

Anticipated moments: temporal structure in attention

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Abstract | We have come to recognize the brain as a predictive organ, anticipating attributes of the incoming sensory stimulation to guide perception and action in the service of adaptive behaviour. In the quest to understand the neural bases of the modulatory prospective signals that prioritize and select relevant events during perception, one fundamental dimension has until recently been largely overlooked: time. In this Review, we introduce the burgeoning field of temporal attention and illustrate how the brain makes use of various forms of temporal regularities in the environment to guide adaptive behaviour and influence neural processing.

Temporal structures

Any repeating sets of intervals among two or more items.

Selective attention

The set of functions that prioritize and select relevant information to guide adaptive behaviour.

Receptive field

(RF). The aspect of the sensory environment to which a neuron is responsive — for example, a spatial location or a stimulus feature such as auditory pitch or visual orientation.

Temporal expectation

The state of the cognitive or neural system associated with the predicted timing of an event. The term has no implications concerning volition, awareness or conscious deliberation.

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doi:10.1038/nrn.2017.141
Published online 7 Dec 2017

Our environment unfolds dynamically, affording us boundless stimulation and possibilities. Although the incoming stream of information is ever new, not all of it is unpredictable. Embedded relationships among the attributes of events over different timescales carry predictions that guide proactive sensory and motor preparation in the brain. The same holds for the temporal structuring of events. Recurring temporal structures enable proactive and temporally selective preparation for anticipated relevant events.

The field of selective attention has uncovered many mechanisms by which the brain anticipates and selects relevant events to guide adaptive perception and action — for example, the filtering of competing sensory inputs, the upregulation of firing rates and inter-areal synchronization. At the core of most of these mechanisms is the modulation of neuronal activity and of neuronal communication on the basis of receptive field (RF) properties, leading to the prioritization of items that occur at the relevant location or contain a relevant feature^{1–3}. Thus, we have come to a relatively advanced understanding of still frames, or snapshots, of attention. However, how the brain can use predictable temporal structure to anticipate and select relevant events immersed in the continuous flow of stimulation remains less clear. As attention is, by definition, a dynamic process, we need to add ‘time’ to understand attention fully. The study of temporal expectation in attention is finally gaining momentum and joining the mainstream.

The aims of this Review are to introduce the reader to temporal attention and to highlight the emerging principles and interesting findings in this burgeoning field. A first major advance has been to recognize that many types of predictable temporal structure support attention. We illustrate their strong effects on performance and consider how they are utilized by the brain.

Temporal expectations can act through various mechanisms at different stages of neural processing to enhance performance. One interesting observation is that, rather than acting in isolation, temporal expectations often accompany expectations about other identifying attributes of anticipated events, markedly boosting the effects of the latter. We stress that the effects of temporal expectation are not confined to typical attention laboratory experiments but also influence our perception of complex streams of information as well as many other fundamental aspects of cognition, such as learning and memory.

Types of temporal structures

The ability to prioritize and select relevant events based on their timing has typically been investigated by manipulating the likelihood of a relevant event occurring at a given moment in time, thus focusing on the role of temporal expectations in attention (see ‘Task relevance versus expectations’ in BOX 1). In attention research, the study of temporal expectations complements the investigation of how perceptual and cognitive functions are limited over time (see ‘Expectations versus limitations’ in BOX 1).

Here, we consider temporal expectations in the context of four types of informative temporal structures commonly found in the environment and manipulated in experimental tasks: associations, hazard rates, rhythms and sequences (FIG. 1). These categories are not intended to be exhaustive, but they provide a good first set from which to showcase the robust effects and distil some of the principles of temporal attention.

The mappings between the types of temporal structures and the brain mechanisms that sense and utilize them are only beginning to be investigated. The extent to which common or different neural systems and

Box 1 | Temporal attention: relevance, expectations and limitations

Definitions and taxonomies in attention research can be inconsistent. In this box, we explain the central terms and concepts used in this Review and highlight how they differ from alternative perspectives.

Task relevance versus expectations

In this Review, we define selective attention as the set of functions that prioritize and select relevant, or potentially relevant, information to guide adaptive behaviour. In this framework, many types of modulatory signals, often referred to as 'biases', contribute to attention. Task goals and expectation based on prior likelihood of events are two prominent types of biases. Other modulatory biases include perceptual salience, motivational drive, emotional valence and associations in long-term memory⁷⁶. Our view differs from a recently proposed strict dichotomy in which attention refers only to task relevance and expectation is a separate construct that corresponds to prior likelihood¹³⁶. In our framework, attention is a broader construct, based on more than just relevance as defined by task goals. Under attention, both goals and probability of items provide modulatory biases that guide perception. These types of biases are conceptually dissociable, but they often work together to prioritize probable task-relevant events for neural processing and/or to filter irrelevant events⁷⁶.

Different consequences of modulation by expectations have been emphasized in different literatures. In the field of attention, researchers have tended to concentrate on how expectations about target events enhance the processing of anticipated relevant items relative to irrelevant distractors. This is also our focus in this Review. By contrast, in the field of predictive coding and in learning theory, the emphasis has often been on the attenuation of processing of anticipated events based on their prior likelihood^{137,138}. Harmonizing the views of these fields is beyond the scope of this Review; however, we propose that the effects of expectation depend critically on the purpose of an individual's task. For example, in tasks that require fine perceptual discriminations, enhancement of perceptual analysis based on expectations will be highly adaptive. By contrast, in tasks that require learning new environments, unexpected outcomes may have higher value, whereas expected events may be redundant.

Expectations versus limitations

In the literature, two separate phenomena have been referred to as 'temporal attention'. In this Review, we focus on how predictive temporal structure is used to prioritize and select relevant items to guide adaptive behaviour. This definition follows the strict definition of attention¹³⁹ and is analogous to the use of expressions such as spatial attention, object-based attention and feature-based attention.

Others have used 'temporal attention' to refer to 'limitations' of information processing over time. Processing items from the sensory stream takes time, and the more in-depth the processing of a stimulus, the longer it takes. Furthermore, some of the operations required to process, respond to or remember a given target may interfere with concurrent analyses of other stimuli. Accordingly, it has been noted that identifying a target among stimuli in rapid serial visual presentation is compromised if the target occurs within a few hundred milliseconds of a preceding target¹⁴⁰ — a widely studied effect known as the 'attentional blink' (REF. 141). Similarly, individuating separate instances of the same item is also compromised if they occur in close temporal proximity — an effect known as 'repetition blindness' (REF. 142). Behavioural decrements also occur when individuals are required to perform two tasks contemporaneously (for example, when responding to two visual stimuli that are associated with different response rules and presented in close temporal proximity), with a period of lingering interference between demands of one task on those of another, known as the 'psychological refractory period' (REF. 143). Although these phenomena are often referred to as 'temporal attention', they do not reflect attention-related processes in the strict sense of prioritization and selection. Rather, they reveal the temporal constraints built into our perceptual and cognitive systems. Interestingly, having informative temporal predictions can help to overcome such temporal limitations^{127,128}.

Predictive coding

A theoretical framework in which perceptual inferences are based on the difference between predicted and observed sensory inputs.

Learning theory

A theoretical framework for how learning is shaped by associations between stimuli or between actions and rewards. In reinforcement learning, for example, a key principle is that learning is driven by prediction errors (the differences in value between predicted and observed rewards).

Posner's spatial orienting task

An influential spatial attention task developed by Posner in which symbolic cues inform the most probable location of a future target stimulus.

mechanisms operate in these temporal contexts is yet to be understood. Advances in revealing the neural systems and mechanisms are considered in a following section.

