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Review

Attention in flux

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SUMMARY

Selective attention comprises essential infrastructural functions supporting cognition—anticipating, prioritizing, selecting, routing, integrating, and preparing signals to guide adaptive behavior. Most studies have examined its consequences, systems, and mechanisms in a static way, but attention is at the confluence of multiple sources of flux. The world advances, we operate within it, our minds change, and all resulting signals progress through multiple pathways within the dynamic networks of our brains. Our aim in this review is to raise awareness of and interest in three important facets of how timing impacts our understanding of attention. These include the challenges posed to attention by the timing of neural processing and psychological functions, the opportunities conferred to attention by various temporal structures in the environment, and how tracking the time courses of neural and behavioral modulations with continuous measures yields surprising insights into the workings and principles of attention.

INTRODUCTION

Picking out useful content from the environment and from memory to guide adaptive behavior is a core prerequisite for all neural and cognitive systems. The functions responsible for this infrastructural task make up “selective attention”—responsible for anticipating, prioritizing, selecting, routing, integrating, and preparing signals from external and internal sources to inform the performance of current and upcoming tasks.[1,2]

The primordial temporal dimension frames all our interactions with the environment. To do its job effectively, attention must orchestrate the confluence of dynamics from various sources (Figure 1). As active agents, we move through environments. The environment, too, is always changing. Our brains process the resulting stimulation from our senses and actions over time in dynamic networks. Finally, as cognitive beings, the dispositions of our minds—our goals, expectations, memories, and motivations—also shift regularly and strongly influence how sense turns to experience.

The multiple sources of flux pose extraordinary challenges to attention. We turn to these challenges in the first part of this review. Concomitantly, recurring temporal structures ground predictions and bring opportunities for anticipating and prioritizing incoming relevant events. We turn to these opportunities in the second part of this review. Finally, in the third part, we reflect on how methods that enable tracking behavior and neural activity continuously have proven essential for revealing the temporal choreography of attention functions.

CHALLENGES BY TIME

Given the inescapable importance of timing for attention, it is puzzling how narrowly the topic has been addressed. One may wonder why.

Time is strange. Even assuming a well-behaved Newtonian conception of sequentially advancing time, various challenges surface immediately. Transduction in the various senses follows different time courses, resulting in asynchronous stimulation in the brain. Within the senses, constituent features of items are broken down further and processed and integrated through selective specializations in networks containing many forward, lateral, and re-entrant connections. Processing at each stage takes time, and information flows between stations at different rates depending on the length, width, and myelination of the fibers. The result is a perplexing temporal dimension to the binding problem. Many basic questions remain, such as how to determine when the computational transformations within cell assemblies yield informative signals and how to piece together the resulting asynchronous signals originating from a common event within and across modalities, while also separating relevant and competing events.

Thus, it is baffling enough to consider how the functional architecture of the brain manages to build a cohesive construct from even one single static multisensory source in the environment. The problem is greatly amplified by considering the dynamics in the external environment, our active agency through it, and the mutability of mental dispositions and contents. To find a way through these challenges, theoreticians and researchers have considered ways of reducing the mind-boggling complexity resulting from the multitude of simultaneous temporal fluxes.

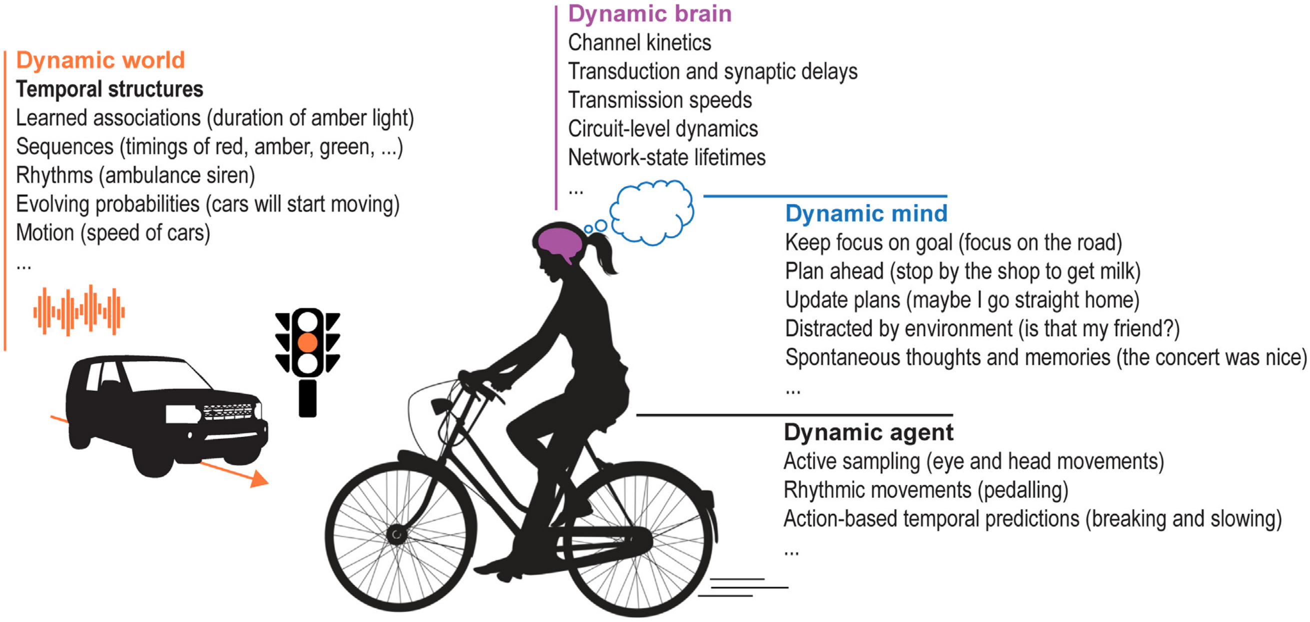

Figure 1. A confluence of dynamic sources
Selective attention functions must maneuver, orchestrate, and capitalize on temporal dynamics in the world, agent, brain, and mind.

Parcellating continuous time into brief sequential chunks could simplify the problem by providing sufficient periods for sampling and integrating signals.[3–6] Along these lines, some researchers propose that oscillatory properties of sensory systems play an important role in pacing perceptual analysis, such as the prevalent alpha oscillations in visual circuits.[7,8] Rhythmic properties of circuits have also been suggested as fundamental for coordinating the communication required to integrate and route features of relevant stimuli.[9] Another related area of research explores the behavioral manifestations of the potential rhythmic pickup of sensory information.[10–12] According to the active-sensing perspective, perception is an active exploration of the sensory world, paced by the natural rhythms of motor systems gating the sensory sampling (e.g., eye movements, whisking).[13] This notion of strong and mutually reinforcing loops between perception and action has rich roots.[14]

Alternatively, or in addition, different temporal windows over which neurons within and between areas integrate signals may help coordinate neural processing by nesting faster local computations within slower, higher-level ones.[15–17] At the network level, the sweep of re-entrant feedback activity has also been proposed to facilitate integration and to mark a separate stage of processing from the faster preceding bottom-up sweep.[18,19]

Yet, we are far from a consistent set of observations and mutually informed lines of investigation that can generate unifying theoretical proposals. For example, reconciling findings from the observed cyclic variation of performance at the alpha range[8] and rhythmic sampling at various estimates in the theta range[10–12] is not straightforward. How the timings of neuronal computation vs. communication relate and influence behavior is also still unclear. Even considering longer time constants of high-level associative networks and feedback sweeps, we remain far from explicating the multiple concurrent timescales governing active cognition up to several seconds and more.

