

# Visual temporal attention from perception to computation

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## Abstract

Visual attention unfolds across space and time to prioritize a subset of incoming visual information. Distinct in key ways from spatial attention, temporal attention is a growing research area with its own conceptual and mechanistic territory. Here I review key conceptual issues, data and models in the field of visual temporal attention, with an emphasis on voluntary temporal attention. I first situate voluntary temporal attention in the broader domains of temporal attention and attentional dynamics, with the goal of organizing concepts and findings related to dynamic attention. Next, I review findings that voluntary temporal attention affects visual perception in a selective fashion – prioritizing certain time points at the expense of other time points. Selectivity is a hallmark of attention and implies a limitation in computational resources that prevents sustained maximal processing of all time points. I discuss a computational model of temporal attention that captures limited resources across time and review other models of attentional dynamics. Finally, I discuss productive future directions for the study of temporal attention.

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## Introduction

Vision is a dynamic sense. The world changes on all timescales, and humans not only watch but actively look around<sup>1,2</sup>, move through<sup>3</sup>, and act on<sup>4</sup> the world, resulting in visual input that is in continuous flux. Although much research simplifies the problem of vision to the perception of still images, the human visual system constructs perceptual experience and guides behaviour from an ongoing, dynamic visual stream.

Like vision itself, visual attention must operate across time to prioritize behaviourally relevant information when that information is most useful. When returning a table tennis serve, for example, it is critical to see the ball well when it hits your opponent's racket but much less useful to see it a half-second before or after<sup>5</sup> (Fig. 1). Likewise, you can daydream while crossing an empty street as long as you pay attention to the curb at the moment you must prepare to step up. The prioritization of visual information at specific points in time is called visual temporal attention<sup>6,7</sup>.

Temporal attention is a growing research area, with ongoing advances in the experimental manipulations, measurement strategies and theoretical approaches applied to the problem of how we attend in time<sup>8–10</sup>. It has long been established that knowing when to expect a visual target can speed reaction times to that target<sup>6,11,12</sup>. Although this improvement was initially thought to be due to enhanced motor preparation<sup>13–15</sup>, later work has demonstrated and characterized the effects of temporal attention on perception. These data have enabled the development of computational models of temporal attention that aim to predict how humans dynamically prioritize and process ongoing visual input. However, data and theory on visual temporal attention still lag behind those for spatial attention<sup>16,17</sup>. This gap presents exciting opportunities to move the study of visual attention – and vision in general – more fully into the dynamic realm.

Space and time are fundamentally different kinds of dimension that raise different conceptual and mechanistic issues for the prioritization of relevant information. At a conceptual level, different spatial locations are stable and symmetric: an image can usually be left–right reversed without fundamental changes to visual spatial processing. By contrast, moments in time are fleeting and asymmetric. Ordering of events in time matters, as demonstrated by a wide array of sequential effects in perception<sup>18–22</sup>. At a mechanistic level, space and time are largely handled differently by the brain. Whereas space is coded in the primate visual system by which neurons respond to a stimulus

(as in retinotopic maps<sup>23</sup>), time is coded in many brain areas through the unfolding dynamics of neural activity itself<sup>24,25</sup>. Thus, the mechanisms for prioritizing locations in space versus moments in time could – and in certain respects must – be quite different. For example, distinct brain areas are involved in attending to points in time versus locations in space<sup>6,26</sup>. These differences between space and time necessitate the dedicated study of temporal attention, as distinct from spatial attention.

Temporal attention involves the prioritization of sensory information, which can be involuntary (stimulus-driven) or voluntary (goal-directed)<sup>16</sup>. Involuntary, or exogenous, temporal attention is driven by salient events, such as a warning signal<sup>27,28</sup> or rhythmic stimulation<sup>29</sup>, and automatically enhances sensory processing<sup>30</sup>. More work is needed to understand when to attribute stimulus-driven behavioural effects to involuntary temporal attention as opposed to other time-varying sensory processes, such as entrainment, and to determine how involuntary temporal attention relates to involuntary spatial attention<sup>31–34</sup> and alerting<sup>35–38</sup>.