In the laboratory tasks described below, perception is typically probed by asking participants to detect, identify or discriminate sensory inputs (such as auditory pitch, visual orientation and so on), and performance is measured in terms of the speed (reaction time) and accuracy of these judgements.

Associations. Temporal associations refer to predictive temporal relations between successive stimuli. A 'go' signal follows predictably in time after the words "on your marks, get set..."; the symphony commences a moment after the conductor's gesture.

The temporal-cueing task has helped bring temporal expectation to the fore of contemporary attention research. The design borrows from Posner's spatial

orienting task⁴ and builds on a rich literature considering the effects of so-called foreperiods (or temporal intervals) preceding a target (reviewed elsewhere^{5,6}). The task uses symbolic cues that predict the time interval after which a target is most likely to occur (after a short interval (for example, 600 ms) or a long interval (for example, 1,400 ms))^{7,8} (FIG. 1a). (Symbolic cues can also be used to instruct participants to focus on stimuli occurring only at a specific time point, independently of how probable stimuli are to occur at that time^{9,10}). The typical observation is that valid predictive cues considerably improve reaction times and accuracy for targets at the short interval^{11,12}. Performance benefits are smaller or absent for targets at the long interval, as expectations can be updated once the short interval elapses^{13,14} (FIG. 1a). This pattern of effects has been replicated across sensory modalities¹⁵ and in different species (non-human primates (NHPs)¹⁶ and rodents¹⁷).

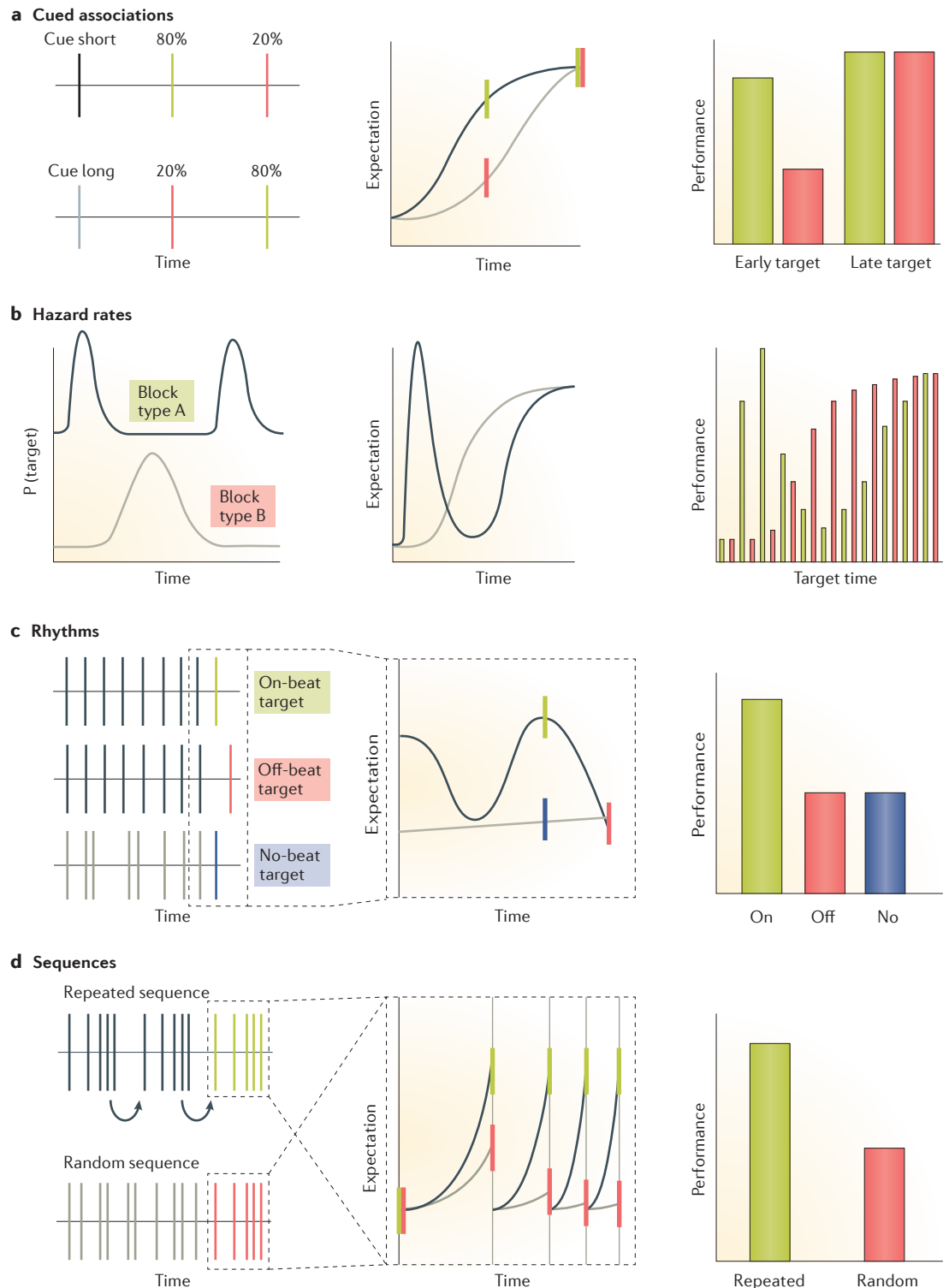


Figure 1 | Types of temporal structures. We consider four types of temporal structures capable of guiding temporal attention: cued associations (part **a**), hazard rates (part **b**), rhythms (part **c**) and sequences (part **d**). For each type (each row), the schematic displays the task structure (left), the expectation profile as a function of time (middle) and the performance profile (right). In the task structure column, vertical lines indicate individual stimuli at their associated timings. In hazard-rate-based tasks, stimuli are often drawn from a particular distribution of target times. The depicted expectation profiles are approximate (not mathematically or empirically derived) schematics that serve exclusively illustrative purposes. Precise expectation profiles will depend on exact target probabilities, exact intervals used (as temporal uncertainty also scales with elapsed time) and inclusion of catch trials (that is, trials with no target), among other aspects. The performance profile column depicts typical patterns of behavioural performance in the task (for example, the speed or accuracy of perceptual judgements).

An adaptation of the temporal-cueing task¹⁸ nicely illustrated that cued temporal orienting is temporally selective, causing trade-offs in perceptual performance between items occurring at cued versus uncued time points. In this task, multiple gratings appeared in succession. A cue indicated (with 75% validity) which subsequent target — the one after the short interval or the one after the longer interval — would most likely be subsequently probed. Relative to neutral cues, valid predictive cues brought benefits, whereas invalid cues brought costs, to accuracy and response-time measures.

Although most cueing tasks rely on short-term associations, in real life, most useful predictions about the characteristics of events to unfold come from long-term associations. Contextual-cueing¹⁹ and memory-based²⁰ orienting tasks confirm that learned spatial contextual associations strongly influence performance. Interestingly, contextual memories also carry temporal associations about when a target occurs within a learned context. Similar to long-term spatial associations^{19,20}, temporal associations strongly improve the detection and discrimination of targets that occur at the learned time interval^{21–23} (FIG. 2).

Hazard rates. Even in the absence of cued temporal associations between successive stimuli, the likelihood of an event occurring may vary predictably over time. The probability that an event will occur given that it has not yet occurred is referred to as the hazard rate²⁴. For example, during a penalty shootout, the probability for a player to initiate the penalty increases as time elapses. Hazard rates can be highly dynamic and need not increase with elapsed time. When a player commits a foul, the probability for the referee to blow the whistle initially increases sharply but then drops off again (the referee may have missed the foul).

