

# Opening Questions in Visual Working Memory

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## ***Abstract***

In this reflective piece on visual working memory, I depart from the laboriously honed skills of writing a review. Instead of integrating approaches, synthesising evidence, and building a cohesive perspective, I scratch my head and share niggles and puzzlements. I expose where my scholarship and understanding are stumped by findings and standard views in the literature.

## ***Keywords:***

Cognition  
Visual working memory  
Attention: visual  
Synaptic plasticity  
Ignorance

The act of self-exposure on paper is unnerving. However, confronting ignorance is a necessary and important step for scientific advancement. In private or, even better, in the good company of a close colleague, surfacing and sharing bafflements can become the most rewarding source of creative energy. For me, many new experimental designs, methods, and conceptualisations were born from open-ended conversations with kindred science friends, comparing and discussing points of contention and confusion. I have been lucky to enjoy the friendship of some brilliant, curious, generous, and unpretentious collaborators. Mark Stokes stands out, playing a vital role in shaping and un-shaping my ideas and methods. I offer this soliloquy as a snapshot of what I might bring to such conversations. I do so in the spirit of spreading the courage and fun of facing and respecting ignorance before building knowledge.

Science shows humankind at its best. By building on evidence with curiosity, ingenuity, logic, and years of preparation, scientists expose the nature of matter, life, and mind with increasing sophistication and dazzling discoveries. Yet, as a human endeavour, science cannot escape our cognitive limitations or the social and political dimensions of our behaviour. Thus, experimental paradigms<sup>1</sup> develop not only for the quality of the methods and the robustness of the results that ground models and theories. They also reflect the technologies of the times, the influence of powerful and charismatic individuals, clannish allegiances driving competition and cooperation, the catchiness of simplistic and categorical ideas, the lure of the novel, and an occasional disregard for earlier foundational discoveries. Clear dichotomies and intuitive models that appeal to folk psychology often have an edge over better nuanced and integrative views.

Science progresses nonetheless, though not without occasionally derailing, reinventing, or getting stuck in local minima. Promoting progress takes seeing through the standard accepted narratives and models in one's field and looking anew with scholarship and a beginner's mindset.

### ***Defining Visual Working Memory***

Working memory is a core psychological construct essential for guiding flexible and adaptive human behaviour. The term working memory was probably first introduced by Miller, Gallanter and Pribram (1960) to refer to a quick-access form of memory for executing plans. In their proposal, uncompleted parts of plans in working memory comprise intentions. Atkinson and Shiffrin (1968) also used the term in their seminal theoretical treatment of memory and its control processes. In their proposal, the short-term memory store makes up the person's working memory, receiving selected inputs from a brief sensory register and the long-term memory store. Flexible and volitional control processes operate in the short-term store, helping to support storage, search, and retrieval. Both accounts echo the information-processing paradigm inspired by advances in communication and computer technologies during the inception of modern cognitive psychology (Neisser, 1967). Baddeley and Hitch (1974) later used the term to describe a specific, multi-component model of short-term

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<sup>1</sup> By paradigm, I mean "a conceptual or methodological model underlying the theories and practices of a science or discipline at a particular time; (hence) a generally accepted world view" (Oxford English Dictionary). This word is often used, incorrectly in my view, to refer to an instance of an experimental design or set-up.

maintenance and manipulation of visual and verbal material. This highly popular model and its various alterations (Baddeley, 2012; Baddeley, Hitch, & Allen 2021) have heavily shaped research, especially in the verbal domain.

Currently, there is some confusion and disagreement concerning how the term “working memory” should be used. Some scholars reserve it for the multi-component model (Baddeley & Hitch, 1974); others use it more generally but contend it implies necessarily more than just temporary storage, requiring the manipulation of contents and/or conscious access. This piece adopts a more basic, bare-bones definition: the ***temporary storage of visual contents to guide behaviour***. The simple definition preserves the essential role in guiding future behaviour from the original definition (Miller et al., 1960) and the separation between mnemonic content and control processes operating upon them (Atkinson & Shiffrin, 1968).

### ***Updating the standard paradigm***

Until recently, most research on visual working memory examined its representational aspects — the nature of its contents and the related psychological and neural mechanisms supporting storage. The standard view was that visual working memory holds contents in a robust format, and these are accessed through an inflexible process of exhaustive search (Sperling, 1960; Sternberg, 1966). Capacity is severely limited, and dichotomies arose to explain the limitations. Polar positions propose that resources are distributed evenly across the contents to be memorised (Bays & Husain 2009; Ma, Husain, & Bays, 2014) vs. that a fixed number of slots are available for contents to occupy (Zhang & Luck, 2008). Another related dichotomy concerns whether there is only one item in the focus of visual working memory (Oberauer, 2002) or the full set of items within the capacity limitations (Cowan, 2010). The primary mechanism proposed for maintaining contents in visual working memory is persistent “delay” activity in neuronal populations signalling attributes of memorised items in prefrontal and sensory areas (Fuster & Alexander 1971; Kubota & Niki, 1971; Kojima & Goldman-Rakic, 1982). The delay activity during working memory is considered a major top-down source for selective attention, guiding sensory processing of task-relevant items (Desimone & Duncan, 1995). The focusing of perception by working memory thus feeds a virtuous cycle, ultimately helping encode relevant memory content, which in turn guides sensory processing... (Nobre & Stokes, 2011).

Current research is breaking from the standard visual working-memory paradigm and upgrading our understanding in various ways.

Work in my group has promoted the realisation that visual working memory is much more flexible than previously envisaged, with selective attention continuing to operate within visual working memory to prioritise maintenance, selection, and access to mnemonic contents (Nobre & Stokes 2019; van Ede & Nobre, 2023). Initial studies revealed that retroactive attention cues (retrocues) during the maintenance period indicating the memory content that is relevant for the upcoming task confer significant performance benefits (Griffin & Nobre 2003; Landman, Spekreijse, & Lamme, 2003). Subsequent studies added observations of selective attention modulating working memory based on changing internal states in the absence of cueing stimuli (van Ede, Niklaus, & Nobre 2017), sensory capture by external stimuli sharing features with working-memory content (van Ede, Board, & Nobre 2020), and intended actions prioritising congruent items (Heuer, Ohl, & Rolfs, 2020). Selective attention can

modulate feature-based (Niklaus, Nobre, & van Ede, 2017; Ye, Hu, Ristaniemi, Gendron, & Liu, 2016) as well as object-based (Lin, Kong, & Fougny, 2021, Peters, Kaiser, Rahm, & Bledowski, 2015) information in visual working memory (Hajonides, van Ede, Stokes, & Nobre, 2020), with other possible substrates still to be tested. Interestingly, selective attention in visual working memory is also reversible, such that priorities can shift flexibly among contents without obligatory trade-offs in their quality or accessibility (Lewis Peacock, Drysdale, Oberauer, & Postle, 2012; Myers, Chekroud, Stokes, & Nobre 2018; Rerko & Oberauer, 2013; van Ede et al., 2017; Zokaei, Board, Manohar, & Nobre, 2019).