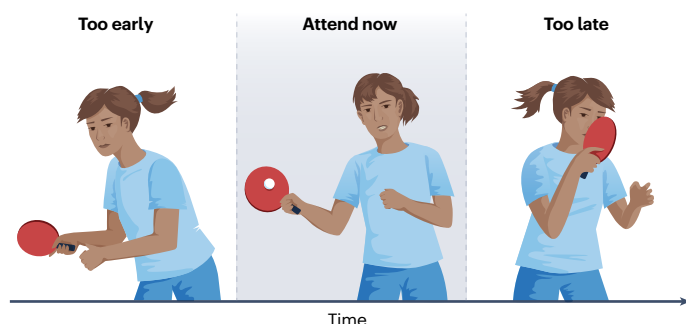
Voluntary temporal attention is the deliberate prioritization of points in time that are known in advance to be relevant to a behavioural goal<sup>27,39,40</sup>. Voluntary temporal attention can be flexibly deployed in the service of a wide range of natural behaviours, whenever the timing of visual input is predictable. It also has the advantage of being accessible to experimental manipulation, with a clear operational definition. As such, it is a useful starting place for investigating the effects of temporal attention on visual perception and for developing computational theories.

In this Review, I synthesize key concepts, data and models in the science of voluntary temporal attention. I first situate voluntary temporal attention within the broader landscape of dynamic attention, a landscape of diverse phenomena whose exact interrelations are still ripe for investigation. Next, I review results showing that temporal attention selectively influences visual perception, revealing temporal constraints in the ability to process ongoing visual input. I describe several proposals for processing limitations that could lead to selectivity. Finally, I review computational models of attentional dynamics and discuss productive future directions for the study of voluntary temporal attention and attention more broadly.

## Defining temporal attention

The term 'temporal attention' has been used to discuss a broad array of dynamic processes in visual perception and attention. To advance the study of temporal attention, it is important to establish working definitions of psychological concepts in this domain and to distinguish concepts with potentially distinct mechanisms. Doing so will enable more rapid progress in understanding the mechanisms underlying various aspects of dynamic perception and attention and will facilitate communication among researchers. I therefore start with a brief overview of phenomena that have been related to temporal attention, and dynamic attention more generally. In all cases, I consider only covert attention – attention without eye movements<sup>16,34</sup>. My goal in this section is to give working definitions for several concepts related to dynamic attention that are broadly consistent with the literature (although inevitably not every researcher will agree), including a definition of voluntary temporal attention that will set the stage for my subsequent discussion of its properties and mechanisms.

Defining attention has proved to be a fraught enterprise<sup>41–43</sup> and these definitional issues also affect temporal attention. I follow a tradition that defines attention as prioritized processing that is selective



**Fig. 1 | Temporal attention in the real world.** When returning a table tennis serve, it is critical to see well at the moment your opponent's paddle hits the ball, incentivizing increased visual attention at that moment. Attending slightly earlier or later would prioritize visual information that is less useful for enabling you to return the serve.

in nature, leading to behavioural tradeoffs across stimuli<sup>16,44,45</sup>. Thus, spatial attention is engaged when a prioritized location is enhanced at the expense of another location. Feature-based attention is engaged when a prioritized feature value (such as the colour red) is enhanced at the expense of another feature value (such as the colour green). Likewise, temporal attention is engaged when a prioritized time point is enhanced at the expense of another time point. These are all kinds of attentional selection in the Jamesian sense, in which attention implies withdrawal from unattended stimuli<sup>44</sup>. Whereas some authors have used ‘selection’ to mean guidance of behaviour<sup>46</sup> or simple enhancement of one item relative to another, I use it in the stronger sense of enhancements of some items yoked to impairments of others. Thus, attention should lead not only to improved performance for attended compared to unattended items but also to performance costs for unattended items, relative to a neutral baseline condition in which attention has not been directed to a particular item. To qualify as voluntary temporal attention further requires that prioritization be goal-directed (voluntary) and that temporal information be the basis for prioritization.

Temporal attention lies within a broader concept – the temporal dynamics of attention – that encompasses how selective prioritization along any dimension unfolds across time. Most studies of attention have used discrete stimulus presentations, which enables an organization of attentional dynamics according to whether they precede or follow a stimulus (Table 1). Pre-stimulus dynamics are proactive, requiring advance knowledge of the stimulus. These include the dynamics of voluntary spatial<sup>31–34</sup> and feature-based<sup>47</sup> attentional allocation, each with its own time course, as well as the dynamics of voluntary temporal attentional allocation<sup>48,49</sup>. Post-stimulus dynamics are reactive, with processing changes triggered by the onset of a stimulus. For example, involuntary spatial attention transiently enhances performance at the location of a salient stimulus onset<sup>31–34</sup>, which is followed by decreased performance at that location, called the ‘inhibition of return’<sup>50–52</sup>. These changes in spatial selectivity across time demonstrate the dynamics of spatial attention, as well as involuntary temporal attention when perceptual benefits are followed by perceptual costs in the same location<sup>53</sup>. In the attentional blink<sup>54</sup>, performance decreases following a task-relevant target stimulus when the second target is 200–500 ms after the first<sup>55–59</sup>, exhibiting temporal selectivity at the stimulus location. Thus, the attentional blink involves temporal attention, but not voluntary temporal attention: temporal information is not the basis for selection in the attentional blink, as targets are randomly timed and are selected based on an orthogonal dimension (such as colour).