Studies manipulating hazard rates — for example, by drawing target-onset times in different experimental blocks from different temporal probability distributions (FIG. 1b) — demonstrate that they have strong effects on performance. Benefits in performance track the hazard rates, even when participants are not informed about the distributions. Similar results have been reported in humans^{25–27} and NHPs^{28–30}.

Rhythms. Some events are characterized by recurring temporal structures. The simplest case is that of regular, isochronous rhythm (FIG. 1c). Many natural stimuli follow regular rhythms: footsteps, speech prosody and musical beats, among others. In regular rhythmic contexts, perception waxes and wanes. Through a pioneering body of psychophysical experiments in the auditory domain, Jones and colleagues demonstrated that discrimination of sound pitch and duration is most accurate when a stimulus occurs exactly at the predicted beat and decreases progressively with increasing temporal discrepancy in either direction^{31,32}. According to Jones' 'dynamic attending theory' (REFS 33,34), the ongoing temporal structure of events entrains attention and affects perception (as also described in REFS 35,36).

Rhythms also enhance perception in vision. Using a similar logic to Jones', another study showed that, after a rhythmic series of stimuli, perceptual discrimination was superior for masked visual targets that occurred on beat³⁷. A complementary approach developed in our laboratory compared the ability of human observers to discriminate stimuli embedded within temporally regular versus irregular streams. Both the threshold and speed for discriminating brief visual gratings improved when stimuli occurred within regular streams (every 400 ms) compared with irregular streams (200–600 ms)^{38,39}. Modelling of the behavioural data⁴⁰ suggested that rhythmic temporal expectation increased the signal-to-noise gain during visual processing.

Facilitation of performance by rhythms occurs independently of whether they are predictive of relevant target events. In both audition and vision, performance is superior for on-beat targets even when targets are more likely to occur off beat^{36,41}.

Sequences. Recurring temporal structures can be more complex than simple rhythms, as in the case of repeating temporal sequences (FIG. 1d). Temporal sequences are a staple in music and dance. In temporal sequences, the timing of the next expected element (for example, the next dance move) depends on the current position within the sequence. In the laboratory, performance benefits conferred by learned sequences are often studied using the serial reaction-time (SRT) task⁴². In the typical SRT task, specific stimulus locations are assigned to specific motor responses (response A to stimulus X, response B to stimulus Y, and so on). Participants' responses are considerably faster when the stimuli occur in a repeating ordinal sequence, even when low-level differences between the sequence and baseline conditions are controlled, such as the frequency of individual elements or element pairs⁴³. Sequence learning usually proceeds incidentally, with participants remaining unaware of the ordinal structure.

SRT tasks can be adapted to introduce temporal sequences. In this case, the onsets of targets follow a well-controlled sequence of temporal intervals. Adding a sequence of temporal intervals over and above the ordinal sequence dramatically improves response times, even when the ordinal and temporal sequences are independent of one another^{44,45}.

SRT tasks are often studied within the domain of memory and are rarely considered within the context of attention. However, the pattern of behavioural enhancements, as well as recordings of brain activity, indicate that temporal sequences are not only learned but also utilized proactively and dynamically to anticipate the timing of the expected target or action and to optimize performance⁴⁶. Similar to what is observed in temporal-cueing tasks, repeating temporal sequences lead to larger benefits at short target-onset times than at longer target-onset times⁴⁷.

Concurrent temporal structures. Until recently, temporal expectation has been treated as a single, unitary construct, with an implicit assumption that all types of

Isochronous

Of a temporal structure with a constant inter-element interval; a regular beat.

Ordinal sequence

The order of elements that make up a sequence. For example, in SRT tasks, this refers to the order of the spatially arranged items to which participants must respond.

Temporal sequence

The timings between elements that make up a sequence.

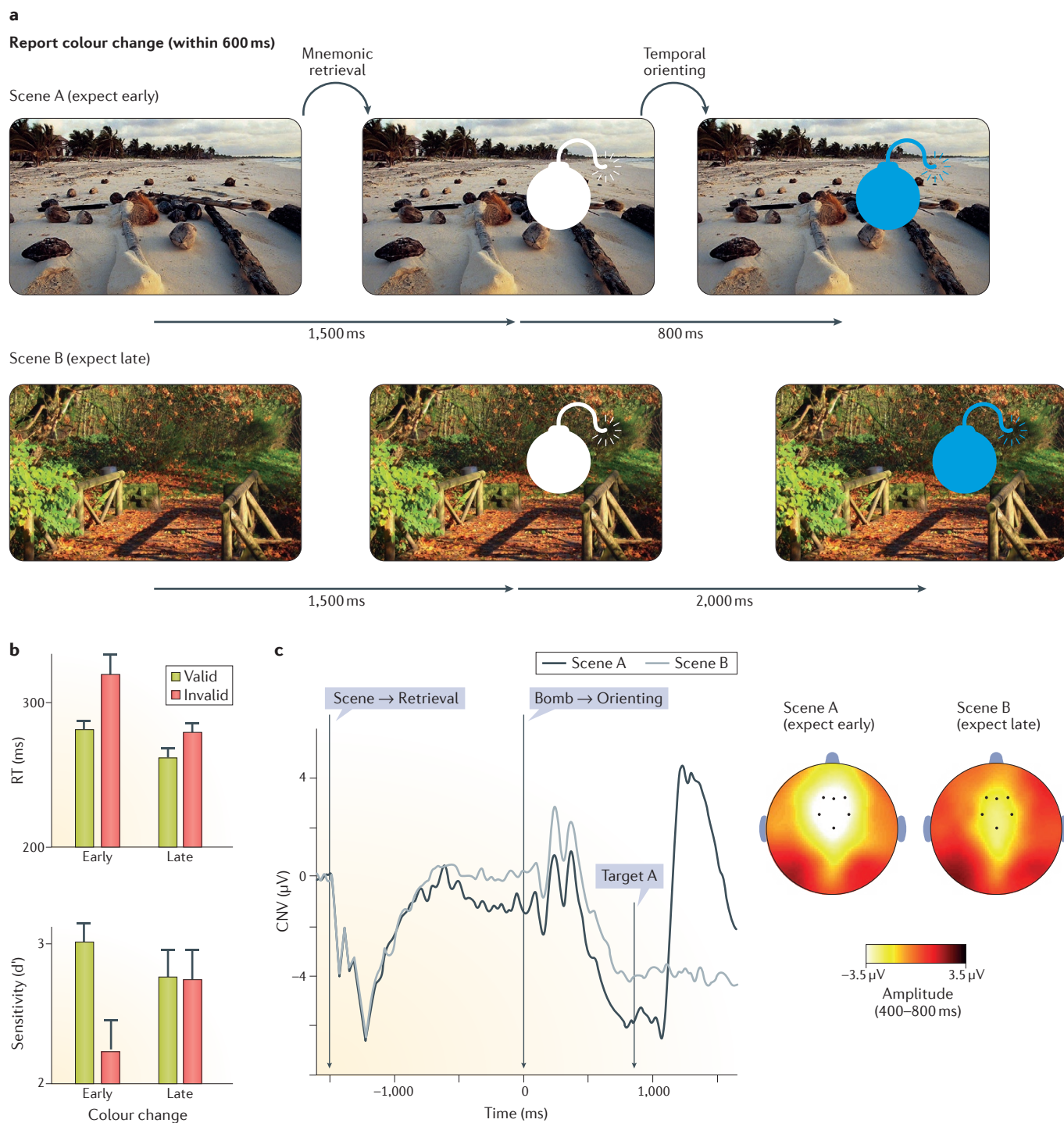


Figure 2 | Memory-guided temporal expectations. This study tested whether specific temporal associations between given contexts and the onset time for target stimuli could be subsequently utilized to prepare brain activity for the timing of the anticipated target and to enhance behavioural performance. **a** | Participants learned to associate images of scenes with one of two intervals (800 or 2,000 ms), after which a placeholder (a schematic of a bomb; placed within the scene) would change colour. Participants were asked to respond with a finger press as quickly as possible after the colour change (detection task) or to indicate to which of two alternative colours the placeholder changed (discrimination task). After an initial learning phase with fully predictable intervals, targets (colour changes) occurred either at learned (valid; 67%) or unlearned (invalid; 33%) intervals after placeholder onset.