Given its scope and sophisticated methodology, the attention research field should embrace the temporal dimension more firmly. By manipulating predictions and goal relevance of stimuli in static sensory displays, attention research has produced impressive insights into the myriad of cell-, circuit-, and network-level modulatory mechanisms that can operate from early sensory to later motor stages of information processing in the service of adaptive behavior.[20–22] Newer studies manipulating predictions and goals concerning memoranda in simple working-memory displays have extended the enquiry to modulatory mechanisms operating on internal representations.[23,24] Many sources of modulatory signals have also been identified, including automatic consequences of differences in sensory salience, top-down consequences of current task goals, and influence of memories of various types and time scales.[25]

The fundamental next step is to situate attention tasks in an ecologically valid temporal context—encompassing dynamics and temporal structures, both in the environment and in the agent. Making headway on how the brain focuses on useful stimulation to guide behavior in this dynamic way requires using powerful continuous measures of brain activity, as well as continuous readouts of behavior, to track the degree and timing of content processing at various levels of organization. Studies on the temporal orienting of attention, or temporal expectations,[26] take the first step in this effort, but there is further to travel.

ATTENTION IN TIME

Cast of timings

Before considering how attention research can embrace timing, brief comments on some pertinent facets of timing may help.

An important and useful distinction exists between explicit and implicit timing,[27] which is often overlooked or confused. The distinction between explicit and implicit timing is about the objective of the task and is independent of whether participants are aware of temporal parameters in the task. Explicit timing refers to situations in which timing is the primary objective of a task and needs to be explicitly reported. Explicit timing tasks include reproducing a stimulus duration—for example, using a manual response—or estimating a stimulus duration, for example, by judging its temporal midpoint or comparing its duration to a previous stimulus. In contrast, implicit timing tasks *utilize* temporal processing but do so for purposes other than timing itself. No awareness or explicit report of timing is required, but the processing of timing impacts performance, nevertheless. Temporal attention-orienting tasks are a typical example of implicit timing tasks in which predictive temporal intervals lead to improvements in performance in perceiving or responding to target stimuli.

Explicit and implicit timing tasks both necessitate clocking mechanisms, but these need not be the same.[27] The brain systems and mechanisms supporting explicit temporal judgments may overlap only partially—or not at all—with those that regulate the impact of temporal durations on sensory processing, attention, decision-making, or action. To understand the relationship between attention and timing, the brain systems and mechanisms that support *implicit* timing are of the essence.

How the brain keeps time is of growing research interest. In our opinion, the field is still wide open, and many possibilities exist. The first and remaining question concerns the functional anatomy of timing. Proposals vary from dedicated internal clocks[28] to fully distributed timing properties intrinsic to neural systems.[29] Evidence for the local coding of timing within various specialized circuits is strong, but these do not negate the existence of one or more general timing systems. Local timing computations could benefit from circuits that coordinate timing functions across sensory, associative, and action systems. These general circuits need not be entirely dedicated to timing but could instead perform important functions for organizing (scaffolding) neural activity in the service of behavior that involves high temporal resolution, such as sensorimotor integration and motor preparation (for discussion see Muller and Nobre[30]).

Complementing the localization question is the quest for timing mechanisms. A range of possible cellular and systems-level mechanisms may operate and differ in their contribution at different time scales. For example, coding for interval durations has been linked to: temporal tuning of receptive field properties of neurons in sensory cortices[31] and the hippocampus[32]; firing rates of neurons in sensory,[33] sensorimotor,[34] and motor[35] neurons; prediction-error signals within reward circuits[36]; delay-line circuits in the cerebellum[37]; oscillations in the basal ganglia[28]; neural sequences[38]; and short-term synaptic plasticity reinforcing states within dynamical neuronal circuits.[29]

Temporal limitations

The temporally extended nature of neural processing constrains information processing and results in various refractory phenomena limiting perception and performance over short intervals. Examples include deficits in identifying two simultaneously occurring targets in the same sensory modality,[39] identifying a target occurring shortly after another in a rapidly presented stream (referred to as the attentional blink),[40,41] noticing repeated items occurring in close temporal proximity (repetition blindness),[42] and performing different tasks in rapid succession (psychological refractory period).[43] The precise explanations for each of these well-documented phenomena are still being debated, but they share a common thread of proposing bottlenecks in specific stages of processing due to ongoing processing impeding other simultaneous analyses. Studies containing rapidly presented stimuli have also highlighted confusability between temporally adjacent targets and preceding or succeeding distractor items (distractor intrusion)[44–47] as well as the incorrect combination of features between items (illusory conjunctions in the temporal domain).[48] The swapping and meshing of temporally proximal stimuli suggest a temporal buffer for active processing as well as a limitation within which it is difficult to individuate and select target items. These phenomena are often considered properties of attention. Technically, however, they are better understood as inherent limitations of perceptual and cognitive systems and are not part of selective attention in the sense of functions that prioritize and select signals to guide adaptive behavior.

Varieties of temporal expectations

As a counterpoint, in addition to challenging the brain, the continuous dynamic influx of stimulation from the environment also provides abundant predictive information that is useful for guiding behavior. The burgeoning field of temporal orienting of attention, or temporal expectation, shows how various types of predictable temporal structures in the environment support the selective temporal anticipation, prioritization, processing, and action-preparation of task-relevant stimuli.[26,49] Temporal orienting builds on the rich and longstanding foreperiod literature that revealed systematic variations in response times according to the variability, length, and sequence of intervals (foreperiods) preceding an imperative stimulus (see Niemi and Näätän[50] and Los[51]).