In addition to dispelling the notion of an inflexible store, the growing literature on selective attention in visual working memory also challenges other standard views and opens new questions. The ability to juggle selective attention among contents reversibly argues against strong proposals of fixed resource allocation within capacity limits (Myers, Stokes, & Nobre, 2017). The ability to modulate features as well as object-level representations questions the nature of unitary entities for slots. Reconsidering such concepts as ‘resources’ and ‘slots’ also highlights their underspecified nature, which compromises their utility as theoretical tools. The influence of intended actions on setting internal attention reminds us of the ecological purpose of visual working memory. Whereas emphasis has traditionally been placed on representational properties, the most important aspect of visual working memory is its function of preparing for future behaviour (Myers et al., 2017; van Ede, 2020; see also Fuster & Alexander, 1971). Accordingly, studies re-introducing action links to visual stimuli in working-memory tasks have underlined the major role of action readiness (Boettcher, Gresch, Nobre, & van Ede, 2021; Schneider, Barth, & Wascher, 2017; van Ede, Chekroud, Stokes, & Nobre 2019).

The paradigm is thereby shifting from visual working memory as an inflexible representational state that is severely limited in capacity to a highly flexible pragmatic functional state that adaptively prepares the individual for potential futures and guides action (van Ede & Nobre, 2023). However, this updating of views deepens old questions and opens new ones. Much effort lies ahead before a full understanding emerges of how signals derived from experience persist to constitute structured content and prepare possible actions; how control processes, including but not limited to selective attention interact with such traces; and how they relate to long-term traces, both pre-existing long-term memories that scaffold perception and those yet to form based on the recent sensory input. Addressing these puzzles will ultimately require looking under the hood at the changing patterns, dynamics, and transformations of activity in neurons and networks.

### ***Neural Traces***

The dissociation between working memory and long-term memory started as a theoretical one. James (1890), for example, contrasted primary memory (working memory), as never cut off in consciousness from the present moment, with secondary memory (long-term memory), as the knowledge of a former state already dropped from consciousness. The case of HM (Scoville & Milner 1957) provided a striking neuropsychological manifestation of the distinction. Whereas HM had profound episodic amnesia, he was nevertheless able to maintain information in mind over short periods if not interrupted, using elaborate strategies if required (Milner, Corkin, & Teuber, 1968).

Yet, the nature of the relation between working memory and long-term memory is still unresolved. Some of the initial neuropsychological evidence that grounded theories proposing a strong separation between their neural systems may have been overinterpreted (e.g., Warrington & Shallice, 1972). For example, these dissociations were often based on different types of content and tasks with varied performance demands. More recently, some scholars emphasize the association between neural systems supporting working memory and long-term memory for equivalent types of material (e.g., Graham, Barense, & Lee, 2010; Olson, Moore, Stark, & Chatterjee, 2006; Petkov et al., 2013; Zokaei et al., 2019). However, even if the memory systems are co-extensive, the neural processes supporting information maintenance over short and long spans are likely to differ, given the time required for cementing the structural changes involved in enduring plasticity.

Interestingly, early theoretical models are often misinterpreted as proposing a strong division between the memory systems, whereas they did “not require that the two stores necessarily be in different parts of the brain or involve different physiological structures” (Atkinson & Shiffrin, 1971). My own working hypothesis is that overlapping brain areas are involved in storing contents over short and long timespans and that multiple functions operate upon these traces to facilitate performance based on working memory or long-term memory (e.g., selecting, integrating, individuating, relating, or organising contents). However, I have not completely ruled out the possibility that some brain structure(s) may be specifically recruited for an adaptive temporary transient store for task-relevant content (see Duncan, 2001; Xu, 2017).

A clear theoretical proposal for distinct processes to support traces over the short and long term in the brain was introduced by Hebb (1949). He suggested that lingering reverberatory activity within cell assemblies was sufficient for short-term storage, whereas enduring strengthening of functional connections among neurons with correlated activity (through growth process or metabolic change) supported long-term storage.

### Persistent delay activity

The discovery of persistent delay-activity neurons in the prefrontal cortex (Fuster & Alexander 1971; Kubota & Niki 1971; Goldman-Rakic, 1984) and then in many other brain regions (see Christophel et al., 2017) provided a simple and intuitive solution for working-memory maintenance. The idea stuck and has become the standard textbook explanation for working-memory storage.

There are many appealing aspects to the explanation. Persistent neuronal firing yields a simple and effective attractor state for models of working-memory maintenance (Wang, 2001). Persistent activity can also be measured with non-invasive human imaging (Curtis & D’Esposito, 2003) and neurophysiological (Vogel & Machizawa, 2004) methods. The strength of delay activity correlates with working-memory performance variables (e.g., Adam, Robison, & Vogel, 2018; Rypma, Berger, & D’Esposito, 2002).

However, there are also bothersome niggles. I first remember focusing on these with Mark Stokes when we confronted how a stimulus presented during the working-memory delay impaired the CDA (contralateral-delay activity) marker of sustained activity in event-related potentials in an ongoing experiment. The observation cast our mind to how single-unit delay activity in sensory areas is interrupted by intervening stimuli (Miller, Erickson, & Desimone, 1996) and how sustained firing in the prefrontal cortex is interrupted in dual-task contexts (e.g., Watanabe & Funahashi, 2014). Examining the time courses of neuronal activity in various papers also revealed a more dynamic picture (e.g., Fuster & Alexander, 1971; Hussar & Pasternak, 2010). Most of the delayed-response working-memory tasks also conflated maintenance of the memoranda with anticipation of the probe, suggesting delay activity could reflect anticipatory attention instead (see Ikkai & Curtis, 2011; Lepsien & Nobre 2007; Lewis-Peacock & Postle, 2012; Nobre & Stokes, 2011 for similar arguments).

If persistent delay activity is not the full answer, what else could maintain relevant neural traces in readiness for guiding behaviour? One possibility is to return to Hebb's more dynamic notion of reverberation in a cell assembly. Dynamic patterns of activity reverberating across cell assemblies within and across brain areas could lead to more complex but still efficient attractor states (Wang, 2021). Changes in excitability in neuronal populations resulting from membrane kinetics and adaptation could also contribute (see Fitz et al., 2020). Reviewing the evidence and models at the time, Stokes (2015) suggested that activity-dependent short-term synaptic plasticity (STSP) operating upon a spatiotemporally dynamic neural system could provide an effective mechanism for preserving patterns of neuronal signals in an excitable functional state across working-memory delays. Similar models had been proposed for encoding temporal associations between events (Buonomano & Maass, 2009; Karmarkar & Buonomano, 2007).

### Latent functional states

The proposal that short-term synaptic weights silently preserve functional states in neuronal assemblies that serve working memory was simple and elegant, but it also generated controversy and dilemmas. Controversies considered the undeniable existence of delay activity and what specific role it served, as well as the plausibility and evidence for the necessary short-term plasticity. Questions also resurfaced about whether the mere existence of latent functional states counts as working memory and about the appropriate definitions for short-term vs. working memory.