Other processes also substantially change perception across time, but it is less clear whether they lead to selective information processing across time (Table 1). Phenomena in this group often have involuntary components. For example, performance is better when the interval between a warning cue and target (the foreperiod) is fixed across trials than when it is random<sup>9,60,61</sup>, which could be due to voluntary or involuntary anticipatory processes (proactive dynamics). Performance can also fluctuate rhythmically. In the presence of a rhythmic stimulus, performance improves at the expected rhythmic interval<sup>29,62–67</sup>, which could be due to voluntary or involuntary processes of rhythmic expectation (proactive dynamics) and/or to entrainment, an automatic elicitation of periodic neural responses to a rhythmic stimulus sequence<sup>66,68–70</sup> (reactive dynamics). Rhythmic performance fluctuations can also occur endogenously, in a stimulus-independent fashion, a phenomenon called sampling<sup>71–77</sup> (although aperiodic dynamics could also underlie some of these findings<sup>78</sup>).

Table 1 | Categorizing performance fluctuations across time

	Proactive dynamics	Reactive dynamics	Stimulus-independent dynamics
<b>Temporal, spatial and feature-based prioritization</b>	Voluntary temporal attention <sup>48,49</sup> Temporal interval expectation, foreperiod (hundreds of milliseconds to seconds) <sup>9,60,61</sup> Voluntary (endogenous) spatial attention (>300 ms) <sup>31–34</sup> Voluntary feature-based attention (>500 ms) <sup>47</sup>	Attentional blink (200–500 ms) <sup>55–59</sup> Involuntary (exogenous) spatial attention (~100 ms) <sup>31–34</sup> Inhibition of return (>300 ms) <sup>50–52</sup>	Not applicable
<b>Rhythmic processes</b>	Rhythmic expectation (hundreds of milliseconds to seconds) <sup>29,62–67</sup>	Rhythmic entrainment (hundreds of milliseconds to seconds) <sup>66,68–70</sup>	Rhythmic sampling (4–10 Hz) <sup>71–77</sup>
<b>Arousal</b>	Not applicable	Phasic alertness (100–500 ms) <sup>36</sup>	Tonic alertness (minutes to hours) <sup>79</sup>

Performance dynamics can be classified as proactive (preceding a stimulus), reactive (following a stimulus) or stimulus-independent (unrelated to a specific stimulus). Timescales in parentheses give the peak time or time range for each type of performance change, if established.

Finally, performance can vary across time owing to changes in arousal or alertness, broadly defined as a physiological state of readiness<sup>35–38</sup>. Phasic alertness is transient and stimulus-driven: for example, alertness might increase following a warning cue<sup>36</sup> (reactive dynamics). Tonic alertness fluctuates over longer timescales of minutes to hours<sup>79</sup> (stimulus-independent dynamics). Tonic alertness is often probed by continuous monitoring for rare targets<sup>35,80,81</sup>; when a target is missed or has a slow response, it has been called an attentional lapse<sup>37,82</sup>. Not all of these phenomena exhibit temporal selectivity. For example, stimulus rhythmicity can improve performance at an on-beat time without impairing it at an off-beat time, relative to a non-rhythmic condition<sup>8,64,69</sup>. Arousal can also involve enhancements at particular times without yoked impairments at other times – although there is evidence for a refractory period following phasic arousal<sup>83,84</sup>.

In summary, a variety of phenomena involve performance fluctuations across time, many of which have been associated with attention. Performance fluctuations can be classified as proactive, reactive and stimulus-independent. To relate these performance dynamics to attention, I have offered working definitions for the nested concepts of the temporal dynamics of attention, temporal attention and finally voluntary temporal attention. These definitions can be used to classify experimental manipulations and their behavioural effects. A full understanding of attention requires embracing its rich dynamic properties, which probably have a critical role in shaping natural behaviour<sup>10</sup>. In the following sections I detail how advance knowledge about upcoming stimulus timing enables an observer to deliberately and selectively prioritize that point in time.