Temporal-orienting tasks add the element of selective attention by specifically manipulating predictions or goals concerning the temporal intervals of task-relevant stimuli. Benefits in performance occur for target stimuli occurring at intervals predicted or instructed by informative temporal cues (e.g., Coull and Nobre,[52] Denison et al.,[53] and Griffin et al.[54]) or by learned temporal associations (e.g., Cravo et al.,[55] Los et al,[56] Zimmermann et al.,[57] and Olson and Chun[58]). Benefits from specific learned associations extend to incidentally learned sequences of temporal intervals, at least when spatial or action predictions are also available (e.g., O'Reilly et al.[59] and Heideman et al.[60]). In the extreme, items appearing rhythmically at fixed intervals have a strong advantage over those appearing at variable intervals (e.g., Riess Jones[61] and Jones[62]). Temporal expectations can also be derived from the probability of an event occurring at a given time point within a context, given that it has not occurred yet. Performance advantages ebb and flow in tandem with changes in the probability function for the target to appear (e.g., Ghose and Maunsell,[33] Janssen and Shadlen,[34] Cravo et al.,[63] and Grabenhorst et al.[64]). Other, more complex, types of predictive or recurring temporal patterns may also facilitate behavior. For example, benefits are observed when intervals separating events in a stream increase or decrease systematically in a predictable fashion.[65]

The various types of commonly studied predictive temporal structures—associative cues, sequences, probabilities, and rhythms—are not mutually exclusive (see Nobre and van Ede[26] and Nobre and Rohenkohl[49]). The extent to which they can interact, or act independently, deserves further investigation. Functional dissociations have been noted between benefits from rhythms and cues (e.g., Breska and Ivry,[66] Breska and Deouell,[67] and Rohenkohl et al.[68]). For example, participants with basal ganglia damage show a selective impairment in benefiting from rhythms, whereas participants with cerebellum damage show a selective impairment in benefiting from cued temporal associations[66] (Figure 2A). Strong interactions have been highlighted between the effects of predictive cues and probabilities, such that cueing benefits are stronger when the temporal probability is otherwise low or moderate.[69] Furthermore, the effects of continuous temporal probability have been shown to be separable and independent from the discrete probability of the imperative stimulus happening at all during a trial.[70] Mapping the full set of relationships among all temporal structures is still wanting, and their natures may also depend on other task variables and demands.

Interestingly, despite the continuous and dynamic nature of time, most temporal-expectation tasks use simple discrete trial designs. Much of our knowledge so far, therefore, comes from measuring performance in trials with single imperative stimuli that vary in their temporal predictability or relevance. Notable exceptions include continuous performance tasks manipulating the temporal sequence,[59,60] learned probability,[72,73] or rhythm of targets.[74] Interestingly, such results also demonstrate that learning of temporal associations can transcend simple one-to-one timing relations between successive stimuli. Controlling for all applicable experimental variables in extended dynamic tasks can be challenging. For example, several possible temporal structures can combine in tasks that manipulate the temporal probabilities of the targets in addition to their recurring temporal probabilities: the likelihood that a target will occur, sequential effects from temporal priming by the previous interval, the time since the last response, and the passage of time within a trial (e.g., Shalev and Nobre[74] and Salet et al.[75]). Facing the resulting complexity is a necessary step for discovering the workings of attention in its natural dynamic context, but it is not the only one.

The missing final step is to incorporate the natural dynamics of the agent. Participants in typical laboratory studies remain facing a display, usually with their eyes fixed, limiting their movements to delivering responses. Adding natural movement greatly complicates experimental control and is simply not possible with most non-invasive methods for measuring brain activity. This may soon change. Advances in virtual-reality technology are paving the way to rigorous investigations in immersive settings.[76] Tracking eye, head, hand, and body motion with good resolution is already possible and can bring new insights to attention (e.g., Draschkow et al.[77]). The increasing power and portability of human neurophysiology methods (portable electroencephalogram [EEG] and optically pumped magnetometers [OPMs]) should soon enable rigorous neuroscientific investigations while active participants interact with dynamic environments.[78–80] To date, however, as far as we know, studies that consider dynamic temporal structures in both the agent and the environment are still largely missing.

Behavioral consequences of temporal expectations in perception and action

How temporal expectations impact performance depends not only on the type of predictive structure but also on the stimulus properties and response demands of a given task.[26] Temporal expectations driven by a particular type of predictive structure can influence multiple stages of processing across sensory, sensorimotor, and motor areas. The resulting behavioral consequences are multifaceted and heavily depend on factors such as the strength of sensory stimuli, degree of sensory competition, conflict among sensorimotor mappings, and emphasis on accuracy or response time. For example, cue-based temporal expectations about relevant targets in tasks that emphasize accuracy under demanding sensory conditions often yield improvements in perceptual sensitivity and accuracy-related measures. In contrast, temporal expectations in tasks that emphasize speeded responses with little sensory challenge mainly impact response times (see e.g., van Ede et al.[71] and Zokaei et al.[81]). A representative example is depicted in Figure 2B, in which the same temporal-cueing procedure was applied in two tasks, characterized either by predominantly visual demands (tilt identification) or motor demands (speeded response).[71] Temporal expectations in the two tasks did not only drive (latch onto) distinct neural modulations but also had distinct consequences on performance: affecting predominantly accuracy in the visual task but reaction time in the motor task.

Temporal expectations have been observed to influence several psychological functions and the list continues to grow (Figure 3 for a non-exhaustive overview). Examples include: improving visual discriminability,[82] enhancing visual contrast sensitivity,[83,84] increasing processing speed,[85] modulating non-decision processes,[86] expediting the onset of decision-related processes,[87] facilitating multisensory coupling,[88] lowering motor-response thresholds,[89,90] offsetting distraction,[47,91] diminishing the attentional blink,[92,93] increasing fixational stability,[94,95] focusing encoding into working memory,[96,97] improving encoding into long-term memory,[98,99] and enabling phasic modulation of arousal.[74,100]

Distilling the principles regulating the conditions for the expression of given effects still lies ahead. There are multiple variables to consider. The nature of the temporal structure is likely to contribute. For example, the effects of rhythmic expectations appear to be stronger and more automatic than those of cues (e.g., Breska and Deouell[67] and Rohenkohl et al.[68]). The sensory quality of stimulation also matters. In addition to the amount of sensory difficulty or competition, the sensory modality can also play a role (see Nobre[101]). The different senses likely evolved for detecting different types of information in the environment. For example, the auditory system is intrinsically temporal and has a much higher temporal resolution than the visual system, which in turn has a better spatial resolution.[102,103] The source and strength of the temporal prediction are also worth considering. Learned predictive structures may have long or short lifetimes and differ in their precision and reliability. The purpose of the task, too, is likely to be crucial.[71] For example, tasks can