The possibility of information coding in latent functional states additionally provoked the interesting question of how scientific knowledge is distorted by what we can and cannot easily measure. Stokes' group borrowed tricks from sonar technology to 'ping' latent states with a high-contrast neutral visual stimulus (Wolff et al., 2015). The random stimulation interacted with the pattern of stronger synaptic weights associated with the recently encoded item, reactivating the latent state, even if the item was not currently in the focus of attention. Other studies showed that the availability of latent states for pinging with visual or transcranial stimulation depended on the continued task relevance of the memorandum (Rose et al., 2016; Wolff, Jochim, Akyürek, & Stokes, 2017). In addition, cross-temporal decoding analyses revealed working-memory states to be dynamic (Wolff et al., 2015, 2017).

The attractive silent-working-memory proposal and the intriguing pinging results raise many interesting questions.

Experimental evidence for silent, latent representations derives mainly from pinging studies. However, it is important to remember that the stimulation used for pinging can equally well interact with active representations involving neuronal spiking. Therefore, decoding after pinging is not direct evidence for a representation being silent.

Silent working-memory representations depend on synaptic plasticity reinforcing a state within a dynamic system. But what are the implications of finding dynamic patterns of activity for arbitrating between silent vs. active neuronal states? The presentation of a visual stimulus necessarily triggers an initial dynamic cascade of sensory processing early in encoding. After that, spiking activity could continue to support working memory either by settling into a steady state or by continuing to unfold in a more dynamic way within circuits and networks. Therefore, finding dynamic patterns of activity is not enough for concluding that activity-silent mechanisms are sufficient for supporting working memory.

Furthermore, if plasticity is sufficient, what point(s) in time should be reinforced? Would a sequential string of states be reinforced and temporally linked? If not, are there salient or privileged time points? Understanding the role of plasticity in temporally evolving brain signals within extended experience in changing environments can be daunting. Methods for pinpointing the timing of cellular events that contribute to relevant states and computations should prove particularly informative (see Day-Cooney, Cone, & Maunsell, 2022).

One consequence of encoding information through short-term plasticity in a dynamical system is that the associations are vulnerable to disruption from intervening events, which themselves may stamp in new associations. How, therefore, do such models circumvent or overcome interference to deliver adequate working-memory performance in dual-task or multi-stimuli contexts? Would the strong neutral pinging stimulus itself not be expected to disrupt the functional state of associations? In other words, is there a measurable *observer effect* of pinging a silent state – i.e., a disturbance of the representation by the act of observation? Recovering activity following intervening stimulation was one of the motivations for developing an alternative model to persistent delay activity, but it is not clear how plasticity naturally overcomes the limitation.

The differential decodability between potentially relevant vs. irrelevant content in working memory is also puzzling. Pinging studies have shown that it is possible to reactivate the contents of currently unattended items in working memory (Rose et al., 2016; Wolff et al., 2017). However, pinging is only effective when the unattended item may still become relevant for subsequent task performance. Pinging leads to significant decoding of unattended items after the first of two retrocues, when the unattended item may still become relevant for a subsequent phase of the trial. However, pinging is ineffective after the final retrocue, which renders the unattended item fully irrelevant (Fulvio & Postle, 2020; Rose et al., 2016, Wolff et al., 2017). It is not obvious how changing item relevance based on task goals can selectively disrupt some but not other latent functional states. Is an active process suggested to flush out the functional connectivity state associated with the irrelevant items? How would an active

control process interact with the patterns of synaptic weights related to different contents within a dynamic system?

Answers to some of these questions may rest in the transformations of neural states, but what exactly is meant by this and how transformations occur are underspecified. For example, focusing on an item in working memory has been proposed to engage an output-gating process, placing the attended content in a state of action readiness (Chatham & Badre, 2015; Myers et al., 2017; Muhle-Karbe, Myers, & Stokes, 2021; Panichello & Buschman, 2021, van Ede & Nobre, 2021). Additionally, items with similar sensory content have been proposed to occupy different states depending on their associated task demands (Nobre & Stokes, 2019). Multivariate and state-space analyses facilitate testing such proposals, but the neurophysiological underpinnings remain elusive. Does information preservation in different states rely mainly on changing the involvement of brain areas or the pattern of synaptic changes within regions? (How) Do rhythmic events at different frequencies implicated in working memory play into the process (e.g., Miller, Lundqvist, & Bastos, 2018)? Addressing these questions will undoubtedly benefit from improving methods in animal models to measure rapid shifts in brain states and functional connectivity (e.g., Benisty et al. 2021; Perrenoud et al. 2022; Marshall et al., 2021).

Short-term changes in synaptic plasticity are likely to exist and contribute to the storage and accessibility of signals deriving from recent experience. However, they may not provide a full account of working-memory maintenance. Perhaps the most valuable contribution of the proposal is to rouse researchers out of a complacent state of not questioning the standard paradigm. This new alertness to other possibilities must now endure, so that we explore all options with an open mind and additionally consider how different processes (e.g., tonic sustained activity, plasticity, adaptation, dynamical reverberation) may come together and interact to support working-memory encoding, maintenance, prioritisation, and selection.

### ***Future directions***

#### Refining methods

A fuller understanding of working memory will benefit from the relentless breakthroughs in measurement and analysis methods in human neuroscience plus from the ability to relate the research on humans to that in model systems.

Advances in human neuroscience methods have transformed the research agenda (see Nobre & van Ede, 2020). The sensitivity and spatiotemporal acuity of brain imaging and neurophysiological methods have increased continuously. Measures have shifted from group averages to single trials. Analyses have progressed from univariate variables related to the amount and timing of information processing to multivariate variables that also tap into information content and quality. Neurophysiological studies can examine activity across the frequency spectrum, with data-driven methods to separate frequencies that preserve the morphology and phase of physiological signals (Quinn et al., 2021). Large-scale functional networks can be studied in terms of their activity strength, connectivity, and dynamics (Brookes et al., 2011; Quinn et al., 2019). Statistics have evolved to include Bayesian approaches. Methods borrowed from other disciplines help analyse and compare structures,



dynamics, and trajectories of functional networks. Computational models have increased their sophistication and physiological validity (e.g., Langdon & Engel, 2022).

Human neuroscience researchers should continue to exercise creativity and ingenuity to push the boundaries of what we can investigate. Developing the ping method is a great example (Wolff et al., 2015). Other possibilities should be pursued. For example, could invisible visual tagging (Zhigalov et al., 2019) include stochastic stimulation to yield information about the timing of non-invasive neural markers causally influencing performance (see Day-Cooney et al. 2022)?

Importantly, we should enhance and upgrade methods for capturing behavioural signals. While skill and cleverness have gone into measuring and analysing brain activity, the rich repertoire of behavioural activity has been underappreciated (Nobre & van Ede, 2020). For example, continuous recordings of pupil diameter and microsaccades have started yielding new insights into the dynamics of attention within working memory (Zokaei et al., 2019, van Ede, Board, & Nobre, 2020; van Ede, Chekroud, & Nobre, 2019). Continuous measures of motor excitability and spatiotemporal aspects of response trajectories are similarly promising (Dotan, Pinheiro-Chagas, Roumi, & Deheane, 2020; Echeverria-Altuna et al., 2022; Novembre et al., 2019). Rather than discard external behavioural markers correlated with psychological functions (Mostert et al., 2018, Quax et al., 2019), we should embrace their information value to unlock new questions.