b | Participants were significantly faster and more sensitive to targets occurring at learned intervals. **c** | This memory-guided orienting of attention in time was further corroborated by concurrent recordings of a classic electrophysiological marker of anticipatory attention (the contingent negative variation; CNV), which was enhanced early after the scene and placeholder onset for scenes predicting early as opposed to late targets. Depicted time courses are taken from the electrodes indicated in the topographical maps. RT, reaction time. Figure adapted from Cravo, A. M., Rohenkohl, G., Santos, K. M. & Nobre, A. C. Temporal Anticipation Based on Memory. *Journal of Cognitive Neuroscience*. **29**:12, 2081–2089 (December, 2017) © 2017 by the Massachusetts Institute of Technology, reprinted by permission of the MIT Press (REF. 22).

temporal structures guide attention through common mechanisms. It is becoming increasingly clear that this is probably too simplistic. Rhythms, for example, can facilitate performance independently of concurrent temporal cues^{41,48}. Furthermore, whereas the effects of symbolic temporal cues are strongly influenced by task instructions⁴⁸ and competing task demands^{49–51}, the effects of rhythms remain robust and unaffected by task instruction⁴⁸, competing demands⁵¹ or their predictive utility^{36,41}. Studies in individuals with brain lesions and studies using repetitive transcranial magnetic stimulation (rTMS) further suggest that there are dissociable mechanisms for temporal expectation that follow different types of temporal structures^{52–54}.

Multiple sources of temporal structure may operate in tandem. For example, when cues and rhythms are simultaneously present, both influence performance in an additive manner^{41,48}. In hazard-rate-based tasks, reaction times may be shaped not only by the current hazard rate but also by memory for hazard rates experienced one week earlier²³. In addition, the effects of different temporal structures may interact. For example, the predictability of targets by hazard rates can markedly diminish the effects of temporal cues or rhythms^{13,55}.

The plurality of sources of predictable temporal structures and their distinct behavioural consequences must be recognized when seeking to understand the mechanisms involved. We should also note that, whereas this Review is predominantly concerned with expectations about the onsets of events, expectations about event durations⁵⁶ and response urgency⁵⁷ are also likely to steer adaptive perception, particularly when monitoring continuous input streams such as speech^{58,59} or extended visual displays⁵⁶.

Neural bases

The challenge for investigating the neural mechanisms of temporal expectation is exacerbated by our limited understanding of how timing is coded in the brain at the interval-time range⁶⁰. Whereas some researchers propose the existence of dedicated timing circuits and mechanisms⁶¹, others emphasize the intrinsic timing properties distributed across most, if not all, neural circuits⁶². Whatever its source or sources, information about temporal structures can be used to guide adaptive behaviour. Here, we focus on the neural bases of this utilization.

In sensory cortices, spatial and feature-based RF properties are organized and interconnected in an orderly way, providing a convenient substrate for top-down spatial and feature-based biases on processing. For example, connections among neurons in different visual areas follow retinotopy and enable communication and coordination of top-down biases that are based on the spatial location of relevant anticipated stimuli. No equivalent organization for temporal RF properties is recognized. (This is not to say that neurons are insensitive to timing; indeed, there are increasing demonstrations that neurons within sensory and associative areas can, with learning, become temporally tuned to stimulus properties⁶³ or within a context⁶⁴.) Modulatory mechanisms based on RF properties alone, therefore, are unlikely to have much explanatory power for temporal expectation. To make progress, we

must consider the dynamics of brain activity and how they can support prospective and temporally selective modulation of information processing. Initial discoveries have started to provide the grounding for a much richer and more dynamic conceptualization of attention. They reveal that multiple mechanisms may be at work. As the mappings between internal mechanisms for temporal expectation and the external varieties of temporal structure are yet to be defined, it remains prudent to note differences in task contexts at this stage. In highlighting some of the advances thus far, it is convenient to consider three separate stages of processing of temporal expectation: control, anticipation and modulation.

Control. The large-scale networks that control temporal expectation have been investigated primarily through cueing tasks. Coull and Nobre⁷ assessed regional blood flow while participants were cued to either the spatial location or temporal interval of a target. Compared with spatial cueing, temporal cueing preferentially engaged the left inferior parietal cortex and the ventral premotor–prefrontal cortex. Activation of left parietal cortex and, to a lesser extent, of left ventral premotor–prefrontal cortex in temporal-cueing tasks has been replicated repeatedly^{65,66}. Activations in the left inferior parietal cortex have also been noted when targets occur on strong beats of an auditory rhythmic stream⁶⁷ and following temporal updating according to hazard rates⁶⁸.

These observations suggest a role for a left-dominant sensorimotor network in the control of temporal attention in humans. One interesting proposal is that sensorimotor circuits for limb and hand control provide supporting representations and computations for temporal attention in a way analogous to that in which the dorsal frontoparietal network that is involved in oculomotor control supports spatial attention^{7,69,70}. However, further investigation is required to elucidate what causal role the left-dominant sensorimotor network plays in the control of temporal attention. Whether these areas provide the source of temporal expectation or are modulated by temporal expectation during evidence accumulation or motor preparation remains to be settled.

Recently, navigation studies in rodents have identified hippocampal time cells that respond at particular intervals within a context⁶⁴. Similar to the properties of place cells (such as the size and mapping of place fields), time-cell properties (such as interval duration) are plastic and change in different environments. Hippocampal neurons also have a role in representing the time interval between temporally separate stimuli during learning — for example, signalling the precise timing of conditioned eye-blink responses during trace conditioning^{71,72}. The possibility that hippocampal cells contribute to temporal anticipation of events⁷³ is worth testing. The proactive use of hippocampal spatial signals to guide performance is being increasingly recognized^{74,75} — for example, in tasks in which long-term memory guides attention⁷⁶. Tasks for testing memory-based temporal expectation^{22,23,45} (as in FIG. 2) will enable the investigation of whether and how temporal, as well as spatial, information from the hippocampal region is used proactively to guide adaptive performance.

Interval-time range

Cognitively relevant time range that ranges from several hundreds of milliseconds to several seconds.

Temporal updating

Updating of cognitive variables — such as expectations, the allocation of attention or movement plans — on the basis of estimates of elapsed time.

Evidence accumulation

The build-up of evidence for one of multiple perceptual decisions. In the literature on perceptual decision making, this is often studied using perceptual streams in which individual samples are insufficiently reliable, thus necessitating the integration of perceptual evidence over time.

Trace conditioning

A variation of classical conditioning in which the conditioned stimulus (such as a tone) and unconditioned stimulus (for example, an air puff) are separated by an empty time interval of a given duration.