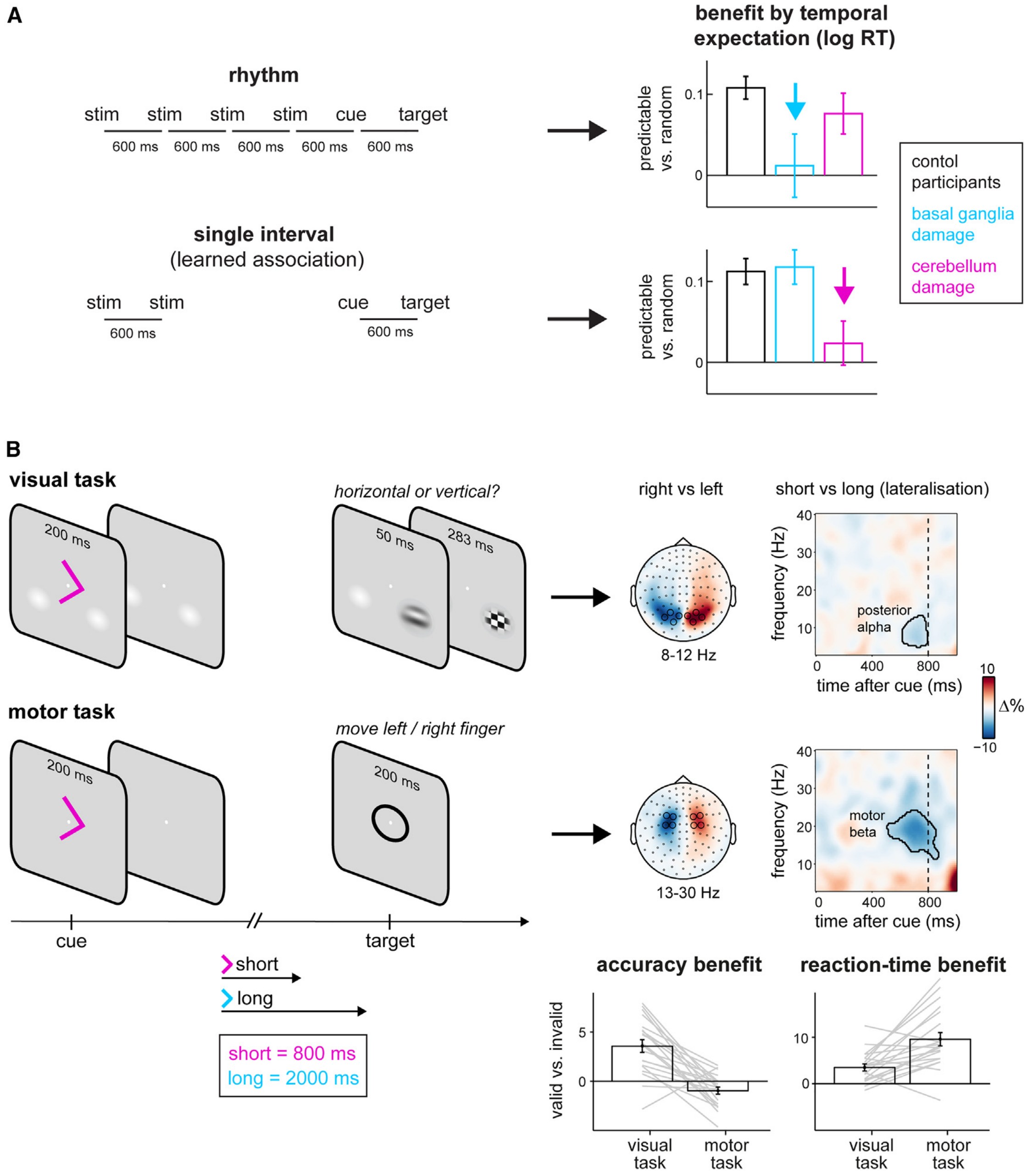

Figure 2. Mechanisms and consequences of temporal expectations depend on temporal structures and task demands

(A) Performance benefits of rhythms and single-interval cued associations rely on distinct brain circuits. Participants with basal ganglia damage are selectively impaired in benefiting from predictable rhythms, while participants with cerebellum damage are selectively impaired in benefiting from single-interval cued temporal associations. Error bars denote ±1 SEM. Data from Breska and Ivry[66].

(B) Performance benefits and neural modulations by cued temporal expectations depend on task demands. When cueing the timing of an anticipated visual task (tilt identification at the left or right of fixation), temporal expectations shape neural modulations in the visual cortex and predominantly affect accuracy. When the same cues inform about the timing of an anticipated motor task (speeded button press with the left or right index finger), temporal expectations shape neural modulations in motor cortex and predominantly affect reaction time. Error bars denote ±1 SEM. Data from van Ede et al[71].

emphasize perceptual sensitivity, learning, decision-making, accurate deliberation, or speed of responding. The precise nature of the task goal determines the critical, limiting stage(s) of neural processing informing performance. Hence, different task goals may tap into the different types of temporal modulatory mechanisms within different stages of processing.

Behavioral consequences of temporal expectations in working memory

The consequences of temporal expectation go beyond the immediate sensory-motor arc, extending to internal representations within working memory (see van Ede and Nobre[23]). In working-memory tasks, significant performance benefits result from

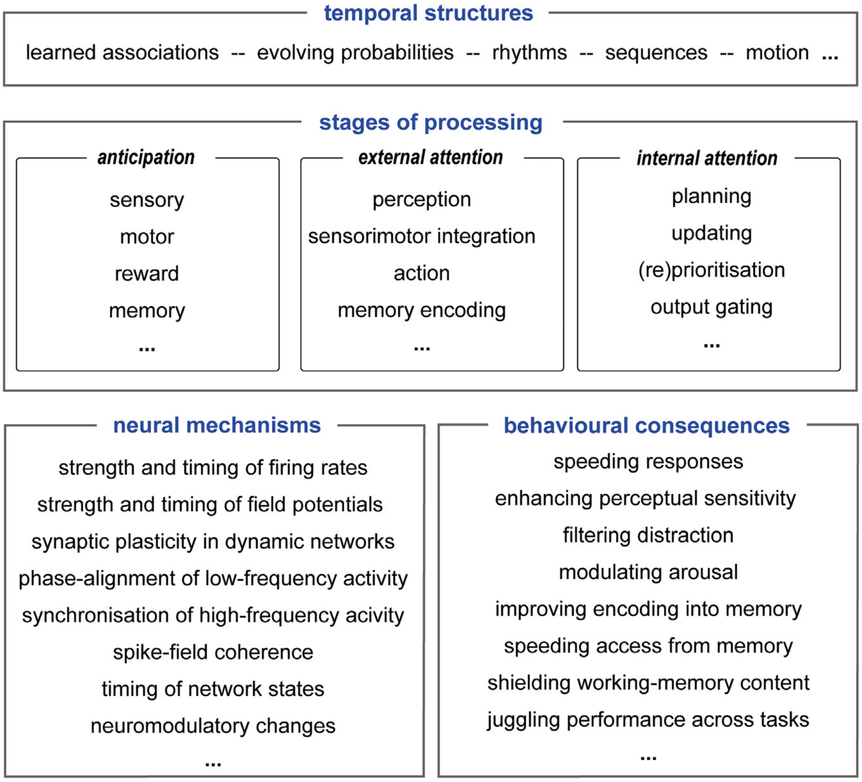

Figure 3. Dimensions of temporal attention
Temporal expectations can be driven by multiple temporal structures, act through multiple stages of processing, be supported by multiple neural mechanisms, and result in multiple behavioral consequences. Entries in this schematic are not intended to be mutually exclusive nor exhaustive.

informative cues presented during the delay period that retroactively predict which stimulus is likely to be goal-relevant (retrocues) (for reviews see van Ede and Nobre[23] and Souza and Oberauer[104]). When retrocues also indicate the order in which an orientation item from the memory array will be probed, benefits are temporally specific.[105] In the absence of order information, prioritizing one item leads to biases in the report of the orientation of other (uncued) items. When participants are probed on an uncued item first, they report a distorted orientation away from the retrocued item. However, if participants know that the cued item will be probed last, no biasing of orientations occurs during the first probing interval. The findings suggest the temporally specific prioritization of items. More direct demonstrations of temporally specific prioritization of contents in working memory come from studies manipulating the temporal probability of items being probed at certain intervals, in the absence of retrocues. In a change-detection task using two intervals for comparing the sample and probe arrays, both accuracy and response times improved at the short interval when this duration was more probable within the block,[106] akin to what is typically observed in perceptual tasks.[26]