However, characterising specific dynamical circuits in the human brain may remain out of reach for current or forthcoming non-invasive methods, either for defining computations within microcircuits or in networks across brain areas. The problem is challenging for tracking neuronal firing or extracellular field potentials, and the challenge is magnified manifold for revealing latent functional states in circuits or networks. Methods development in animal models increasingly allows the individuation and manipulation of specific circuits and networks. For example, mini-scope calcium imaging in rodents can reveal activation and changes in neuronal ensembles resulting from experimental manipulations (Mau et al., 2022). Optogenetic methods enable the targeting of neuronal subpopulations, and methods for genetically sequencing and classifying neurons are developing at a staggering pace (e.g., Krienen et al 2020; BICNN, 2021). Exciting innovative optogenetic protocols using random (white-noise) trains of stimulation are opening the doors for investigating the timings of critical neuronal contributions to performance in tasks (Day-Cooney et al. 2022).

### Integrating research camps

Researchers studying working memory in humans and animal models will need to work together for real progress. Task developments and whole-brain measurements in humans can expose principles of psychological and neural organisation to frame in-depth investigations at the network, circuit, and cellular levels. In turn, mechanistic discoveries can prompt the search for related markers in non-invasive measurements and test for their functional contributions. We are far from a coordinated collaboration in working-memory research. Alignment of work in humans and non-human primates is better, although the conceptual and task advances from human research have been slow to percolate into non-human-primate research, for example

on the flexible attention functions operating in working memory (but see Panichello & Buschman, 2021, van Ede, & Nobre, 2021). In rodents, the very term working memory carries different connotations and tasks employed typically diverge substantially from those in primates.

Virtual reality (VR) provides a promising opportunity for cross-linking research across species while also upgrading the ecological validity of experimental tasks. The methodology allows for capturing varied continuous behavioural and brain measures with strong experimental control in naturalistic immersive settings (Draschkow, 2022). VR is already widely used in rodent studies to great effect. Working-memory studies are just starting in humans and already changing our understanding of natural working memory (Draschkow, Kallmayer, & Nobre 2021). A propitious way forward would see the development of closely matched experimental tasks across species, although recognising that no task can be fully equated given their different evolutionary adaptations and the training methods required. Analytical tools that can describe functional states, relationships, and dynamics in data at various scales may help interrelate findings.

Work within species, including humans, also needs to proceed in a better-integrated way. Focusing on certain brain markers is a natural tendency, but this seeds different strands of research which can be difficult to reconcile. In human visual working memory, for example, different sets of studies concentrate on developmental trajectories; neuropsychological dissociations; and various types of neural measures: sustained activity, theta oscillations and cross-frequency coupling, alpha oscillations, decoding of contents, and dynamics in state-space. Are the various lines of findings compatible? Are there systematic differences in the types of tasks associated with different measurement types? Can we build cohesive models that harmonise the various strands to guide future research? It is time to remove the blinders and pull groups together to discuss points of tension and how to resolve them.

Rifts between research subfields are even deeper and can be similarly counterproductive. Fault lines follow folk psychological concepts – attention, memory, decision-making, action, language, planning, etc. In reality, these concepts are highly interrelated and one day we may reach a very different description of the natural kinds supporting cognition (Churchland, 1981). For now, researchers stand to gain from considering concepts and experimental approaches across the textbook psychological domains. Working memory is a special point in case. As a bridge between sensory experience and adaptive behaviour, working memory should be considered from an evolutionary and ecological perspective (Cisek, 2019) and not just for its phenomenological qualities. Working memory is an essential building block for orienting attention, decision making, long-term memory formation, action control, language, planning, etc. As such, emphasis is increasingly falling on the functional and pragmatic aspects of working memory (Nobre & Stokes, 2019; van Ede & Nobre, 2023).

When integrating findings and perspectives across species, strands from different experimental methods, and psychological domains, it is also important to preserve relevant distinctions. Early neuropsychological studies revealed many important dissociations between psychological functions. Some of the dissociations may have been misleading, such as dividing short-term and long-term memory based on performance in tasks with disparate materials and demands. Some of the dissociations, however, may still stand, such as HM's ability to maintain

online behaviour that relies on working memory without the ability to commit those contents to long-term memories. By their nature, neuropsychological milestones become associated with specific brain areas. In the case of memory, the hippocampus and medial temporal area became the territory dedicated to episodic long-term memory, characterised by contextual and relational associations. Increasingly, studies indicate the involvement of these areas in working memory and perception, depending on the type of content required for task performance (e.g., Graham et al., 2010). Thus, alternative models of hippocampal function are developing (e.g., Maguire & Mullaly, 2013; Barry & Maguire, 2019). These advances, however, do not negate the important distinction between perception, working memory, and long-term memory. The challenge ahead is to refine the understanding of how brain areas contribute to different extents and in different ways to larger-scale networks supporting psychological functions and to uncover the critical structural, activity, plasticity, connectivity, and computational parameters for performing natural tasks based on different types of content. Developing tasks that equate stimulus materials and task demands for assaying performance based on perception, working memory and long-term memory should prove particularly fruitful (e.g., Richter et al., 2016).

Another fundamental distinction to preserve, at least in human studies, is the obvious separation between the mental (subjective) and neural (implementational) levels of description. Most of us, as reductionists, believe in a mapping between the neural and the mental. However, centuries of musing, theorising, and experimenting rule out simple one-to-one isomorphic mappings. In the case of working memory, the subjective experience of apprehending the rich gamut of sensory experience contrasts sharply with the limited capacity to report memoranda objectively. Most working-memory studies focus primarily on objective behavioural measures, leaving subjective phenomenology untapped. We study humans as what philosophers describe as zombies (Kirk, 1974; Chalmers, 1996). Yet, conflating or flip-flopping between these levels is a frequent bad habit when generating hypotheses and interpreting findings. Holding something fixed in mind does not imply a sustained fixed neural mechanism. Conversely, many consciously inaccessible short-term traces of experience impact behaviour. Stitching across this ultimate divide requires a careful and critical appreciation of their conceptual distinctions.

## ***Conclusions***

Recent research findings and theoretical proposals have disrupted the relatively calm field of working memory, highlighting just how enigmatic this fundamental building block of adaptive cognition remains. We are not ‘there yet,’ so should maintain the level of inquisitive alertness toward the new standard views that are forming. Fuller understanding may require conciliating and integrating multiple perspectives that still seem antagonistic. Breaking some scientific bad habits could help set the field on a more productive path.

Agreeing on a core nomenclature would be transformative. For example, is it enough to consider the traces of recent experience for guiding behaviour as working memory or is active manipulation required? What functions would count? Could terminology usefully differentiate the neural and subjective states? Short of a shared taxonomy, defining terms would be a start. Keywords carry different connotations in the working-memory field and vary even more

between neighbouring fields. Papers rarely spell out definitions and premises, causing readers to project their own intellectual biases, which may distort the intended messages.

Stepping outside the comfort zone will be essential. Dialogue between divergent and even opposing camps should help distil what notions are mutually incompatible or reconcilable, develop falsifiable models, and inspire pivotal experimental hypotheses. Scientific niches have formed across many domains, such as species of study, methods, methodological markers, level of analysis, and experimental tasks. Small communities thus independently develop repertoires of findings, ideas, and terminology in parallel, with few attempts to build bridges. Workshops and symposia in larger conferences often convene like-minded scientists. Instead, intensive meetings and sessions exploring points of disconnection and tension within a safe environment might prove much more instructive and possibly even more enjoyable.