Motor potential

Change in voltage associated with activity recorded from the muscle (electromyogram) upon stimulating the corresponding area of the primary motor cortex.

Event-related potentials

(ERPs). The average electrophysiological responses that are locked in time to a particular event of interest, such as a stimulus, action or other physiological marker.

Contingent negative variation

(CNV). A negative potential broadly distributed over the scalp that builds up before a target stimulus. Its intracranial sources include brain areas linked to motor preparation.

Phase

A point in an oscillatory period between 0 and 2π , corresponding to trough, rising slope, peak and so on.

Much is still to be learned about the networks and mechanisms for the control of temporal attention, such as the causal involvement of the cortical areas highlighted thus far and the additional possible contributions of subcortical structures. Another important consideration is that haemodynamic-based methods are poorly suited to reveal modulations in the dynamics, as opposed to the strength, of neural activity. Furthermore, any temporal correlation between successive events, which is a hallmark of temporal-expectation studies, can greatly complicate interpretation. Methods with high temporal resolution are therefore required to break ground in the understanding of how temporal expectations are controlled and utilized in the brain.

Anticipation. A central hypothesis for how temporal expectations serve attention is that they prospectively align a state of optimal sensitivity among relevant neuronal ensembles with the anticipated onset of a relevant event. There may be multiple ways of timing neuronal sensitivity.

A simple but convincing demonstration of temporally specific changes in neuronal excitability comes from a study using TMS to probe corticospinal excitability in a cued-response task⁷⁷. After a preparatory cue, a go stimulus occurred at one of four equally probable intervals, prompting participants to respond with a finger movement. The TMS-evoked motor potential recorded at the relevant hand muscle was significantly larger at the specific moments when the go signal could (but did not) occur than during the intervals in between possible go signals. The motor potential furthermore increased over the successive moments at which go signals could occur, in line with the increasing hazard rate.

Studies measuring event-related potentials (ERPs) to investigate cued temporal expectations in humans were the first to suggest systematic changes in anticipatory neural activity, putatively associated with increased 'readiness'. Predictive temporal cues considerably amplify a potential link to anticipation and motor preparation, known as the contingent negative variation (CNV)⁷⁸. The CNV develops more steeply when targets are expected after a short interval than when they are expected after a long interval⁸ (FIG. 2c). This effect of temporal expectation on ERPs has been extensively replicated^{41,49,79–81} and has also been observed in the context of hazard rates^{26,82} and rhythms⁸³.

Studies in NHPs have mainly manipulated temporal anticipation by using hazard rates. They reveal systematic changes in firing rates associated with the subjective hazard rate in various brain areas — the lateral intraparietal area (LIP)²⁹, visual area V4 (REF. 28) and primary visual area (V1)^{84,85}. In one study, changes in V1 firing rate (and gamma power) were also observed in a temporal-cueing task⁸⁴. Studies in humans and NHPs have also shown timed increases in neuronal synchronization in motor areas in preparation for temporally anticipated responses^{25,86}.

In addition to changes in neuronal firing, modulation of oscillatory activity has also been noted. In human electrophysiological studies, a striking and

consistent effect of preparatory spatial attention is the relative attenuation of alpha-band (8–12 Hz) and beta-band (15–30 Hz) activity across sensory and motor cortices associated with anticipated stimuli and responses, putatively reflecting preparatory increases in excitability^{87,88}. Several studies reveal that temporal expectations can alter oscillatory dynamics such that moments of heightened sensitivity align with temporally predicted events. Preparatory alpha-band attenuation in visual areas occurs more quickly when cues predict a short versus a long interval before a visual event⁸⁰. Temporally specific attenuation in the alpha and beta bands in somatosensory areas has also been reported during anticipation of somatosensory events⁸⁹. Similar effects are observed when temporal expectations are induced by rhythms^{83,90}, hazard rates²⁵ or sequences⁴⁶. For example, the power of the alpha-band oscillation continued to wax and wane with the tempo of the preceding stimulus-onset rhythm during a period of stimulus occlusion as participants prepared to discriminate a visual stimulus⁹⁰. In NHPs, V1 recordings revealed that temporal anticipation following cues or hazard-rate manipulations is associated with an attenuation of alpha oscillatory power in this region⁸⁴. In addition, some researchers have suggested that temporal expectations also align the phase of alpha oscillations relative to anticipated target times^{91–93}, although this issue remains unsettled⁹⁴.

Thus, though still at an early stage, research reveals that multiple mechanisms may be at play — including modulations in the rate and synchronization of neuronal firing and in the strength and timing of oscillatory activity. In addition, patterns of neuronal activity in cortical networks have been proposed to encode time intrinsically⁶². A specific interval could be encoded when a specific network pattern induced by the first stimulus is reinforced by the onset of the second stimulus. Network states learned through such reinforcement would thus carry embedded temporal predictions. Testing whether and how reinforcement of dynamic network states contributes to temporal expectation will be fascinating, if challenging.

Entrainment. An idea that has been gaining strength is that temporal expectations during rhythmic stimulation may capitalize on the tempos of the naturally occurring oscillatory brain dynamics, such that moments of heightened excitability (corresponding to particular oscillatory phases^{95–97}) become aligned to the timing of relevant events (FIG. 3). This type of mechanism has come to be known as entrainment and has been noted especially in the delta (1–4 Hz) frequency range. A complementary line of research considers whether these endogenous oscillations also constrain perception of non-periodic stimuli (BOX 2).

A landmark study by Lakatos *et al.*⁹⁸ sparked interest in rhythmic entrainment as a major attention mechanism⁹⁶. They presented NHPs with quasi-rhythmic streams of visual and auditory stimuli in antiphase. When the monkey attended one of the two streams, the low-frequency delta oscillations in both

