, Summerfield J, Griffin I, Nobre AC. 2012. Orienting attention to locations in mental representations. *Atten. Percept. Psychophys.* 74(1):146–62
- Atkinson AL, Berry EDJ, Waterman AH, Baddeley AD, Hitch GJ, Allen RJ. 2018. Are there multiple ways to direct attention in working memory? *Ann. N.Y. Acad. Sci.* 1424(1):115–26
- Atkinson RC, Shiffrin RM. 1968. Human memory: a proposed system and its control processes. In *Psychology of Learning and Motivation: Advances in Research and Theory*, Vol. 2, ed. KW Spence, JT Spence, pp. 89–195. New York: Academic
- Backer KC, Alain C. 2012. Orienting attention to sound object representations attenuates change deafness. *J. Exp. Psychol. Hum. Percept. Perform.* 38(6):1554–66
- Backer KC, Buchsbaum BR, Alain C. 2020. Orienting attention to short-term memory representations via sensory modality and semantic category retro-cues. *eNeuro* 7(6):ENEURO.0018-20.2020
- Baddeley A. 2012. Working memory: theories, models, and controversies. *Annu. Rev. Psychol.* 63:1–29
- Baddeley AD, Hitch G. 1974. Working memory. *Psychol. Learn. Motiv.* 8:47–89
- Baldauf D, Deubel H. 2010. Attentional landscapes in reaching and grasping. *Vis. Res.* 50(11):999–1013
- Ballard DH, Hayhoe MM, Pook PK, Rao RPN. 1997. Deictic codes for the embodiment of cognition. *Behav. Brain Sci.* 20(4):723–42; discuss. 743–67
- Bartsch LM, Singmann H, Oberauer K. 2018. The effects of refreshing and elaboration on working memory performance, and their contributions to long-term memory formation. *Mem. Cognit.* 46(5):796–808
- Boettcher SE, Gresch D, Nobre AC, van Ede F. 2021. Output planning at the input stage in visual working memory. *Sci. Adv.* 7:eabe8212
- Boettcher SEP, van Ede F, Nobre AC. 2020. Functional biases in attentional templates from associative memory. *J. Vis.* 20(13):7
- Brady TF, Konkle T, Alvarez GA. 2011. A review of visual memory capacity: beyond individual items and toward structured representations. *J. Vis.* 11(5):4
- Brass M, Liefoghe B, Braem S, De Houwer J. 2017. Following new task instructions: evidence for a dissociation between knowing and doing. *Neurosci. Biobehav. Rev.* 81:16–28
- Burgess N. 2006. Spatial memory: how egocentric and allocentric combine. *Trends Cogn. Sci.* 10(12):551–57
- Cabeza R, Ciaramelli E, Olson IR, Moscovitch M. 2008. The parietal cortex and episodic memory: an attentional account. *Nat. Rev. Neurosci.* 9(8):613–25
- Camos V, Johnson M, Loaiza V, Portrat S, Souza A, Vergauwe E. 2018. What is attentional refreshing in working memory? *Ann. N.Y. Acad. Sci.* 1424(1):19–32
- Carrasco M. 2011. Visual attention: the past 25 years. *Vis. Res.* 51(13):1484–525
- Chatham CH, Badre D. 2015. Multiple gates on working memory. *Curr. Opin. Behav. Sci.* 1:23–31
- Christophel TB, Iamshchinina P, Yan C, Allefeld C, Haynes JD. 2018. Cortical specialization for attended versus unattended working memory. *Nat. Neurosci.* 21:494–96
- Chun MM, Golomb JD, Turk-Browne NB. 2011. A taxonomy of external and internal attention. *Annu. Rev. Psychol.* 62:73–101

- Cisek P. 2019. Resynthesizing behavior through phylogenetic refinement. *Atten. Percept. Psychophys.* 81(7):2265–87
- Cisek P, Kalaska JF. 2010. Neural mechanisms for interacting with a world full of action choices. *Annu. Rev. Neurosci.* 33:269–98
- Cohen NJ, Squire LR. 1980. Preserved learning and retention of pattern-analyzing skill in amnesia: dissociation of knowing how and knowing that. *Science* 210(4466):207–10
- Corneil BD, Munoz DP. 2014. Overt responses during covert orienting. *Neuron* 82(6):1230–43