Finally, as scientists, we are trained to “pontificate”. Our presentations and writings carefully synthesize what we have learned and understood, preferably in a cohesive and engaging narrative. However, we also need to find a voice for our complementary and equally important ignorance. Ignorance, after all, is the true engine of science (Firestein, 2012). Openly admitting ignorance is not a natural or comfortable activity. Those lingering confusions, nagging doubts, methodological preoccupations, and unyielding questions are often saved for solitary contemplation. Sometimes though, you find a kindred spirit in a close colleague with whom you can share and learn from ignorance. Frank, broad, probing, meandering conversations then turn into creative fuel and intellectual advancement. I am lucky to count on some close mind-opening colleagues, including Mark Stokes. My hunch is that finding a way to open similar exchanges more widely would turbocharge our science and improve us as scientists.

Meanwhile, I remain open-minded and will be curious to look back in another decade to check how our understanding of working memory has progressed. Who knows? By then, we may have done away with working memory as a separate psychological domain altogether, and rather consider it as an intrinsic memory function embedded within other psychological domains that evolved to support adaptive behaviour. But, whether an independent domain or a ubiquitous property of neural systems, working memory will always be that remarkable bridge between the past and the future essential for so much intelligent and flexible human behaviour.

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## References

- Adam, K. C. S., Robison, M. K., & Vogel, E. K. (2018). Contralateral Delay Activity Tracks Fluctuations in Working Memory Performance. *Journal of Cognitive Neuroscience*, 30(9), 1229–1240. [https://doi.org/10.1162/jocn\\_a\\_01233](https://doi.org/10.1162/jocn_a_01233)
- 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
- Atkinson, R. C., & Shiffrin, R. M. (1971). The Control of Short-Term Memory. *Scientific American*, 225(2), 82–90. <https://doi.org/10.1038/scientificamerican0871-82>
- Baddeley, A. (2012). Working Memory: Theories, Models, and Controversies. *Annual Review of Psychology*, 63(1), 1–29. <https://doi.org/10.1146/annurev-psych-120710-100422>
- Baddeley, A. D., & Hitch, G. (1974). Working Memory. In *Psychology of Learning and Motivation* (Vol. 8, pp. 47–89). Elsevier. [https://doi.org/10.1016/S0079-7421\(08\)60452-1](https://doi.org/10.1016/S0079-7421(08)60452-1)
- Baddeley, A. D., Hitch, G. J., & Allen, R. J. (2019). From short-term store to multicomponent working memory: The role of the modal model. *Memory & Cognition*, 47(4), 575–588. <https://doi.org/10.3758/s13421-018-0878-5>
- Barry, D. N., & Maguire, E. A. (2019). Remote Memory and the Hippocampus: A Constructive Critique. *Trends in Cognitive Sciences*, 23(2), 128–142. <https://doi.org/10.1016/j.tics.2018.11.005>
- Bays, P. M., & Husain, M. (2008). Dynamic Shifts of Limited Working Memory Resources in Human Vision. *Science*, 321(5890), 851–854. <https://doi.org/10.1126/science.1158023>
- Benisty, H., Moberly, A. H., Lohani, S., Barson, D., Coifman, R. R., Mishne, G., Cardin, J. A., & Higley, M. J. (2021). Rapid fluctuations in functional connectivity of cortical networks encode spontaneous behavior. *bioRxiv*. <https://doi.org/10.1101/2021.08.15.456390>
- Boettcher, S. E. P., Gresch, D., Nobre, A. C., & van Ede, F. (2021). Output planning at the input stage in visual working memory. *Science Advances*, 7(13), eabe8212. <https://doi.org/10.1126/sciadv.abe8212>
- BICNN (BRAIN Initiative Cell Census Network). (2021). A multimodal cell census and atlas of the mammalian primary motor cortex. *Nature*, 598(7879), 86–102. <https://doi.org/10.1038/s41586-021-03950-0>
- Brookes, M. J., Woolrich, M., Luckhoo, H., Price, D., Hale, J. R., Stephenson, M. C., Barnes, G. R., Smith, S. M., & Morris, P. G. (2011). Investigating the electrophysiological basis of resting state networks using magnetoencephalography. *Proceedings of the National Academy of Sciences of the United States of America*, 108(40), 16783–16788. <https://doi.org/10.1073/pnas.1112685108>

Buonomano, D. V., & Maass, W. (2009). State-dependent computations: spatiotemporal processing in cortical networks. *Nature Reviews Neuroscience*, 10(2), 113-125.

Chalmers, D. (1996). *The Conscious Mind: in Search of a Fundamental Theory*. Oxford University Press.

Christophel, T. B., Klink, P. C., Spitzer, B., Roelfsema, P. R., & Haynes, J.-D. (2017). The Distributed Nature of Working Memory. *Trends in Cognitive Sciences*, 21(2), 111–124. <https://doi.org/10.1016/j.tics.2016.12.007>

Chatham, C. H., & Badre, D. (2015). Multiple gates on working memory. *Current Opinion in Behavioral Sciences*, 1, 23–31.

Churchland, P. M. & Journal of Philosophy Inc. (1981). Eliminative Materialism and Propositional Attitudes: *Journal of Philosophy*, 78(2), 67–90. <https://doi.org/10.5840/jphil198178268>

Cisek, P. (2019). Resynthesizing behavior through phylogenetic refinement. *Attention, Perception & Psychophysics*, 81(7), 2265–2287. <https://doi.org/10.3758/s13414-019-01760-1>

Cowan, N. (2010). The Magical Mystery Four: How Is Working Memory Capacity Limited, and Why? *Current Directions in Psychological Science*, 19(1), 51–57. <https://doi.org/10.1177/0963721409359277>

Curtis, C. E., & D’Esposito, M. (2003). Persistent activity in the prefrontal cortex during working memory. *Trends in Cognitive Sciences*, 7(9), 415–423. [https://doi.org/10.1016/S1364-6613\(03\)00197-9](https://doi.org/10.1016/S1364-6613(03)00197-9)

Day-Cooney, J., Cone, J. J., & Maunsell, J. H. R. (2022). Perceptual Weighting of V1 Spikes Revealed by Optogenetic White Noise Stimulation. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, 42(15), 3122–3132. <https://doi.org/10.1523/JNEUROSCI.1736-21.2022>

Desimone, R., & Duncan, J. (1995). Neural mechanisms of selective visual attention. *Annual Review of Neuroscience*, 18, 193–222. <https://doi.org/10.1146/annurev.ne.18.030195.001205>

Dotan, D., Pinheiro-Chagas, P., Al Roumi, F., & Dehaene, S. (2019). Track it to crack it: dissecting processing stages with finger tracking. *Trends in cognitive sciences*, 23(12), 1058-1070.