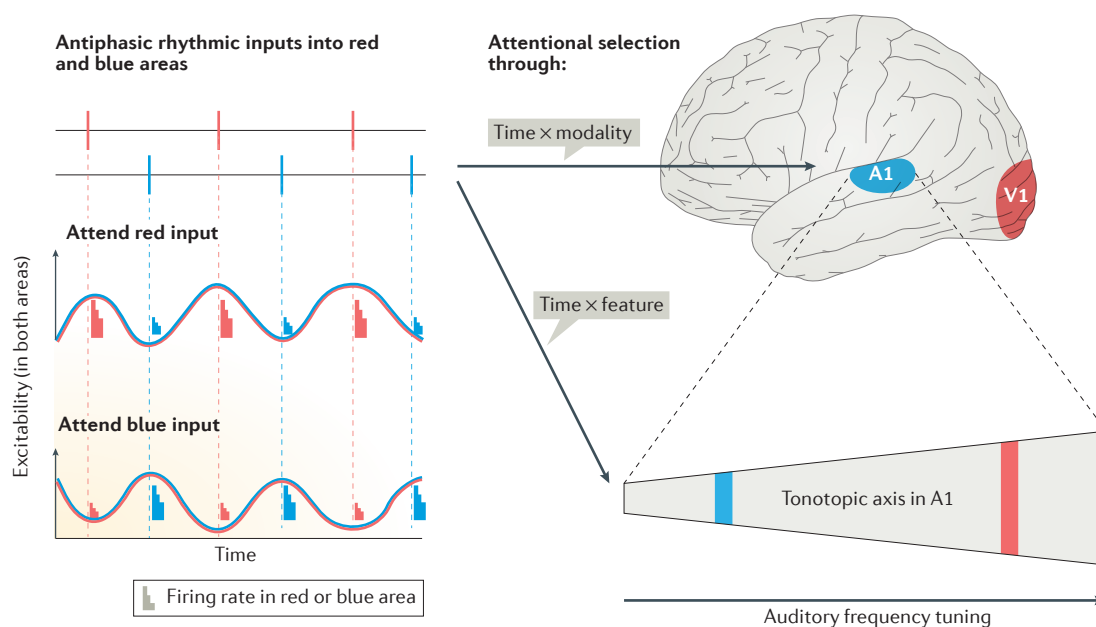


Figure 3 | Selective entrainment to relevant stimulus modality or feature. In this entrainment task, two rhythmic input streams are presented approximately in antiphase. Each is processed by a spatially segregated neuronal population — for example, populations processing different modalities (such as primary auditory cortex (A1; blue) and primary visual cortex (V1; red), which process auditory and visual input streams, respectively) or populations with distinct sensory tuning within a modality (for example, low-pitch and high-pitch input streams, for which the corresponding A1 tonotopic zones are depicted as blue and red, respectively). The central observation is that when attention is deployed to either input stream, neuronal oscillations (typically somewhere in the 1–4 Hz, delta range) in supragranular layers in both areas become aligned to this stream, such that moments of heightened excitability coincide with (expected) inputs in the attended stream (as indicated on the left-hand side). In the population processing the attended stream, this modulatory phase alignment translates into an enhanced firing-rate response (depicted by clustered blue and red bars in the graphs on the lower left). Schematic based on REF. 98 (for the modality case) and REF. 102 (for the feature case).

V1 and in the primary auditory area (A1) became entrained to the relevant modality, such that maximal excitability coincided with expected events in the attended stimulus stream (FIG. 3). The effect was concentrated in the supragranular (upper) cortical layers, in line with involving a modulatory, as opposed to driving, input.

Entrainment of neural activity to the rhythms of relevant events has also been reported in human electroencephalogram (EEG) and magnetoencephalogram (MEG) studies^{38,99,100} (but see REF. 101). By relating psychophysical analysis and modelling to the phase of oscillatory activity, one study showed that the degree of delta-phase alignment in rhythmic contexts correlated with signal-to-noise gain in visual processing and perceptual performance³⁸.

In rhythmic contexts, it can be difficult to separate anticipatory and proactive entrainment effects from responsive and reactive target-driven effects. In favour of the notion of anticipatory effects, neural oscillations can persist for a few cycles after rhythmic stimulation has ceased¹⁰². Moreover, entrainment of neural oscillations can be observed in the absence of any evoked neuronal activity. Examples are entrainment of visual or auditory cortex to stimuli in the other modality when they are relevant for performance in NHPs⁹⁸ and

entrainment to subliminal stimulus streams in humans that are below threshold for conscious perception and that do not elicit observable evoked MEG responses¹⁰³.

Modulation. Many types of modulatory consequences of temporal expectation on subsequent stimulus processing have been documented, and the list is certain to grow. Selective temporal expectation can modulate the strength, timing and synchronization of neuronal responses and may ultimately improve the quality and efficiency of information communicated about relevant events.

The most direct evidence for the modulatory effects of temporal expectation on sensory processing comes from single-unit studies. Anderson and Sheinberg¹⁶ showed increases in the firing rates of inferotemporal neurons in NHPs for relevant inputs at expected moments in a temporal-cueing task. Similar increases have also been reported in monkey V1 (REF. 84) and in rodent V1 (REF. 104) and A1 (REF. 17), thus revealing modulations at early stages of cortical processing. Non-invasive recordings in temporal-cueing tasks in humans have also shown increases in the strength of visual¹⁰⁵, auditory¹⁰ and somatosensory¹⁵ ERPs with valid cues. Decreases in the latency of target-related potentials have also been observed in cueing and

Box 2 | Rhythms of perceptual sampling

In addition to the psychological anticipatory functions that prepare perception, the role played by effector systems in the active sampling of external stimulation is increasingly recognized^{144,145}. Our sense organs are not passive receptacles for stimulation; they are part of exploratory organisms and are bound by their own temporal structures. Many of the actions used to sample the world are intrinsically rhythmic, such as whisking in rodents and eye movements in humans. Our saccadic eye movements, for example, exhibit prominent rhythmicity at approximately 3–4 Hz. It has been proposed that such rhythmic sampling provides a potent and reliable scaffold for aligning attention in time¹⁴⁶.

Temporal sampling of external stimulation may not be restricted to the rhythms of overt action. The characteristic intrinsic time courses associated with neural systems for controlling perception may be sufficient to impose periodicity even during covert sampling of the environment. Some have proposed that motor regions, through interaction with sensory areas, set the periodicity of perceptual sampling⁷⁰. Others have suggested that perception itself is inherently periodic, capturing external stimulation over successive discrete quanta^{147,148}.

Studies are beginning to chart the quality of perception over time relative to the phase of endogenous brain oscillations^{149,150} as well as to transient attentional cues^{151,152} and movements¹⁵³. The precise perceptual rhythms recorded across studies vary within the range between delta and alpha, and one could speculate that they reflect the temporal sampling rates that are intrinsic to different task-related brain networks at play, although other factors, such as the number of locations to be sampled, may also contribute to the variability in the frequencies observed. More research is needed to establish the reliability, and to derive the principles, of rhythmic perceptual sampling mechanisms¹⁵⁴. It will also prove interesting to understand how endogenous sampling rhythms and external sensory stimulation come together to provide sensible objects of perception.

rhythmic tasks^{8,16,105}. In tasks with recurrent temporal relations among stimuli, ERPs also signal breaches in temporal expectations^{106–108}.

Ultimately, the success of a preparatory process is measured by its ability to enhance the quality of information extracted from a relevant target relative to competing distractors. Multivariate decoding of electrophysiological recordings provides a powerful analytic tool for investigating how stimulus-related information is dynamically modulated¹⁰⁹. Recent EEG data suggest that temporal warning cues selectively boost target-identity representations and help to protect the processing of target-identity information against temporally adjacent, competing distractors¹¹⁰.

Interactions

Above, we have considered temporal expectations in isolation. Although it is conceptually possible and experimentally convenient to isolate temporal expectation, expectations about forthcoming events often blend ‘what’, ‘where’ and ‘when’. An important question, therefore, is whether and how temporal expectation combines with spatial and feature-based expectations to influence brain activity and behaviour.

Perhaps counter-intuitively, spatial attention and feature-based attention seem to operate largely independently^{2,111} (although interactions have also been reported^{112,113}). For example, increases in neuronal responses to stimuli that contain relevant versus irrelevant features (such as motion direction or colour hue) are of similar values regardless of whether the stimuli are presented at attended or unattended locations^{114,115}.

By contrast, the effects of temporal expectation do seem to interact strongly with expectations regarding target location and identity.

Time and space. The interaction between temporal and spatial expectations in guiding perceptual discrimination was tested in a human psychophysical task using predictive temporal and spatial cues¹¹⁶. Temporal cues enhanced perceptual discrimination only when targets appeared at their expected location as well as at their expected time. Spatial and temporal expectations show a similar synergistic interaction during sequence learning in SRT tasks. Temporal sequences strongly magnify the influence of spatial sequences on reducing response times, whereas the temporal sequences in isolation are ineffective⁴⁵.