- Cowan N. 2001. The magical number 4 in short-term memory: a reconsideration of mental storage capacity. *Behav. Brain Sci.* 24(1):87–114
- Cowan N. 2010. The magical mystery four: How is working memory capacity limited, and why? *Curr. Dir. Psychol. Sci.* 19(1):51–57
- de Vries IEJ, van Driel J, Karacaoglu M, Olivers CNL. 2018. Priority switches in visual working memory are supported by frontal delta and posterior alpha interactions. *Cereb. Cortex* 28(11):4090–104
- de Vries IEJ, van Driel J, Olivers CNL. 2017. Posterior α EEG dynamics dissociate current from future goals in working memory-guided visual search. *J. Neurosci.* 37(6):1591–603
- Desimone R, Duncan J. 1995. Neural mechanisms of selective visual attention. *Annu. Rev. Neurosci.* 18:193–222
- D’Esposito M, Postle BR. 2015. The cognitive neuroscience of working memory. *Annu. Rev. Psychol.* 66:115–42
- Deubel H, Schneider WX. 1996. Saccade target selection and object recognition: evidence for a common attentional mechanism. *Vis. Res.* 36(12):1827–37
- Dewey J. 1896. The reflex arc concept in psychology. *Psychol. Rev.* 3(4):357–70
- Draschkow D, Kallmayer M, Nobre AC. 2021. When natural behavior engages working memory. *Curr. Biol.* 31(4):869–74.e5
- Draschkow D, Nobre AC, van Ede F. 2022. Multiple spatial frames for immersive working memory. *Nature Hum. Behav.* 6:536–44
- Egley R, Driver J, Rafal RD. 1994. Shifting visual attention between objects and locations: evidence from normal and parietal lesion subjects. *J. Exp. Psychol. Gen.* 123(2):161–77
- Eichenbaum H, Yonelinas AP, Ranganath C. 2007. The medial temporal lobe and recognition memory. *Annu. Rev. Neurosci.* 30:123–52
- Engel AK, Maye A, Kurthen M, König P. 2013. Where’s the action? The pragmatic turn in cognitive science. *Trends Cogn. Sci.* 17(5):202–9
- Fan JE, Turk-Browne NB. 2013. Internal attention to features in visual short-term memory guides object learning. *Cognition* 129(2):292–308
- Fan Y, Han Q, Guo S, Luo H. 2021. Distinct neural representations of content and ordinal structure in auditory sequence memory. *J. Neurosci.* 41(29):6290–303
- Fawcett JM, Risko EF, Kingstone A, eds. 2015. *The Handbook of Attention*. Cambridge, MA: MIT Press
- Fuster JM. 1973. Unit activity in prefrontal cortex during delayed-response performance: neuronal correlates of transient memory. *J. Neurophysiol.* 36(1):61–78
- Fuster JM, Bressler SL. 2012. Cognit activation: a mechanism enabling temporal integration in working memory. *Trends Cogn. Sci.* 16(4):207–18
- Garavan H. 1998. Serial attention within working memory. *Mem. Cogn.* 26(2):263–76
- Gehring WJ, Bryck RL, Jonides J, Albin RL, Badre D. 2003. The mind’s eye, looking inward? In search of executive control in internal attention shifting. *Psychophysiology* 40(4):572–85
- Goldberg ME, Wurtz RH. 1972. Activity of superior colliculus in behaving monkey. II. Effect of attention on neuronal responses. *J. Neurophysiol.* 35(4):560–74
- Gong M, Li S. 2014. Learned reward association improves visual working memory. *J. Exp. Psychol. Hum. Percept. Perform.* 40(2):841–56
- González-García C, Formica S, Liefoghe B, Brass M. 2020. Attentional prioritization reconfigures novel instructions into action-oriented task sets. *Cognition* 194:104059
- Goodale MA, Westwood DA, Milner AD. 2004. Two distinct modes of control for object-directed action. *Prog. Brain Res.* 144:131–44
- Griffin IC, Nobre AC. 2003. Orienting attention to locations in internal representations. *J. Cogn. Neurosci.* 15(8):1176–94

- Groen IIA, Dekker TM, Knapen T, Silson EH. 2022. Visuospatial coding as ubiquitous scaffolding for human cognition. *Trends Cogn. Sci.* 26(1):81–96