Draschkow, D. (2022). Remote virtual reality as a tool for increasing external validity. *Nature Reviews Psychology*. <https://doi.org/10.1038/s44159-022-00082-8>

Draschkow, D., Kallmayer, M., & Nobre, A. C. (2021). When Natural Behavior Engages Working Memory. *Current Biology*, 31(4), 869-874.e5. <https://doi.org/10.1016/j.cub.2020.11.013>

Duncan, J. (2001). An adaptive coding model of neural function in prefrontal cortex. *Nature Reviews. Neuroscience*, 2(11), 820–829. <https://doi.org/10.1038/35097575>

Echeverria-Altuna, I., Quinn, A. J., Zokaei, N., Woolrich, M. W., Nobre, A. C., & van Ede, F. (2022). Transient beta activity and cortico-muscular connectivity during sustained motor behaviour. *Progress in Neurobiology*, 214, 102281. <https://doi.org/10.1016/j.pneurobio.2022.102281>

Firestein, S. (2012). *Ignorance: How it drives science*. Oxford University Press.

Fitz, H., Uhlmann, M., van den Broek, D., Duarte, R., Hagoort, P., & Petersson, K. M. (2020). Neuronal spike-rate adaptation supports working memory in language processing. *Proceedings of the National Academy of Sciences*, 117(34), 20881–20889. <https://doi.org/10.1073/pnas.2000222117>

Fulvio, J. M., & Postle, B. R. (2020). Cognitive control, not time, determines the status of items in working memory. *Journal of Cognition*, 3(1).

Fuster, J. M. (1973). Unit activity in prefrontal cortex during delayed-response performance: Neuronal correlates of transient memory. *Journal of Neurophysiology*, 36(1), 61–78. <https://doi.org/10.1152/jn.1973.36.1.61>

Fuster, J. M., & Alexander, G. E. (1971). Neuron Activity Related to Short-Term Memory. *Science*, 173(3997), 652–654. <https://doi.org/10.1126/science.173.3997.652>

Goel, A., & Buonomano, D. V. (2014). Timing as an intrinsic property of neural networks: Evidence from in vivo and in vitro experiments. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 369(1637), 20120460. <https://doi.org/10.1098/rstb.2012.0460>

Goldman-Rakic, P. S. (1984). The frontal lobes: Uncharted provinces of the brain. *Trends in Neurosciences*, 7(11), 425–429. [https://doi.org/10.1016/S0166-2236\(84\)80147-2](https://doi.org/10.1016/S0166-2236(84)80147-2)

Graham, K. S., Barense, M. D., & Lee, A. C. H. (2010). Going beyond LTM in the MTL: A synthesis of neuropsychological and neuroimaging findings on the role of the medial temporal lobe in memory and perception. *Neuropsychologia*, 48(4), 831–853. <https://doi.org/10.1016/j.neuropsychologia.2010.01.001>

Griffin, I. C., & Nobre, A. C. (2003). Orienting Attention to Locations in Internal Representations. *Journal of Cognitive Neuroscience*, 15(8), 1176–1194. <https://doi.org/10.1162/089892903322598139>

Hajonides, J. E., van Ede, F., Stokes, M. G., & Nobre, A. C. (2020). Comparing the prioritization of items and feature-dimensions in visual working memory. *Journal of Vision*, 20(8), 25. <https://doi.org/10.1167/jov.20.8.25>

Hebb, D. O. (1949). *The organization of behavior; a neuropsychological theory*. Wiley.



Heuer, A., Ohl, S., & Rolfs, M. (2020). Memory for action: A functional view of selection in visual working memory. *Visual Cognition*, 28(5–8), 388–400. <https://doi.org/10.1080/13506285.2020.1764156>

Hussar, C., & Pasternak, T. (2010). Trial-to-trial variability of the prefrontal neurons reveals the nature of their engagement in a motion discrimination task. *Proceedings of the National Academy of Sciences*, 107(50), 21842–21847. <https://doi.org/10.1073/pnas.1009956107>

Ikkai, A., & Curtis, C. E. (2011). Common neural mechanisms supporting spatial working memory, attention and motor intention. *Neuropsychologia*, 49(6), 1428–1434. <https://doi.org/10.1016/j.neuropsychologia.2010.12.020>

James W. 1890. *The Principles of Psychology*. New York: Henry Holt and Company

Karmarkar, U. R., & Buonomano, D. V. (2007). Timing in the Absence of Clocks: Encoding Time in Neural Network States. *Neuron*, 53(3), 427–438. <https://doi.org/10.1016/j.neuron.2007.01.006>

Kirk, R. (1974). Sentience and Behaviour. *Mind*. **83** (329): 43–60.

Kojima, S., & Goldman-Rakic, P. S. (1982a). Delay-related activity of prefrontal neurons in rhesus monkeys performing delayed response. *Brain Research*, 248(1), 43–50. [https://doi.org/10.1016/0006-8993\(82\)91145-3](https://doi.org/10.1016/0006-8993(82)91145-3)

Kojima, S., & Goldman-Rakic, P. S. (1982b). Delay-related activity of prefrontal neurons in rhesus monkeys performing delayed response. *Brain Research*, 248(1), 43–50. [https://doi.org/10.1016/0006-8993\(82\)91145-3](https://doi.org/10.1016/0006-8993(82)91145-3)

Krienen, F. M., Goldman, M., Zhang, Q., C H Del Rosario, R., Florio, M., Machold, R., Saunders, A., Levandowski, K., Zaniewski, H., Schuman, B., Wu, C., Lutservitz, A., Mullally, C. D., Reed, N., Bien, E., Bortolin, L., Fernandez-Otero, M., Lin, J. D., Wysoker, A., ... McCarroll, S. A. (2020). Innovations present in the primate interneuron repertoire. *Nature*, 586(7828), 262–269. <https://doi.org/10.1038/s41586-020-2781-z>

Kubota, K., & Niki, H. (1971). Prefrontal cortical unit activity and delayed alternation performance in monkeys. *Journal of Neurophysiology*, 34(3), 337–347. <https://doi.org/10.1152/jn.1971.34.3.337>

Landman, R., Spekreijse, H., & Lamme, V. A. F. (2003). Large capacity storage of integrated objects before change blindness. *Vision Research*, 43(2), 149–164. [https://doi.org/10.1016/S0042-6989\(02\)00402-9](https://doi.org/10.1016/S0042-6989(02)00402-9)

Langdon, C., & Engel, T. A. (2022). Latent circuit inference from heterogeneous neural responses during cognitive tasks. *bioRxiv* <https://doi.org/10.1101/2022.01.23.477431>