Tasks manipulating the evolving temporal probability for probing different contents of a memory array have revealed striking flexibility in the dynamic prioritization of internal contents. For example, using two-item arrays, we varied the probability of each item being probed early vs. late. Items were colored oriented bars, and the probe color prompted the report of the item's orientation.[107] One color consistently had a high probability (80%) of being probed after a short interval and the other after a long interval. Errors and response times for reproducing the probed orientation diminished according to the predicted probe time. Furthermore, item prioritization shifted from favoring the likely-early item to favoring the likely-late item purely based on internal states tracking the passage of time. Thus, attention can be allocated reversibly within memory contents without notable trade-offs between the information available between items. Similar behavioral benefits were observed for another task employing a similar arrangement and logic. In this case, left and right items had complementary probabilities of being probed after a short or long interval.[108] Items were light and dark orientation gratings. Probes indicated the side of the item for reproducing its orientation. Response precision and response times improved at the predicted probe time, favoring first the likely-early and then the likely-late item. Interestingly, the internal focus of attention could also be tracked by the pupillary response. The size of the pupil adjusted according to the brightness of the attended stimulus within the internal memory array, even though stimulus brightness was irrelevant for task performance and no change in luminance occurred during the working-memory delay. The findings reinforce the flexible reversibility of attention in working memory according to internal states of temporal expectation. They also suggest embodied mechanisms for attention in working memory that may have evolved for anticipating interactions with events in the environment. In this laboratory task, no other change in luminance was involved during the delay or probe phase but, in everyday situations, we often retain items in working memory to interact with them shortly (see van Ede and Nobre[23] and Draschkow et al.[109]).

Working-memory tasks incorporating interfering events have further broadened the set of modulatory mechanisms by temporal expectations. Interference during a working-memory delay typically impairs performance, whether it is just a distracting stimulus to be ignored or a secondary task that needs to be performed in the interim. Temporal expectation about the onset of the interfering distracting or interrupting event significantly reduces the degree of this interference and suggests shielding of the memory contents.[91] After encoding two orientation stimuli, an interfering tilted stimulus occurred at fixed or variable temporal intervals, which could be ignored (distraction) or required a simple leftward/rightward response (interruption). At the end of the trial, a color prompted the reproduction of the corresponding orientation. Temporal expectation about the interfering stimulus counteracted its disruptive effects on reproducing the orientation from memory. The protective effects occurred for both types of interference and, furthermore, also improved response times in the interruption task itself. The effects, therefore, show that temporal expectations do more than dampen the processing of interfering sensory stimuli because the improved performance of the interruption task confirms the ability to engage flexibly with interfering events when necessary. Instead, the findings show that temporal expectations can additionally shield working-memory contents from sensory stimuli.[91] In a related follow-up study, the timing of the interruption task was held constant, while temporal expectation about the working-memory report was manipulated. Temporal expectation about the working-memory report diminished both errors and response times for the orientation reproduction. In addition, performance on the interruption task also improved, suggesting the ability of temporal expectation to organize the setting of priorities across multiple tasks.[110]

Neural mechanisms of temporal expectations

When hypothesizing about the mechanisms through which temporal structures influence neural processing, two strong temptations are best avoided. The first is to look for THE mechanism. Gone are the days of pinpointing the singular bottleneck of capacity limitation in the brain or arbitrating between simple dichotomies regarding the locus of attention.[1] Instead, as we have learned from the rich literature on visual spatial attention, changes in many cellular, ensemble, and communication parameters can contribute. The same applies to effects of selective temporal expectations (Figure 3 for a non-exhaustive overview).

The second trap is to confine the search to the known modulatory mechanisms for spatial, object-based, and feature-based attention. It is instinctive to draw from the repertoire of familiar mechanisms, such as increased firing rates related to anticipated stimuli, filtering of irrelevant stimuli competing for processing, different types of gain control (to prioritize coding of relevant vs. irrelevant stimulation), changes in the intrinsic and correlated noise of neurons, and synchronization of neuronal activity (see Maunsell,[20] Moore and Zirnsak,[21] and Buschman and Kastner[22]). Yet, incorporating timing into the equation should also prompt us to consider additional ways in which the brain may anticipate, prioritize, and gate events occurring at temporally predicted or relevant moments.

Human studies

Research in humans using neurophysiology has revealed that spatial vs. temporal expectation can yield similar patterns of behavioral improvement through divergent neural effects.[54,111] In addition to changing the strength of neural processes, as often observed during spatial attention, the timing of neural processes can also be affected. Temporal expectations can result in faster progression through successive stages of processing.[101] Changes in the duration of processing stages also apply to protecting relevant information from distraction. Temporal preparation for a target orientation improved performance when the target was shortly followed by another interfering orientation.[47] Multivariate decoding of target and distractor orientations revealed that temporal preparation led to prolonged as well as strengthened analysis of the target orientation, with little effect on distractor processing. As previously mentioned, temporal expectation can also shield working-memory representations from interference,[91] though the neural counterparts of the effect have not yet been revealed.

Predictive rhythmic structures with fixed durations can entrain natural endogenous slow brain rhythms in the delta and theta bands[112,113] (cf. Breska and Deouell[114] and Haegens and Zion Golumbic[115]). Excitability for sensory stimuli varies with the phase of the entrained neural rhythm.[84] Rhythmic stimulation in one modality can also entrain excitability in other modalities.[88,116] For example, a rhythmic-frequency-modulated sound resulted in related changes in the discrimination of a brief visual stimulus, depending on its timing relative to the phase of the auditory rhythm. Neural entrainment occurred in both auditory and visual cortices.[88]

In addition to bringing new mechanisms to the table, temporal expectations can potentiate the effects of other attention-related modulatory mechanisms. The first demonstration came in a task that manipulated the predictable location and/or interval for a visual target to reappear after moving across the display in discrete steps and disappearing behind an occluding band.[111] The amplitude of the early visual P1 potential was increased by spatial expectation—when the circle moved along a linear compared with a meandering trajectory. This increase in P1 was greatly amplified by temporal expectation—when the target moved in fixed rhythmic steps compared with variable-duration steps. The strong synergy between temporal and spatial expectations was not reflected in the behavioral performance measures, probably because perceptual demands were not a limiting factor for performance. A follow-up behavioral study designed to stress perceptual demands did instead reveal the hypothesized synergy between temporal and spatial expectations at the behavioral outcome level.[117]

The interaction between temporal and other expectations also plays out during attention-related anticipation. In the occlusion task, the alpha-band marker of visual excitability follows the cadence of the preceding predictable rhythm during the occlusion period in anticipation of the target re-appearance.[118] In temporal-cueing tasks, cues combining temporal and spatial expectation pace oscillatory markers of visual[71,119] (see Figure 2B, visual task) and somatosensory[120] excitability. When temporally predictive cues indicate the response hand required to report a simple central stimulus in a speeded reaction-time task, they instead pace the timing of beta-band activity related to motor preparation[71] (see Figure 2B, motor task). Together, the findings reinforce the notion that predictive temporal information can work through other attention mechanisms related to different types of information. They also highlight the plurality of mechanisms and systems through which temporal expectations can improve behavior (Figure 3).