- Hajonides JE, van Ede F, Stokes MG, Nobre AC. 2020. Comparing the prioritization of items and feature-dimensions in visual working memory. *J. Vis.* 20(8):25
- Hanning NM, Deubel H. 2018. Independent effects of eye and hand movements on visual working memory. *Front. Syst. Neurosci.* 12:37
- Hanning NM, Jonikaitis D, Deubel H, Szinte M. 2016. Oculomotor selection underlies feature retention in visual working memory. *J. Neurophysiol.* 115(2):1071–76
- Harrison SA, Tong F. 2009. Decoding reveals the contents of visual working memory in early visual areas. *Nature* 458(7238):632–35
- Helmholtz H. 1867. Handbuch der Physiologischen Optik. In *Allgemeine Encyclopädie der Physik*, ed. G Karsten, pp. 37–51. Leipzig, Ger.: Voss
- Heuer A, Ohl S, Rolfs M. 2020. Memory for action: a functional view of selection in visual working memory. *Vis. Cogn.* 28(5–8):388–400
- Heuer A, Rolfs M. 2021a. A direct comparison of attentional orienting to spatial and temporal positions in visual working memory. *Psychon. Bull. Rev.* 29:182–90
- Heuer A, Rolfs M. 2021b. Incidental encoding of visual information in temporal reference frames in working memory. *Cognition* 207:104526
- Heuer A, Schubö A. 2016. Feature-based and spatial attentional selection in visual working memory. *Mem. Cogn.* 44(4):621–32
- Heuer A, Schubö A. 2017. Selective weighting of action-related feature dimensions in visual working memory. *Psychon. Bull. Rev.* 24(4):1129–34
- Hommel B, Müsseler J, Aschersleben G, Prinz W. 1994. The theory of event-coding (TEC): a framework for perception and action planning. *Behav. Brain Sci.* 24:849–78
- Hu Y, Hitch GJ, Baddeley AD, Zhang M, Allen RJ. 2014. Executive and perceptual attention play different roles in visual working memory: evidence from suffix and strategy effects. *J. Exp. Psychol. Hum. Percept. Perform.* 40(4):1665–78
- James W. 1890. *The Principles of Psychology*. New York: Henry Holt & Co.
- Janczyk M, Berryhill ME. 2014. Orienting attention in visual working memory requires central capacity: decreased retro-cue effects under dual-task conditions. *Atten. Percept. Psychophys.* 76(3):715–24
- Johnson MK. 1992. MEM: mechanisms of recollection. *J. Cogn. Neurosci.* 4(3):268–80
- Jonides J. 1981. Voluntary versus automatic control over the mind's eye's movement. In *Attention and Performance*, ed. JB Long, AD Baddely, pp. 187–203. Mahwah, NJ: Lawrence Erlbaum
- Kalogeropoulou Z, Jagadeesh AV, Ohl S, Rolfs M. 2017. Setting and changing feature priorities in visual short-term memory. *Psychon. Bull. Rev.* 24(2):453–58
- Katus T, Grubert A, Eimer M. 2017. Intermodal attention shifts in multimodal working memory. *J. Cogn. Neurosci.* 29(4):628–36
- Kikumoto A, Mayr U. 2020. Conjunctive representations that integrate stimuli, responses, and rules are critical for action selection. *PNAS* 117(19):10603–8
- Kiyonaga A, Egner T. 2013. Working memory as internal attention: toward an integrative account of internal and external selection processes. *Psychon. Bull. Rev.* 20(2):228–42
- Kong G, Fougine D. 2019. Visual search within working memory. *J. Exp. Psychol. Gen.* 148(10):1688–700
- Kowler E, Anderson E, Doshier B, Blaser E. 1995. The role of attention in the programming of saccades. *Vis. Res.* 35(13):1897–916
- Krauzlis RJ, Lovejoy LP, Zénon A. 2013. Superior colliculus and visual spatial attention. *Annu. Rev. Neurosci.* 36:165–82
- Kuo B-C, Rao A, Lepsien J, Nobre AC. 2009. Searching for targets within the spatial layout of visual short-term memory. *J. Neurosci.* 29(25):8032–38