- Lepsien, J., & Nobre, A. C. (2007). Attentional modulation of object representations in working memory. *Cerebral Cortex (New York, N.Y.: 1991)*, 17(9), 2072–2083. <https://doi.org/10.1093/cercor/bhl116>
- Lewis-Peacock, J. A., Drysdale, A. T., Oberauer, K., & Postle, B. R. (2012). Neural Evidence for a Distinction between Short-term Memory and the Focus of Attention. *Journal of Cognitive Neuroscience*, 24(1), 61–79. [https://doi.org/10.1162/jocn\\_a\\_00140](https://doi.org/10.1162/jocn_a_00140)
- Lewis-Peacock, J. A., & Postle, B. R. (2012). Decoding the internal focus of attention. *Neuropsychologia*, 50(4), 470-478.
- Lin, Y., Kong, G., & Fougine, D. (2021). Object-based selection in visual working memory. *Psychonomic Bulletin & Review*, 28(6), 1961–1971. <https://doi.org/10.3758/s13423-021-01971-4>
- Ma, W. J., Husain, M., & Bays, P. M. (2014). Changing concepts of working memory. *Nature Neuroscience*, 17(3), 347–356. <https://doi.org/10.1038/nn.3655>
- Maguire, E. A., & Mullally, S. L. (2013). The hippocampus: A manifesto for change. *Journal of Experimental Psychology: General*, 142(4), 1180–1189. <https://doi.org/10.1037/a0033650>
- Marshall, N. J., Glaser, J. I., Trautmann, E. M., Amematsro, E. A., Perkins, S. M., Shadlen, M. N., Abbott, L. F., Cunningham, J. P., & Churchland, M. M. (2021). Flexible neural control of motor units. *bioRxiv*. <https://doi.org/10.1101/2021.05.05.442653>
- Mau, W., Morales-Rodriguez, D., Dong, Z., Pennington, Z. T., Francisco, T., Baxter, M. G., Shuman, T., & Cai, D. J. (2022). Ensemble remodeling supports memory-updating. *bioRxiv*. <https://doi.org/10.1101/2022.06.02.494530>
- Miller, E. K., Erickson, C. A., & Desimone, R. (1996). Neural mechanisms of visual working memory in prefrontal cortex of the macaque. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, 16(16), 5154–5167.
- Miller, G.A., Galanter E., Pribram K.H. 1960. *Plans and the Structure of Behavior*. New York: Henry Holt & Co.
- Miller, E. K., Lundqvist, M., & Bastos, A. M. (2018). Working Memory 2.0. *Neuron*, 100(2), 463–475. <https://doi.org/10.1016/j.neuron.2018.09.023>
- Milner, B., Corkin, S., & Teuber, H.-L. (1968). Further analysis of the hippocampal amnesic syndrome: 14-year follow-up study of H.M. *Neuropsychologia*, 6(3), 215–234. [https://doi.org/10.1016/0028-3932\(68\)90021-3](https://doi.org/10.1016/0028-3932(68)90021-3)
- Mostert, P., Albers, A. M., Brinkman, L., Todorova, L., Kok, P., & de Lange, F. P. (2018). Eye Movement-Related Confounds in Neural Decoding of Visual Working Memory Representations. *ENeuro*, 5(4), <https://doi.org/10.1523/ENEURO.0401-17.2018>

Muhle-Karbe, P. S., Myers, N. E., & Stokes, M. G. (2021) A hierarchy of functional states in working memory. *Journal of Neuroscience*, 41(20):4461–4475

Myers, N. E., Chekroud, S. R., Stokes, M. G., & Nobre, A. C. (2018). Benefits of flexible prioritization in working memory can arise without costs. *Journal of Experimental Psychology: Human Perception and Performance*, 44(3), 398–411. <https://doi.org/10.1037/xhp0000449>

Myers, N. E., Stokes, M. G., & Nobre, A. C. (2017). Prioritizing Information during Working Memory: Beyond Sustained Internal Attention. *Trends in Cognitive Sciences*, 21(6), 449–461. <https://doi.org/10.1016/j.tics.2017.03.010>

Neisser, U. (1967). *Cognitive Psychology*. New York: Appleton-Century-Crofts.

Niklaus, M., Nobre, A. C., & van Ede, F. (2017). Feature-based attentional weighting and spreading in visual working memory. *Scientific Reports*, 7(1), 42384. <https://doi.org/10.1038/srep42384>

Nobre, A. C., & Stokes, M. G. (2011). Attention and short-term memory: Crossroads. *Neuropsychologia*, 49(6), 1391–1392. <https://doi.org/10.1016/j.neuropsychologia.2011.04.014>

Nobre, A. C., & Stokes, M. G. (2019). Premembering Experience: A Hierarchy of Time-Scales for Proactive Attention. *Neuron*, 104(1), 132–146. <https://doi.org/10.1016/j.neuron.2019.08.030>

Nobre, A. C., & van Ede, F. (2020). Under the Mind’s Hood: What We Have Learned by Watching the Brain at Work. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, 40(1), 89–100. <https://doi.org/10.1523/JNEUROSCI.0742-19.2019>

Novembre, G., Pawar, V. M., Kilintari, M., Bufacchi, R. J., Guo, Y., Rothwell, J. C., & Iannetti, G. D. (2019). The effect of salient stimuli on neural oscillations, isometric force, and their coupling. *NeuroImage*, 198, 221–230. <https://doi.org/10.1016/j.neuroimage.2019.05.032>

Oberauer, K. (2002). Access to information in working memory: Exploring the focus of attention. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 28(3), 411–421. <https://doi.org/10.1037/0278-7393.28.3.411>

Olson, I. R., Moore, K. S., Stark, M., & Chatterjee, A. (2006). Visual Working Memory Is Impaired when the Medial Temporal Lobe Is Damaged. *Journal of Cognitive Neuroscience*, 18(7), 1087–1097. <https://doi.org/10.1162/jocn.2006.18.7.1087>

Panichello, M. F., & Buschman, T. J. (2021). Shared mechanisms underlie the control of working memory and attention. *Nature*, 592(7855), 601–605. <https://doi.org/10.1038/s41586-021-03390-w>

Perrenoud, Q., Fonseca, A. H. de O., Airhart, A., Bonanno, J., Mao, R., & Cardin, J. A. (2022). Flexible perceptual encoding by discrete gamma events. *bioRxiv*. <https://doi.org/10.1101/2022.05.13.491832>

Pertzov, Y., Miller, T. D., Gorgoraptis, N., Caine, D., Schott, J. M., Butler, C., & Husain, M. (2013). Binding deficits in memory following medial temporal lobe damage in patients with voltage-gated potassium channel complex antibody-associated limbic encephalitis. *Brain*, 136(8), 2474–2485. <https://doi.org/10.1093/brain/awt129>

Peters, B., Kaiser, J., Rahm, B., & Bledowski, C. (2015). Activity in Human Visual and Parietal Cortex Reveals Object-Based Attention in Working Memory. *Journal of Neuroscience*, 35(8), 3360–3369. <https://doi.org/10.1523/JNEUROSCI.3795-14.2015>

Quax, S. C., Dijkstra, N., van Staveren, M. J., Bosch, S. E., & van Gerven, M. A. J. (2019). Eye movements explain decodability during perception and cued attention in MEG. *NeuroImage*, 195, 444–453. <https://doi.org/10.1016/j.neuroimage.2019.03.069>

Quinn, A. J., van Ede, F., Brookes, M. J., Heideman, S. G., Nowak, M., Seedat, Z. A., Vidaurre, D., Zich, C., Nobre, A. C., & Woolrich, M. W. (2019). Unpacking Transient Event Dynamics in Electrophysiological Power Spectra. *Brain Topography*, 32(6), 1020–1034. <https://doi.org/10.1007/s10548-019-00745-5>