The synergy between temporal and spatial attention is also revealed in the pattern of neural modulation. A clear example in humans was provided by a study in which participants covertly attended a disc that moved across the monitor in steps until it became transiently ‘occluded’ (REF. 105). The spatial trajectory and temporal rhythm of the steps were manipulated orthogonally to each other. When the disc reappeared after occlusion, the amplitude of the P1 visual potential elicited by the target was enhanced by spatial attention, and this effect was further amplified by temporal expectation. In the absence of spatial expectation, however, there was no effect of temporal expectation on P1.

Spatial-temporal interactions are also observed during the anticipatory period. In humans, temporal expectation enhances the lateralization of alpha and beta oscillations linked to spatial attention at the times at which targets were anticipated⁸⁹. Similarly, in NHPs, increases in spike rates in areas V4 and LIP associated with spatial attention co-varied with hazard rates^{28,29}. However, not all temporal expectation modulations are necessarily spatially specific. For example, in NHPs, temporal modulations of gamma-band oscillations occurred at both foveal and peripheral sites in V1, even though expected targets appeared only foveally⁸⁴.

Time and feature. Temporal expectations also interact with feature-based expectations. One recent study¹¹⁷ showed that rhythm-based auditory temporal expectations improved perceptual sensitivity when combined with valid expectations regarding the spectral content in which target sounds were embedded, but not when these spectral feature expectations were invalid.

The interaction between temporal and feature-based expectations is again evident from the patterns of neural anticipation and modulation. For example, when presented tones with different frequencies compete for attention, entrainment occurs such that the high-excitability phase of ongoing oscillations became aligned with tones with the relevant pitch, whereas the low-excitability phase became aligned with the irrelevant tones¹⁰² (FIG. 3). Temporal expectation may also sharpen the neural code by modulating neural activity in a feature-specific manner. Such modulation has been observed in rodent A1, where the increase in firing rates by temporal expectation

P1 visual potential

A stereotypical event-related potential response that is characterized by a positive deflection in posterior sites approximately 100 ms after a visual input.

is not equal in all neurons but is largely specific to the preferred auditory frequency of neurons¹⁷. In a similar vein, temporal-expectation-associated increases in the gamma-band response to gratings in monkey V1 are largest for preferred grating orientations⁸⁴.

Studies of human brain activity also support interactions between temporal and feature expectations. One EEG study showed that responses to an expected, but omitted, auditory tone occurred only when both the timing and the pitch of the tone could be anticipated¹¹⁸. Interactions between temporal and feature expectations have also been documented in human functional MRI visual responses to gratings with predictably changing orientations¹¹⁹.

Mechanisms of interaction. In many cases, therefore, the effects of temporal expectation may be expressed through the timing of modulations of other, RF-based properties. Studies suggest that modulation in the gain and synchronization of neuronal activity based on RF properties becomes temporally sculpted according to learned temporal structures to facilitate prioritization and selection of relevant items at their anticipated timings. The question of where these temporally dependent, sculpting influences on neuronal activity come from is a fundamental and exciting one to address. They could arise through plasticity within neuronal populations with specialized RFs, such that the RF properties of these populations acquire a fourth, temporal dimension^{63,64} or such that network patterns carry temporal information⁶². Alternatively, non-specialized

temporal signals (such as subcortical arousal signals or non-selective oscillatory entrainment) could differentially influence neuronal populations that show high versus low levels of activity. In addition, one should not yet rule out the possibility of temporal-expectation effects that are independent of other, RF-based biases. Moreover, the boundary conditions for when interactions occur still need to be charted. Future studies investigating the conditions and mechanisms of three-way interactions among temporal, spatial and feature-based expectations should prove particularly interesting.

The broader landscape

Most tasks that have demonstrated the effects of temporal attention explore psychological and neural mechanisms within the confines of simple perceptual discrimination or speeded response tasks. However, the importance of temporal expectation in guiding adaptive behaviour has much greater reach. Temporal expectation facilitates perception in the context of dynamic streams of complex stimuli, such as in language^{120,121} and music^{122,123}. The effects occur at multiple stages of processing and can influence many critical operations, including multisensory integration¹²⁴, sensorimotor integration¹²⁵, semantic analysis¹²⁶ and conscious perception^{127,128}.

Temporal expectation is likely to have a primary role in learning. Temporal contingency and contiguity strongly influence the strength of associative and reinforcement learning. In classical conditioning, an

Report orientation of item indicated by colour after short or long delay

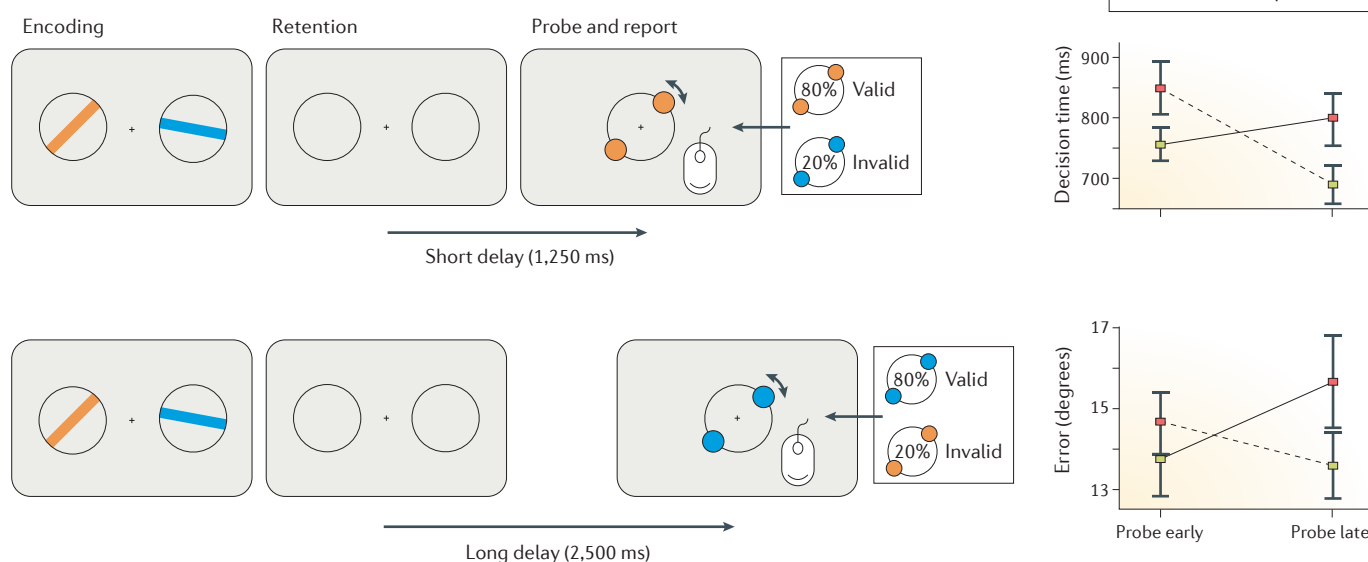


Figure 4 | Temporal expectations in working memory. Participants were instructed to retain the orientation of two coloured bars in working memory and to reproduce the orientation of one of them after either a short (1,250 ms) or a long (2,500 ms) delay. Participants learned that the differently coloured bars were each associated with a different delay after which they were most likely to be probed (for

example, orange early (top) and blue late (bottom); 80% valid). At both delays, mnemonic performance was faster and more accurate when expected items were probed, demonstrating dynamic, item-specific prioritization in working memory governed by temporal expectations. Figure adapted with permission from REF. 134, Society for Neuroscience.

important aspect of learning involves timing the conditioned response relative to the anticipated unconditioned stimulus, especially in trace conditioning⁷¹. In reinforcement learning, a classic observation is that when an expected reward is omitted, dopamine neurons in the midbrain signal the omission with a transient decrease in spiking rate that is aligned to the expected time of the reward¹²⁹. The timing of expected rewards even governs firing rates in early sensory cortices such as in rodent V1 (REF. 130). Thus, the brain uses not merely

the order of events but also precise temporal expectations to evaluate and signal the contingency between a reward and its antecedent stimulus or action — a critical building block of effective learning.