- Kuo B-C, Stokes MG, Murray AM, Nobre AC. 2014. Attention biases visual activity in visual short-term memory. *J. Cogn. Neurosci.* 26(7):1377–89
- Kuo B-C, Stokes MG, Nobre AC. 2012. Attention modulates maintenance of representations in visual short-term memory. *J. Cogn. Neurosci.* 24(1):51–60

- Landman R, Spekreijse H, Lamme VAF. 2003. Large capacity storage of integrated objects before change blindness. *Vis. Res.* 43(2):149–64
- Lee J, Geng JJ. 2019. Flexible weighting of target features based on distractor context. *Atten. Percept. Psychophys.* 82(2):739–51
- Lepsien J, Nobre AC. 2007. Attentional modulation of object representations in working memory. *Cereb. Cortex* 17(9):2072–83
- Lewis-Peacock JA, Drysdale AT, Oberauer K, Postle BR. 2012. Neural evidence for a distinction between short-term memory and the focus of attention. *J. Cogn. Neurosci.* 24(1):61–79
- Li J, Huang Q, Han Q, Mi Y, Luo H. 2021. Temporally coherent perturbation of neural dynamics during retention alters human multi-item working memory. *Prog. Neurobiol.* 201:102023
- Lin Y-t, Kong G, Fougner D. 2021a. Object-based selection in visual working memory. *Psychon. Bull. Rev.* 28(6):1961–71
- Lin Y-t, Sasin E, Fougner D. 2021b. Selection in working memory is resource-demanding: concurrent task effects on the retro-cue effect. *Atten. Percept. Psychophys.* 83(4):1600–12
- Liu B, Nobre AC, van Ede F. 2022. Functional but not obligatory link between microsaccades and neural modulation by covert spatial attention. *Nat. Commun.* 13:3503
- Luck SJ, Vogel EK. 1997. The capacity of visual working memory for features and conjunctions. *Nature* 390(6657):279–81
- Makovski T, Sussman R, Jiang YV. 2008. Orienting attention in visual working memory reduces interference from memory probes. *J. Exp. Psychol. Learn. Mem. Cogn.* 34(2):369–80
- Maunsell JHR, Newsome WT. 1987. Visual processing in monkey extrastriate cortex. *Annu. Rev. Neurosci.* 10:363–401
- McElree B, Doshier BA. 1989. Serial position and set size in short-term memory: the time course of recognition. *J. Exp. Psychol. Gen.* 118(4):346–73
- Miller GA, Galanter E, Pribram KH. 1960. *Plans and the Structure of Behavior*. New York: Henry Holt & Co.
- Mok RM, Myers NE, Wallis G, Nobre AC. 2016. Behavioral and neural markers of flexible attention over working memory in aging. *Cereb. Cortex* 26(4):1831–42
- Moore T, Armstrong KM, Fallah M. 2003. Visuomotor origins of covert spatial attention. *Neuron* 40(4):671–83
- Muhle-Karbe PS, Myers NE, Stokes MG. 2021. A hierarchy of functional states in working memory. *J. Neurosci.* 41(20):4461–75
- Murray AM, Nobre AC, Clark IA, Cravo AM, Stokes MG. 2013. Attention restores discrete items to visual short-term memory. *Psychol. Sci.* 24(4):550–56
- Myers NE, Chekroud SR, Stokes MG, Nobre AC. 2018. Benefits of flexible prioritization in working memory can arise without costs. *J. Exp. Psychol. Hum. Percept. Perform.* 44(3):398–411
- Myers NE, Stokes MG, Nobre AC. 2017. Prioritizing information during working memory: beyond sustained internal attention. *Trends Cogn. Sci.* 21(6):449–61
- Nasrawi R, van Ede F. 2022. Planning the potential future during multi-item visual working memory. *J. Cogn. Neurosci.* 34(8):1534–46
- Nee DE, Jonides J. 2008. Neural correlates of access to short-term memory. *PNAS* 105(37):14228–33
- Nee DE, Jonides J. 2013. Trisecting representational states in short-term memory. *Front. Hum. Neurosci.* (7):796
- Nelissen N, Stokes M, Nobre AC, Rushworth MFS. 2013. Frontal and parietal cortical interactions with distributed visual representations during selective attention and action selection. *J. Neurosci.* 33(42):16443–58