Quinn, A., Lopes-dos-Santos, V., Dupret, D., Nobre, A., & Woolrich, M. (2021). EMD: Empirical Mode Decomposition and Hilbert-Huang Spectral Analyses in Python. *Journal of Open Source Software*, 6(59), 2977. <https://doi.org/10.21105/joss.02977>

Rerko L., & Oberauer K. (2013). Focused, unfocused, and defocused information in working memory. *J. Exp. Psychol. Learn. Mem. Cogn.* 39(4), 1075–96

Richter, F. R., Cooper, R. A., Bays, P. M., & Simons, J. S. (2016). Distinct neural mechanisms underlie the success, precision, and vividness of episodic memory. *ELife*, 5, e18260. <https://doi.org/10.7554/eLife.18260>

Rose, N. S., LaRocque, J. J., Riggall, A. C., Gosseries, O., Starrett, M. J., Meyering, E. E., & Postle, B. R. (2016). Reactivation of latent working memories with transcranial magnetic stimulation. *Science (New York, N.Y.)*, 354(6316), 1136–1139. <https://doi.org/10.1126/science.aah7011>

Rypma, B., Berger, J. S., & D’Esposito, M. (2002). The Influence of Working-Memory Demand and Subject Performance on Prefrontal Cortical Activity. *Journal of Cognitive Neuroscience*, 14(5), 721–731. <https://doi.org/10.1162/08989290260138627>

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

Scoville, W. B., & Milner, B. (1957). Loss of recent memory after bilateral hippocampal lesions. *Journal of Neurology, Neurosurgery, and Psychiatry*, 20(1), 11–21. <https://doi.org/10.1136/jnnp.20.1.11>

Sperling, G. (1960). The information available in brief visual presentations. *Psychological Monographs: General and Applied*, 74(11), 1–29. <https://doi.org/10.1037/h0093759>

- Sternberg, S. (1966). High-Speed Scanning in Human Memory. *Science*, 153(3736), 652–654. <https://doi.org/10.1126/science.153.3736.652>
- Stokes, M. G. (2015). ‘Activity-silent’ working memory in prefrontal cortex: A dynamic coding framework. *Trends in Cognitive Sciences*, 19(7), 394–405. <https://doi.org/10.1016/j.tics.2015.05.004>
- van Ede, F. (2020). Visual working memory and action: Functional links and bi-directional influences. *Visual Cognition*, 28(5–8), 401–413. <https://doi.org/10.1080/13506285.2020.1759744>
- van Ede, F., Board, A. G., & Nobre, A. C. (2020). Goal-directed and stimulus-driven selection of internal representations. *Proceedings of the National Academy of Sciences*, 117(39), 24590–24598. <https://doi.org/10.1073/pnas.2013432117>
- van Ede, F., Chekroud, S. R., & Nobre, A. C. (2019). Human gaze tracks attentional focusing in memorized visual space. *Nature Human Behaviour*, 3(5), 462–70.
- van Ede, F., Chekroud, S. R., Stokes, M. G., & Nobre, A. C. (2019). Concurrent visual and motor selection during visual working memory guided action. *Nature Neuroscience*, 22(3), 477–483. <https://doi.org/10.1038/s41593-018-0335-6>
- van Ede, F., Niklaus, M., & Nobre, A. C. (2017). Temporal Expectations Guide Dynamic Prioritization in Visual Working Memory through Attenuated  $\alpha$  Oscillations. *The Journal of Neuroscience*, 37(2), 437–445. <https://doi.org/10.1523/JNEUROSCI.2272-16.2016>
- van Ede, F., & Nobre, A. C. (2021). Toward a neurobiology of internal selective attention. *Trends in Neurosciences*, 44(7), 513–515. <https://doi.org/10.1016/j.tins.2021.04.010>
- van Ede, F., & Nobre, A. C. (2023). Turning Attention Inside Out: How Working Memory Serves Behavior. *Annual Review of Psychology*, 74, Forthcoming. DOI: <https://doi.org/10.1146/annurev-psych-021422-041757>
- Vogel, E. K., & Machizawa, M. G. (2004). Neural activity predicts individual differences in visual working memory capacity. *Nature*, 428(6984), 748–751. <https://doi.org/10.1038/nature02447>
- Wang, X.-J. (2001). Synaptic reverberation underlying mnemonic persistent activity. *Trends in Neurosciences*, 24(8), 455–463. [https://doi.org/10.1016/S0166-2236\(00\)01868-3](https://doi.org/10.1016/S0166-2236(00)01868-3)
- Wang, X.-J. (2021). 50 years of mnemonic persistent activity: Quo vadis? *Trends in Neurosciences*, 44(11), 888–902. <https://doi.org/10.1016/j.tins.2021.09.001>
- Warrington, E. K., & Shallice, T. (1972). Neuropsychological Evidence of Visual Storage in Short-term Memory Tasks. *Quarterly Journal of Experimental Psychology*, 24(1), 30–40. <https://doi.org/10.1080/14640747208400265>

Watanabe, K., & Funahashi, S. (2014). Neural mechanisms of dual-task interference and cognitive capacity limitation in the prefrontal cortex. *Nature Neuroscience*, 17(4), 601–611. <https://doi.org/10.1038/nn.3667>

Wolff, M. J., Ding, J., Myers, N. E., & Stokes, M. G. (2015). Revealing hidden states in visual working memory using electroencephalography. *Frontiers in Systems Neuroscience*, 9. <https://doi.org/10.3389/fnsys.2015.00123>

Wolff, M. J., Jochim, J., Akyürek, E. G., & Stokes, M. G. (2017). Dynamic hidden states underlying working-memory-guided behavior. *Nature Neuroscience*, 20(6), 864–871. <https://doi.org/10.1038/nn.4546>

Xu, Y. (2017). Reevaluating the Sensory Account of Visual Working Memory Storage. *Trends in Cognitive Sciences*, 21(10), 794–815. <https://doi.org/10.1016/j.tics.2017.06.013>

Ye, C., Hu, Z., Ristaniemi, T., Gendron, M., & Liu, Q. (2016). Retro-dimension-cue benefit in visual working memory. *Scientific Reports*, 6(1), 35573. <https://doi.org/10.1038/srep35573>

Zhang, W., & Luck, S. J. (2008). Discrete fixed-resolution representations in visual working memory. *Nature*, 453(7192), 233–235. <https://doi.org/10.1038/nature06860>

Zhigalov, A., Herring, J. D., Herpers, J., Bergmann, T. O., & Jensen, O. (2019). Probing cortical excitability using rapid frequency tagging. *NeuroImage*, 195, 59–66. <https://doi.org/10.1016/j.neuroimage.2019.03.056>

Zokaei, N., Board, A. G., Manohar, S. G., & Nobre, A. C. (2019). Modulation of the pupillary response by the content of visual working memory. *Proceedings of the National Academy of Sciences*, 116(45), 22802–22810. <https://doi.org/10.1073/pnas.1909959116>

Zokaei, N., Nour, M. M., Sillence, A., Drew, D., Adcock, J., Stacey, R., Voets, N., Sen, A., & Husain, M. (2019). Binding deficits in visual short-term memory in patients with temporal lobe lobectomy. *Hippocampus*, 29(2), 63–67. <https://doi.org/10.1002/hipo.22998>