Studies in animal models

Studies of temporal expectation in animal models are still relatively few, but they vindicate the plurality of possible sites and mechanisms of modulation. Investigations have probed brain areas and cellular mechanisms during visual, auditory, and reward processing in non-human primates and rodents. Most studies have used temporal probability manipulations,[33,34,121,122] but others have relied on specific learned temporal associations between stimuli,[36,123,124] temporally structured sequences,[125] and rhythms.[126,127] Neural changes following temporal expectations have been observed in the motor cortex[35]; sensorimotor regions, such as in posterior parietal areas[34]; and subcortical and cortical regions linked to reward.[36,125] Modulatory effects are also prevalent in sensory areas, such as the auditory,[121,128] somatosensory,[129] and visual[33,122–124,130,131] cortices. A study inactivating A1 in rodents suggests that sensory areas may be causally involved in generating or expressing temporal expectations.[121] In addition, the hippocampus was shown to be necessary to mediate temporal-expectation effects in the visual cortex during sequence learning,[130] and dopamine modulation in prefrontal and brainstem areas was causally implicated in temporal expectation during simple reaction-time tasks.[125] The emerging picture is thus one of the widely distributed temporal-expectation effects in which heteromodal and limbic regions may further play a prominent role in coordinating effects in specialized sensory and motor regions.[132]

Relevant cellular changes noted so far include changes in the strength and timing of neuronal firing and local field potentials,[33–36,121–125,128–131] improvements in signal-to-noise ratios,[129] changes in higher-frequency oscillatory signals,[35,123,124] and strengthening of the spike-field coherence.[123] Within rhythmic contexts, relevant stimulus streams can entrain intrinsic low-frequency oscillations.[126] Phase alignment within sensory areas can act crossmodally to impact neural excitability in other modalities[126] and can help to differentiate target vs. distracting stimuli in different streams across the tonotopic map in the auditory cortex, according to phase alignment.[127]

Practical and theoretical implications

It is worth noting that temporal structure exists in every attention experiment. Inevitably, choices are made about the durations of stimuli, the intervals separating them, the responding window, and so on. Over trials, these result in temporal probability functions about stimulus onsets and offsets and response deadlines. In turn, temporal predictions may influence the strength, latency, and duration of processing at many different stages, including sensory, motor, and mnemonic. Understanding how temporal orienting influences neural processing is therefore indispensable for clear interpretations concerning many other variables of interest that may be under investigation.

Acknowledging the temporal limitations in neural systems as well as the role of temporal structuring of attention in turn poses major challenges and constraints for theories concerning the routing, coordination, or integration of brain signals at the network level. Such theories need to account for endogenous rhythms possibly pacing the sampling of sensory stimuli, salient events possibly resetting neural activity, external rhythmic stimulation pushing around endogenous rhythms, temporal predictions changing the timing of processing stages, temporal expectations interacting with other biasing signals, and more. Then, theories must be placed in their actual dynamic setting, in which incoming stimulation from the changing environment is streaming in through non-synchronized modality channels while the agent engages in active behavior.

TIME IN ATTENTION

So far, we have reflected on how the temporal dimension both challenges and guides attention. In this final section, we consider how studying the temporal progression in neural and behavioral measures during attention control and modulation can illuminate the workings of these core scaffolding functions (cf. van Wassenho et al.[133]). By using continuous measures to examine the timings of unfolding neural activity and behavioral outputs, some surprising insights are beginning to emerge.

Time course and stages of attention

Since the earliest investigations, scientists have naturally wondered about the time course of attention. One prominent question has been: how long does it take to shift attention? Early behavioral studies systematically manipulated the time between predictive attention cues and sensory targets, discovering that hundreds of milliseconds elapse until full behavioral benefits from voluntary goal-directed shifts of attention (e.g., Posner et al.[134] and Müller and Rabbitt[135]). In contrast, automatic capture of attention follows a distinct temporal profile with a bi-phasic pattern of early facilitation followed by a slower inhibition-of-return.[136] Interestingly, the answer to the time course of attention may depend on which behavioral outcome measure you use for interrogation. For example, eye-movement measures can reveal periods in which attention is neither driven by goals nor by saliency,[137] and attentional benefits in accuracy and reaction times can develop at different rates and match different neural modulatory mechanisms.[138,139]

Another sticky question has been: how early does attention act? A long-lasting debate was based heavily on how sensory and semantic manipulations changed performance in dichotic listening tasks.[140] In such tasks, participants hear two competing auditory streams and attend to one to repeat the words as they come through. Interestingly, here too, the answer could change depending on the behavioral outcome measures, for example, varying between explicit reports and automatic responses concerning the contents in the target vs. distracting stream (see Nobre[1]).

Neurophysiology methods, with their high temporal resolution, can track the workings of selective attention continuously through modulation of neural activity.[141] They made it possible to map the stages of attention that result in behavioral advantages. The first event-related-potential (ERP) investigations in humans tested when attention acted, providing definitive evidence for early sensory modulations.[142,143] More subtly, ERP studies also indicated that multiple stages could be affected in functionally dissociable ways. For example, successive early P1 and N1 visual potentials were sensitive to different experimental manipulations, such as having to inhibit distractors of discriminate target features.[144] In animal models, studies have identified attention-related modulation across the visual hierarchy and charted their respective timings[145,146] (see also Michalareas[147]). Complementary studies examined the sites and timings of attentional control signals (e.g., Buschman and Miller[148] and Siegel[149]). Such investigations have helped delineate the "stages" and "networks" of attention. They have reinforced how many sites can undergo attention modulation and revealed that relative timing in areas controlling attention depends on the