- Newsome RN, Duarte A, Pun C, Smith VM, Ferber S, Barense MD. 2015. A retroactive spatial cue improved VSTM capacity in mild cognitive impairment and medial temporal lobe amnesia but not in healthy older adults. *Neuropsychologia* 77:148–57
- Niklaus M, Nobre AC, van Ede F. 2017. Feature-based attentional weighting and spreading in visual working memory. *Sci. Rep.* 7:42384
- Niklaus M, Singmann H, Oberauer K. 2019. Two distinct mechanisms of selection in working memory: additive last-item and retro-cue benefits. *Cognition* 183:282–302
- Nobre AC, Coull JT, Maquet P, Frith CD, Vandenberghe R, Mesulam MM. 2004. Orienting attention to locations in perceptual versus mental representations. *J. Cogn. Neurosci.* 16(3):363–73

- Nobre AC, Griffin IC, Rao A. 2008. Spatial attention can bias search in visual short-term memory. *Front. Hum. Neurosci.* 1(4):10.3389/neuro.09.004.2007
- Nobre AC, Kastner S, eds. 2014. *The Oxford Handbook of Attention*. Oxford, UK: Oxford Univ. Press
- Nobre AC, Mesulam MM. 2014. Large-scale networks for attentional biases. In *The Oxford Handbook of Attention*, ed. AC Nobre, S Kastner, pp. 105–51. Oxford, UK: Oxford Univ. Press
- Nobre AC, Stokes MG. 2019. Premembering experience: a hierarchy of time-scales for proactive attention. *Neuron* 104(1):132–46
- Nobre AC, van Ede F. 2020. Under the mind's hood: what we have learned by watching the brain at work. *J. Neurosci.* 40(1):89–100
- Oberauer K. 2002. Access to information in working memory: exploring the focus of attention. *J. Exp. Psychol. Learn. Mem. Cogn.* 28(3):411–21
- Oberauer K. 2010. Declarative and procedural working memory: common principles, common capacity limits? *Psychol. Belg.* 50(3–4):277–308
- Ohl S, Rolfs M. 2017. Saccadic eye movements impose a natural bottleneck on visual short-term memory. *J. Exp. Psychol. Learn. Mem. Cogn.* 43(5):736–48
- Ohl S, Rolfs M. 2018. Saccadic selection of stabilized items in visuospatial working memory. *Conscious. Cogn.* 64:32–44
- Ohl S, Rolfs M. 2020. Bold moves: inevitable saccadic selection in visual short-term memory. *J. Vis.* 20(2):11
- Olivers CNL, Peters J, Houtkamp R, Roelfsema PR. 2011. Different states in visual working memory: when it guides attention and when it does not. *Trends Cogn. Sci.* 15(7):327–34
- Olivers CNL, Roelfsema PR. 2020. Attention for action in visual working memory. *Cortex* 131:179–94
- Panichello M, Buschman T. 2021. Shared mechanisms underlie the control of working memory and attention. *Nature* 592:601–5
- Park YE, Sy JL, Hong SW, Tong F. 2017. Reprioritization of features of multidimensional objects stored in visual working memory. *Psychol. Sci.* 28(12):1773–85
- Pelz JB, Canosa R. 2001. Oculomotor behavior and perceptual strategies in complex tasks. *Vis. Res.* 41(25–26):3587–96
- Pertsov Y, Bays PM, Joseph S, Husain M. 2013. Rapid forgetting prevented by retrospective attention cues. *J. Exp. Psychol. Hum. Percept. Perform.* 39(5):1224–31
- Peters B, Kaiser J, Rahm B, Bledowski C. 2015. Activity in human visual and parietal cortex reveals object-based attention in working memory. *J. Neurosci.* 35(8):3360–69
- Poch C, Capilla A, Hinojosa JA, Campo P. 2017. Selection within working memory based on a color retro-cue modulates alpha oscillations. *Neuropsychologia* 106:133–37
- Posner MI, Cohen Y. 1984. Components of visual orienting. In *Attention and Performance*, ed. H Bouma, D Bouwhuis, pp. 531–54. Mahwah, NJ: Lawrence Erlbaum