The consequences of temporal expectation are beginning to be documented in human memory. Temporal expectation can enhance encoding of information for memories at different timescales. One study¹³¹ demonstrated the utility of cued temporal expectation in improving working memory performance for speech

Box 3 | Open research questions

Basic mechanisms

Compared with the well-established fields of spatial, object-based and feature-based attention, very little is understood about the basic mechanisms that contribute to control, anticipation and modulation in the varieties of temporal expectation. In order to develop a cohesive theoretical account of temporal attention, many basic questions still need to be addressed:

- Are there dedicated brain areas and networks causally involved in controlling temporal attention? Addressing this question will require lesion-based and stimulation-based studies using tasks with different stimulus modalities and response requirements.
- Do different pharmacological systems contribute to temporal attention, and if so, how? Pharmacological manipulations of temporal attention remain rare. In one notable example, administration of the noradrenergic agonist clonidine was shown to have selective and dissociable effects on behavioural measures and functional MRI responses in different brain regions following spatial cues, temporal cues and spatially and temporally non-informative alerting cues¹⁵⁵. Such studies can provide important insights into commonalities and interactions among modulatory biases based on different types of temporal structures and receptive-field properties.
- What cellular mechanisms contribute to modulation by temporal expectations? Manipulations of temporal expectation in non-human primate and rodent single-unit studies (for example, by manipulating hazard rates for task-relevant stimuli) would be highly informative.
- To what extent do similar mechanisms contribute to control, anticipation and modulation based on different types of predictable temporal structures in the environment (associations, hazard rates, rhythms and sequences)? Is it possible to derive a better taxonomy based on neural mechanisms?

Temporal expectations and other control mechanisms

An emerging property of temporal expectation is its strong interaction with other mechanisms for behavioural control. How exactly temporal expectations interact with, and influence, other circuits remains to be understood:

- What, if any, is the relation between the brain networks involved in duration estimation and in controlling temporal attention?
- What circuit-level and cellular mechanisms contribute to the synergies between temporal and other sources of expectations?
- Are the timings of individuals' motor effectors (for example, saccade rates and articulation speed) related to rhythmic attention capabilities in related modalities (such as the visual and auditory streams, respectively)?

Implications for behaviour

Revealing the basic mechanisms of temporal expectations and their relations to other control-related mechanisms will shed light on new, dynamic aspects of control of adaptive behaviour.

- Do the frequencies of endogenous brain rhythms constrain the ability to attend to rhythmic streams?
- Do we extract nested or multiplexed temporal structures to facilitate perception? How is this achieved?
- How do temporal expectations influence decision-making and foraging behaviour in continuous environments?

Clinical implications

Deficits in temporal expectation may feature in many disorders. To date, deficits in temporal processing or temporal expectation have been proposed to occur in disorders involving dopamine dysfunction, including schizophrenia¹⁵⁶, Parkinson disease^{157,158} and attention-deficit hyperactivity disorder^{159,160}. Cerebellar lesions have also been linked to deficits in perceptual and motor timing¹⁶¹, although the cerebellar contribution specifically to temporal expectation is just beginning to be tested^{162,163}.

- Are these temporal deficits causal to these disorders or secondary to other, more basic deficits?
- Can specific deficits in temporal expectation contribute to phenotypic information to improve stratification, diagnosis and prognosis of individuals? If so, how?
- In what situations may training regimens that impose external rhythms and cues improve symptoms? Indications of the efficacy of such interventions — for example, in the contexts of Parkinson disease¹⁶⁴ and stuttering¹⁶⁵ — are highly encouraging.

sounds embedded in noise. Another¹³² showed that human long-term recognition memory is improved when items are encoded within a structured temporal sequence.

Temporal expectation is useful not only for enhancing the encoding of relevant information into memory but also for accessing information from memory at the right time. Evidence suggesting this came from a continuous performance task in which human observers monitored a series of visual gratings to detect occasional stimuli that matched a target orientation template held in memory¹³³. Multivariate decoding analyses of MEG and EEG data suggested that the brain did not sustain a tonically elevated representation of the template but rather transiently upregulated the representation according to the quasi-rhythmic temporal structure of the task, starting just before the presentation of each grating.

In a more direct test of flexible temporal prioritization of representations in working memory, we recently designed a simple task in which participants encoded two peripheral, differently coloured bars and were subsequently probed to reproduce the orientation of either bar at one of two intervals (1,250 ms or 2,500 ms)¹³⁴. The participants learned through association that on 80% of trials, the length of the interval was predictive of which coloured bar would be probed. Response times and accuracy in reproducing orientations were better when items were probed at their expected times, thus marking temporally selective prioritization of items held in visual working memory (FIG. 4). Furthermore, the temporal updating between the items in working memory (that is, shifting attention between items once the short interval had passed) was tracked by lateralization of alpha oscillations (see also REF. 135), which also predicted faster access to working memory on a trial-wise basis.

As our appreciation of the important and pervasive effects of temporal expectations grows, it is natural to consider how the breakdown of temporal expectations may contribute to various psychological, psychiatric and neurological disorders. We suspect that deficits in temporal expectation feature in many disorders, and that they may contribute to symptoms and provide useful phenotypic information that could improve the stratification, diagnosis, characterization and prognosis of individuals (see BOX 3 for elaboration on these and further important open questions).

Time ahead

As highlighted in this Review, temporal expectations act along several stages of neural processing and across many brain regions to guide adaptive behaviour. Many neural mechanisms may support temporal attention based on various predictable temporal structures in the environment. These mechanisms may act in tandem and interact with other, RF-based biases to magnify their effects. Research into the neural mechanisms of control, anticipation and modulation is only just beginning (BOX 3).

When the volume of research increases to match the fundamental importance of temporal expectation, new insights will be gained about dynamic modulatory mechanisms of brain activity. As the principles emerge, we will progress from having static pictures of attention to developing dynamic theories about how predictable temporal structures in the environment interact with temporally evolving brain activity to prioritize and select objects for perception, action and memory. Lessons from the field of temporal attention should have wide-ranging implications for most, if not all, cognitive domains and are also likely to carry important clinical utility.

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Acknowledgements

The authors acknowledge support from a Wellcome Trust

Senior Investigator Award (A.C.N.) (104571/Z/14/Z), a Marie Skłodowska-Curie Individual Fellowship from the European Commission (F.v.E.) (grant code ACCESS2WM) and the UK National Institute for Health Research (NIHR) Oxford Health Biomedical Research Centre. The Wellcome Centre for Integrative Neuroimaging is supported by core funding from the Wellcome Trust (203139/Z/16/Z). The authors also wish to thank K. Nussenbaum, A. Cravo, R. Auksztulewicz, S. Heideman and N. Myers for their thoughtful comments in the course of preparing this review, as well as A. Irvine and A. Board for their help with the bibliography. The authors also thank the reviewers for excellent constructive comments.

Author contributions

A.C.N. and F.v.E. researched data for the article, made substantial contributions to discussions of the content, wrote the article and reviewed and/or edited the manuscript before submission.

Competing interests statement

The authors declare no competing interests.

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