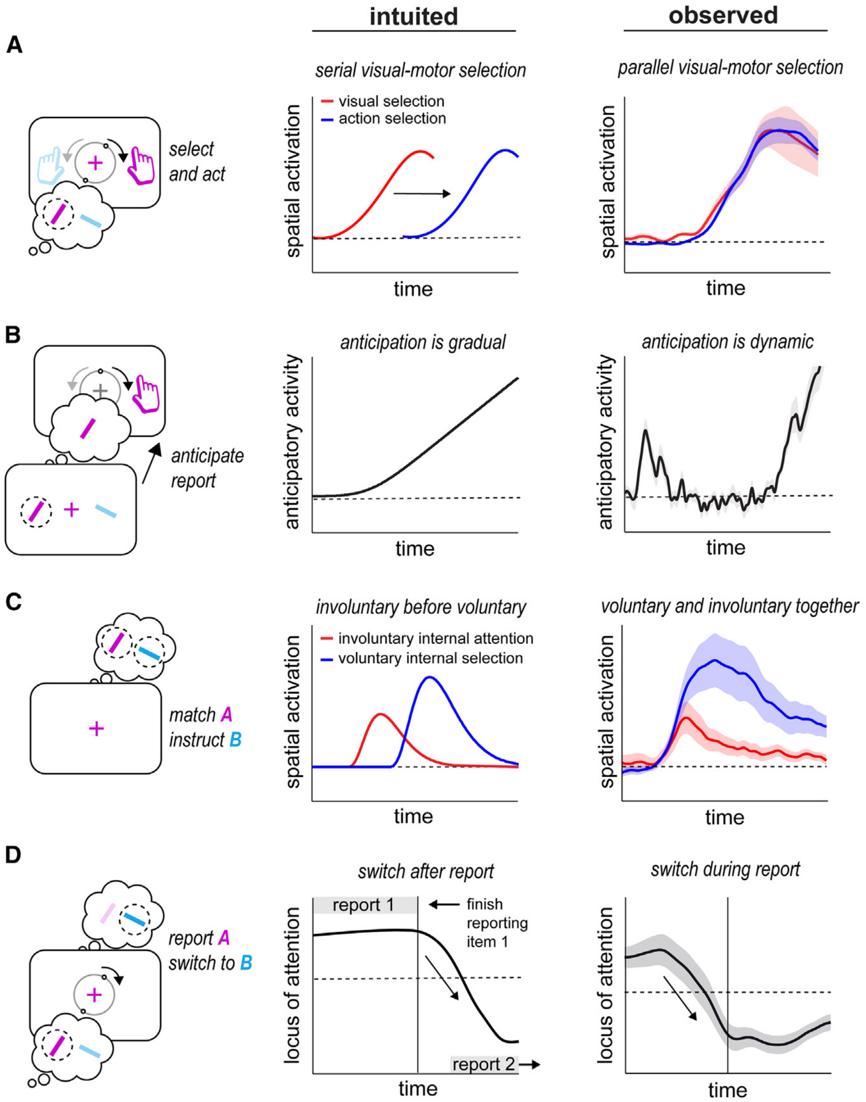

Figure 4. Temporal profiles in neural and behavioral measurements can reveal insights into the principles of attention, such as parallel processing in internal selective attention

Intuited vs. observed temporal profiles in the four studies described in the text. Data in (A) from van Ede et al.[150] Data in (B) from Boettcher et al.[151] Data in (C) from van Ede et al.[152] Data in (D) from van Ede et al.[153] Data in (A) and (B) consist of continuous EEG recordings, while data in (C) and (D) consist of continuous behavioral gaze-position measurements.

source driving attention orienting. For example, changes in posterior parietal activity lead when sensory salience drives attention to a visual display, but changes in frontal activity lead when working memory drives attention.[148] Invasive recordings studies can further shed light on the extent to which attention-related mechanisms are shared across different situations, for example, when directing attention externally to the sensory world or internally to the contents of working memory (e.g., Panichello and Buschman[24]).

Understanding the various stages of attentional modulations in the brain is not merely a matter of cataloging. It is critical for understanding how distinct behavioral outputs of attention come about, such as the processing stages that contribute to changes in detection thresholds, distractor filtering, or response speeds. Understanding the relationship between brain networks, modulatory mechanisms, and behavioral outcomes can help draw out the principles for attentional effects across different situations, depending on stimulus parameters and task demands (see Maunsell,[20] Moore and Zirnsak,[21] and Buschman and Kastner[22]).

Informative temporal profiles of attention modulations

Tracing the timing of attentional modulations can yield knowledge beyond just the staging of attention effects. As methods advance for revealing the contents of information processing and measuring behavioral outcomes with high temporal resolution, surprising findings lead to novel insights and fresh theorizing. In what follows, we highlight four recent examples from our own work on internal selective attention. This is intended to bring to life how the temporal profiles of the modulatory effects of attention can shed new light on our understanding of core attention functions—such as the parallel workings of attentional functions inside working memory (Figure 4).

Visual and motor selection unfold concurrently in working memory

The timing of sensory and motor neural markers in the study described in van Ede et al.[150] (Figure 4A) revealed that selecting motor action plans occurs concurrently with, and not after, selecting the visual attributes of memoranda in working memory. Participants maintained two peripheral visual oriented bars in working memory that were each linked to a different manual action (Figure 4A, left). We were interested in the cascade of the selection of relevant visual and motor memory attributes at the end of the memory delay, when one of the two memoranda became relevant for behavior.

The intuitive model is that participants would maintain the sensorial visual representations of both items and that, when probed, they would first select the visual information and only then derive the motor plan for the appropriate action (Figure 4A, middle). Instead, we observed concurrent selection of both the visual attribute and the appropriate action plan (Figure 4A, right). The lesson was that participants encode and maintain more than just the visual attributes during delay. They also prepare potential action plans for each memorandum, and these are ready to go when either memorandum becomes selected for behavior. The implication is a much richer conceptualization of the nature of visual working-memory representations, in which sensory items are poised for action, highlighting the future-facing and pragmatic, behavior-enabling role of working memory.[23]

Upon reflection, our sensory-then-motor serial intuition likely stemmed from projecting what happens during perception to working memory. When processing incoming stimulation, action plans necessarily depend upon, and therefore follow, the sensory attributes. In contrast, once visual information has been encoded in working memory, plans for potential actions can be assembled and held available for joint visual-motor selection, whenever memory contents become relevant for behavior.

Anticipation in working memory is bi-phasic

The timing of anticipatory neural modulations in the study described in Boettcher et al.[151] (Figure 4B) revealed how plans for future actions are formed surprisingly early and made clear how signals related to anticipation can follow a dynamic, bi-phasic profile. When anticipating delivering a response, the intuition is that motor preparation builds gradually toward the anticipated moment (Figure 4B, middle), as is also typical of other signatures of anticipation such as the contingent negative variation (CNV; e.g., Cravo et al.,[55] Jin et al.,[106] and Miniussi et al.[154]) or the ramping of neuronal firing rates.[34]

In the study, participants selected and encoded visual contents into working memory that would become relevant several seconds later (Figure 4B, left). As in the study described above, visual contents were linked to specific manual actions. We were interested in when action plans would be formed during the working-memory delay. The pattern of action anticipation that we observed did not build gradually. Rather, it was bi-phasic (Figure 4B, right). Early action planning overlapped with attentional selection of visual items during memory encoding (putatively linked to the *formation* of the action plan in working memory). This was followed by a later phase of getting ready for action execution. Interestingly, unlike the late phase, the early phase did not scale with temporal expectation but nevertheless correlated with the speed and quality of performance in the working-memory task.

These findings highlight again how the temporal profile of anticipatory neural signals themselves can prompt new insights into the processes that constitute anticipation. Using other neural readouts in neuronal recordings, others too have advocated moving beyond the gradual ramping of activity during neural preparation and considering, for example, evolving attractor dynamics.[155]

Voluntary and involuntary attention start concurrently in working memory

Importantly, temporal profiles that reveal relevant properties of attention are not limited to neural measurements. Time-resolved behavioral markers of attention can also be highly revealing, as the final two studies make clear.