- Rademaker RL, Chunharas C, Serences JT. 2019. Coexisting representations of sensory and mnemonic information in human visual cortex. *Nat. Neurosci.* 22:1336–44
- Rasoulzadeh V, Sahan MI, Van Dijck JP, Abrahamse E, Marzecova A, et al. 2021. Spatial attention in serial order working memory: an EEG study. *Cereb. Cortex* 31(5):2482–93
- Rerko L, Oberauer K. 2013. Focused, unfocused, and defocused information in working memory. *J. Exp. Psychol. Learn. Mem. Cogn.* 39(4):1075–96
- Rerko L, Souza AS, Oberauer K. 2014. Retro-cue benefits in working memory without sustained focal attention. *Mem. Cogn.* 42(5):712–28
- Rizzolatti G, Riggio L, Dascola I, Umiltà C. 1987. Reorienting attention across the horizontal and vertical meridians: evidence in favor of a premotor theory of attention. *Neuropsychologia* 25(1):31–40
- Rose NS, LaRocque JJ, Riggall AC, Gosseries O, Starrett MJ, et al. 2016. Reactivation of latent working memories with transcranial magnetic stimulation. *Science* 354(6316):1136–39
- Schacter DL, Addis DR, Buckner RL. 2007. Remembering the past to imagine the future: the prospective brain. *Nat. Rev. Neurosci.* 8:657–61
- Schneegans S, Bays PM. 2017. Neural architecture for feature binding in visual working memory. *J. Neurosci.* 37(14):3913–25
- Schneider D, Barth A, Wascher E. 2017. On the contribution of motor planning to the retroactive cuing benefit in working memory: evidence by mu and beta oscillatory activity in the EEG. *Neuroimage* 162:73–85

- Schneider D, Mertes C, Wascher E. 2016. The time course of visuo-spatial working memory updating revealed by a retro-cuing paradigm. *Sci. Rep.* 6:21442
- Schroeder CE, Wilson DA, Radman T, Scharfman H, Lakatos P. 2010. Dynamics of active sensing and perceptual selection. *Curr. Opin. Neurobiol.* 20(2):172–76
- Serences JT, Ester EF, Vogel EK, Awh E. 2009. Stimulus-specific delay activity in human primary visual cortex. *Psychol. Sci.* 20(2):207–14
- Shimi A, Nobre AC, Astle D, Scerif G. 2014. Orienting attention within visual short-term memory: development and mechanisms. *Child Dev.* 85(2):578–92
- Sligte IG, Scholte HS, Lamme VAF. 2008. Are there multiple visual short-term memory stores? *PLOS ONE* 3(2):e1699
- Sligte IG, Scholte HS, Lamme VAF. 2009. V4 activity predicts the strength of visual short-term memory representations. *J. Neurosci.* 29(23):7432–38
- Soto D, Humphreys GW. 2007. Automatic guidance of visual attention from verbal working memory. *J. Exp. Psychol. Hum. Percept. Perform.* 33(3):730–37
- Souza AS, Oberauer K. 2016. In search of the focus of attention in working memory: 13 years of the retro-cue effect. *Atten. Percept. Psychophys.* 78(7):1839–60
- Souza AS, Rerko L, Lin HY, Oberauer K. 2014. Focused attention improves working memory: implications for flexible-resource and discrete-capacity models. *Atten. Percept. Psychophys.* 76(7):2080–102
- Souza AS, Rerko L, Oberauer K. 2015. Refreshing memory traces: Thinking of an item improves retrieval from visual working memory. *Ann. N.Y. Acad. Sci.* 1339:20–31
- Sperling G. 1960. The information available in brief visual presentations. *Psychol. Monogr. Gen. Appl.* 74(11):1–29
- Spitzer B, Blankenburg F. 2011. Stimulus-dependent EEG activity reflects internal updating of tactile working memory in humans. *PNAS* 108(20):8444–49
- Spivey MJ, Geng JJ. 2001. Oculomotor mechanisms activated by imagery and memory: eye movements to absent objects. *Psychol. Res.* 65(4):235–41
- Sprague TC, Ester EF, Serences JT. 2016. Restoring latent visual working memory representations in human cortex. *Neuron* 91(3):694–707
- Sreenivasan KK, Curtis CE, D’Esposito M. 2014. Revisiting the role of persistent neural activity during working memory. *Trends Cogn. Sci.* 18(2):82–89
- Stokes MG. 2015. “Activity-silent” working memory in prefrontal cortex: a dynamic coding framework. *Trends Cogn. Sci.* 19(7):394–405
- Strunk J, Morgan L, Reaves S, Verhaeghen P, Duarte A, Gutchess A. 2019. Retrospective attention in short-term memory has a lasting effect on long-term memory across age. *J. Gerontol. Ser. B Psychol. Sci. Soc. Sci.* 74(8):1317–25
- Tanji J. 2001. Sequential organization of multiple movements: involvement of cortical motor areas. *Annu. Rev. Neurosci.* 24:631–51
- Tatler BW, Land MF. 2011. Vision and the representation of the surroundings in spatial memory. *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* 366(1564):596–610
- van Ede F. 2020. Visual working memory and action: functional links and bi-directional influences. *Vis. Cogn.* 28(5–8):401–13
- van Ede F, Board AG, Nobre AC. 2020. Goal-directed and stimulus-driven selection of internal representations. *PNAS* 117(39):24590–98
- van Ede F, Chekroud SR, Nobre AC. 2019a. Human gaze tracks attentional focusing in memorized visual space. *Nat. Hum. Behav.* 3(5):462–70
- van Ede F, Chekroud SR, Stokes MG, Nobre AC. 2019b. Concurrent visual and motor selection during visual working memory guided action. *Nat. Neurosci.* 22(3):477–83
- van Ede F, Deden J, Nobre AC. 2021. Looking ahead in working memory to guide sequential behaviour. *Curr. Biol.* 31(12):R779–80
- van Ede F, Niklaus M, Nobre AC. 2017. Temporal expectations guide dynamic prioritization in visual working memory through attenuated α oscillations. *J. Neurosci.* 37(2):437–45
- van Ede F, Nobre AC. 2021. Toward a neurobiology of internal selective attention. *Trends Neurosci.* 44(7):513–15

- van Ede F, Nobre AC. 2022. A neural decision signal during internal sampling from working memory. *bioRxiv*. <https://doi.org/10.1101/2022.03.31.486618>
- van Moorselaar D, Battistoni E, Theeuwes J, Olivers CNL. 2015a. Rapid influences of cued visual memories on attentional guidance. *Ann. N.Y. Acad. Sci.* 1339(1):1–10
- van Moorselaar D, Günseli E, Theeuwes J, Olivers CNL. 2015b. The time course of protecting a visual memory representation from perceptual interference. *Front. Hum. Neurosci.* 8:1053
- van Moorselaar D, Olivers CNL, Theeuwes J, Lamme VAF, Sligte IG. 2015c. Forgotten but not gone: Retro-cue costs and benefits in a double-cueing paradigm suggest multiple states in visual short-term memory. *J. Exp. Psychol. Learn. Mem. Cogn.* 41(6):1755–63
- Verschooren S, Egnér T. 2022. When the mind's eye prevails: the internal dominance over external attention (IDEA) hypothesis. *PsyArXiv*. <https://doi.org/10.31234/osf.io/x34de>
- Wallis G, Stokes M, Cousijn H, Woolrich M, Nobre AC. 2015. Frontoparietal and cingulo-opercular networks play dissociable roles in control of working memory. *J. Cogn. Neurosci.* 27(10):2019–34
- Weber RJ, Burt DB, Noll NC. 1986. Attention switching between perception and memory. *Mem. Cogn.* 14(3):238–45
- Wolff MJ, Jochim J, Akyürek EG, Stokes MG. 2017. Dynamic hidden states underlying working-memory-guided behavior. *Nat. Neurosci.* 20(6):864–71
- Ye C, Hu Z, Ristaniemi T, Gendron M, Liu Q. 2016. Retro-dimension-cue benefit in visual working memory. *Sci. Rep.* 6:35573
- Zokaei N, Board AG, Manohar SG, Nobre AC. 2019. Modulation of the pupillary response by the content of visual working memory. *PNAS* 116(45):22802–10
- Zokaei N, Ning S, Manohar S, Feredoes E, Husain M. 2014. Flexibility of representational states in working memory. *Front. Hum. Neurosci.* 8:853