The study described in van Ede et al.[152] (Figure 4C) tracked the timing of voluntary and involuntary shifts of internal selective attention and revealed that these kick off simultaneously and compete with one another. To track both types of attention orienting, this time we measured small shifts in gaze location associated with directional biases in microsaccades. We previously demonstrated that these gaze biases provide a sensitive and continuous behavioral read-out of selective attention within the spatial layout of in working memory[156] (see also Liu et al.[157]). Participants held two peripheral, colored, oriented bars in working memory until a cue indicated which item was required for behavior. We independently manipulated voluntary and involuntary sources of internal attention by manipulating whether the cues were informative or not (voluntary factor) and whether the cues matched the color of either the relevant or the irrelevant item in working memory (involuntary factor) (Figure 4C, left).

Based on classic spatial orienting studies in perception,[134],[135] we imagined that involuntary shifts would occur quickly and that voluntary shifts would lag behind (Figure 4C, middle). Instead, the onset of both voluntary and involuntary shifts of attention occurred early and overlapped (Figure 4C, right). Furthermore, their effects were additive, suggesting that they acted independently and in tandem.

From this, we learned that multiple attention operations can run concurrently. Previously, we observed how attention can influence different types of content at the same time in finding concurrent sensory and motor selection.[150] The current study additionally shows how multiple sources of attention control can modulate the same memory content in tandem. Together, the findings point to a highly parallel nature of attention operations. These results also present yet another example of how classic findings from the external-attention literature do not always translate straightforwardly to internally directed attention.

Attention looks ahead in working memory during sequential behavior

Our final example (Figure 4D), described in van Ede et al.,[153] revealed that the focus of attention in working memory moves onto the next relevant content before responding to the currently relevant content is complete. Building on our earlier demonstration of flexible and reversible focusing of attention in working memory,[107] this study again used gaze biases to track how participants juggle the contents of working memory when these are required in sequence. Participants viewed two oriented colored bars and later, when probed, had to reproduce them in sequence, with each report taking approximately 1 s (Figure 4D, left).

Given the serial nature of the task, we expected participants to switch attention to the next memory content only after they had finished reporting the preceding content (i.e., after the reproduction "report 1" in Figure 4D, middle). Surprisingly, what we observed instead was that attention switched to the next memory content before participants completed the initial report (Figure 4D, right). The gaze biases showed that, by the time participants finished their first report (making a button click with the mouse), their attention had already switched all the way to the next memory content.

The findings make clear how internal attention is fundamentally "forward looking," anticipating the next event while still guiding behavior by the previous. This is reminiscent of starting to look for the next instruction while still working on the previous step when assembling a piece of furniture and is consistent with a wider literature on looking-ahead fixations.[158] More important than the take-home that attention switches *earlier* than imagined is the lesson that attention functions can overlap in time with other concomitant processing.

The intuition that processing stages unfold serially is hard to shake, i.e., first we do one thing, then the next. Yet, this seems not to be the case in the brain. Just like the extensive amount of concurrent processing during processing of single events, processing of successive events may also overlap significantly. This psychologically non-intuitive degree of parallelism is likely to have ecological advantage.[159,160] Nevertheless, it also raises difficult questions about how the brain achieves the necessary temporal coordination of all the relevant signals within and between events to create cohesive information to guide behavior. This requires not only resolving the temporal dimension of the binding problem but also incorporating the issues brought by overlapping analysis of sequential events within dynamic contexts. In addition to parallel processing, neural activity within and between separate processing stages may also draw upon serial mechanisms of information sampling to facilitate coordination and integration, such as rhythmic sampling of externally[10–12] or internally[161–163] derived contents.

The examples chosen for illustration used innovative experimental designs and incorporated continuous brain and behavioral measures to track the neural processing of multiple items and follow the focus of attention. Together, they also revealed how the temporal coordination of internal attention functions differs from that in external attention. Selection of internal sensory and motor attributes runs in parallel[150] and different sources of internal attention take off together.[152] These studies also incrementally push our experimentation toward more ecological situations, bringing action back into visual working memory,[150,151] considering multiple sources of attention together,[152] and imposing sequential task demands.[153] Studies can go even further, using extended and dynamic stimulus displays with various forms of embedded temporal structures.[72,73] As the field embraces more dynamic and naturalistic situations, using time-resolved neural and behavioral measurements will become increasingly important and will continue to generate unexpected findings that defy intuition and prompt new ways of thinking.

Concluding remarks

The work discussed in our (non-exhaustive) review shows how the attention field is edging toward the temporal dimension by embracing various sources of relevant dynamics.

So far, studies manipulating temporal expectations have mainly addressed *dynamics in the environment*. Most tasks so far use simple and static displays, and future studies can go further by using natural environments and extended task contexts.

The *dynamics in mental dispositions* are starting to be explored in internal-attention studies using retrocues, sequential probes, and extended displays. It has been possible, therefore, to show flexible and reversible shifts in the prioritization of different items within working memory based on internal states[107] and to reveal the proactive nature of these shifts.[153] Future studies can enrich this line of enquiry by developing experimental frameworks to investigate temporal dynamics when shifting between task sets and by including multi-tasking situations.

Studies using continuous neurophysiological and behavioral methods are beginning to chart the dynamics in neural processing and their effects on performance. Clever task designs have started to separate the time courses of various modulatory functions and their impact on different stimulus content. However, important coding and modulatory effects may also exist under the surface of palpable brain activity, such as changes in synaptic weights that link neural ensembles and regulate excitability.[164] Developing new tools to examine more aspects of neural and behavioral states will surely deepen the enquiry.

Although the field is moving in a good direction, one source of dynamics is often sidestepped—the active agent. In the typical laboratory task, participants remain still and have limited means to interact with the (experimental) world around them. In life, we attend to things while moving and engaging in behavior (Figure 1). We walk and run and dance and jump and ride; we turn and look and point and reach and grab. Controlled laboratory experiments have exposed the tight link between attention and action systems, such as eye and reach movements,[165,166] but few have actually investigated attention in the context of full body movements and natural forms of behavior (see Tatler and Land[167]).

Setting the agent free is an important next step. Virtual reality provides a propitious means to combine agency with experimental control[76] and increasingly allows for simultaneous tracking of neural processing[80] and various behavioral outcomes, such as subtle patterns of gaze behavior that reveal shifts of attention (e.g., Draschkow et al.[77]). Placing moving agents in extended dynamic environments with embedded temporal structures, while measuring brain activity and behavior as mental dispositions shift, will get us much closer to tapping into the fundamental workings of selective attention.

As ever, multiple methods will need to be combined for a full understanding, as each reveals only clues about the full answer. We also stand to gain from a much better partnership between human and animal experimentation. Studies on humans can introduce conceptual innovation regarding the psychological factors shaping attention and point toward some of the neural systems involved, but understanding functional mechanisms at the circuit and cellular levels requires granularity that is only available in animal models.[141]

The moment is ripe to step into the fluxes of attention. The time dimension, in its glorious strangeness, will surely offer new insights about the essential scaffolding functions of adaptive cognition and behavior.

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AUTHOR CONTRIBUTIONS

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DECLARATION OF INTERESTS

A.C.N. is on the advisory board of *Neuron*.

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