## Temporal attention and temporal expectation

Voluntary temporal attention is goal-directed, so it requires the observer to have knowledge of which upcoming time points are likely to contain visual information relevant to achieving their behavioural goals. The time points that are most relevant can change depending on the goal, even for the same physical stimulus. For example, when someone throws a frisbee in your direction and your goal is to catch it, you must attend just before the frisbee reaches you so that you can make fine motor adjustments to grab it out of the air. But if your goal is to avoid getting hit by the frisbee, attending earlier to the broad trajectory of the disc will give you more time to move out of its path. Voluntary temporal attention therefore relies on both predictive information about the timing of future states of the world and knowledge of how task-relevant these upcoming moments are likely to be.

Thus, it is important to differentiate experimentally between the temporal predictability of a stimulus and its relevance to the observer's task goals. A given stimulus can be predictable or unpredictable and task-relevant or task-irrelevant, in any combination (Fig. 2). For example, an experimental trial might contain targets (task-relevant stimuli, requiring a response) and distractors (task-irrelevant stimuli, requiring no response), and either type of stimulus can be temporally predictable or unpredictable. A stimulus can also be partially predictable or sometimes relevant, and these contingencies can be described using probabilities. For each time point  $t$  during an experimental trial, there is a probability that a stimulus event will occur,  $P(X_t = \text{stimulus})$ , reflecting the predictability of the stimulus; and a probability that a target event will occur,  $P(X_t = \text{target})$ , reflecting relevance. These two probabilities define a space of experimental manipulations (Fig. 2a).

The probability that a stimulus will occur at a given time point is independent of whether it is a target, whereas every target is a stimulus. Nevertheless, the probability that a target will occur can be isolated using Bayes' theorem:  $P(X_t = \text{target}) = P(X_t = \text{stimulus})P(X_t = \text{target}|X_t = \text{stimulus})$ . Thus, the relevance of a time point (the probability that a target will occur), is the product of the probability that any stimulus event will occur and the probability that such an event will be task-relevant. This relationship of relevance and predictability means that targets cannot occur with higher probability than stimuli (Fig. 2a, no points in lower triangle). At the same time, the above application of Bayes' theorem shows that relevance can be manipulated independent of predictability by manipulating  $P(X_t = \text{target}|X_t = \text{stimulus})$ , the probability that a stimulus is a target (Fig. 2a, yellow points).

A unique feature of predictability and relevance in dynamic settings is that the probability that a stimulus or target will occur at the next moment in time can change depending on what has happened so far. For example, when waiting for a traffic light to turn green, the longer you wait, the more likely it becomes that the light will turn at the next moment. The probability that an event that has not yet occurred will occur in the next moment is the hazard rate<sup>85</sup>. It is useful for an observer to track the hazard rates of targets, which might depend strongly on stimulus history, and to take these changing probabilities into account when allocating attention<sup>8</sup>.

Similar to the distinction between predictability and relevance, there is a parallel distinction between the cognitive processes of temporal expectation and temporal attention. These terms have sometimes been used interchangeably in the literature, along with the term 'temporal orienting'<sup>26,29,86</sup>. Following a framework established in spatial and feature-based attention<sup>87,88</sup>, temporal attention is associated with relevance, whereas temporal expectation is associated with

predictability<sup>39,40,89,90</sup>. This conceptual framework links experimental manipulations to the terms used to describe cognitive processes, which might improve consistency of terminology among researchers, facilitating communication and aggregation of results. However, the importance of this distinction is not only terminological. In the spatial and feature-based domains, predictability and relevance have different, even opposite effects on neural responses<sup>87,88,91</sup> (although some authors have argued that such studies did not fully dissociate attention and expectation<sup>92,93</sup>), and might influence different stages of processing<sup>93</sup>, suggesting separate mechanisms. In the temporal domain, researchers are just beginning to investigate whether, when and to what extent temporal attention and expectation rely on shared versus separate mechanisms.

Many studies have manipulated temporal attention and expectation together in a protocol in which a single target is presented at a more or less predictable time, which makes different time points during the trial more or less likely to be task-relevant (Fig. 2b). I include these studies in the subsequent discussion of how temporal attention affects perception, although they do not disentangle temporal attention and expectation. Indeed, several of these papers describe their experiments as manipulating temporal expectation, rather than temporal attention.

## Temporal attention selectively affects perception

Voluntary temporal attention affects visual perception in a selective fashion. Attending to a point in time improves perceptual sensitivity at that time and impairs perceptual sensitivity at nearby unattended times, relative to a neutral attention condition in which observers are asked to attend to any possible target time point<sup>39,89</sup>. I discuss first how voluntary temporal attention leads to perceptual benefits at attended times and then how it leads to perceptual costs at unattended times, findings that imply limited computational resources for processing visual stimuli across time.

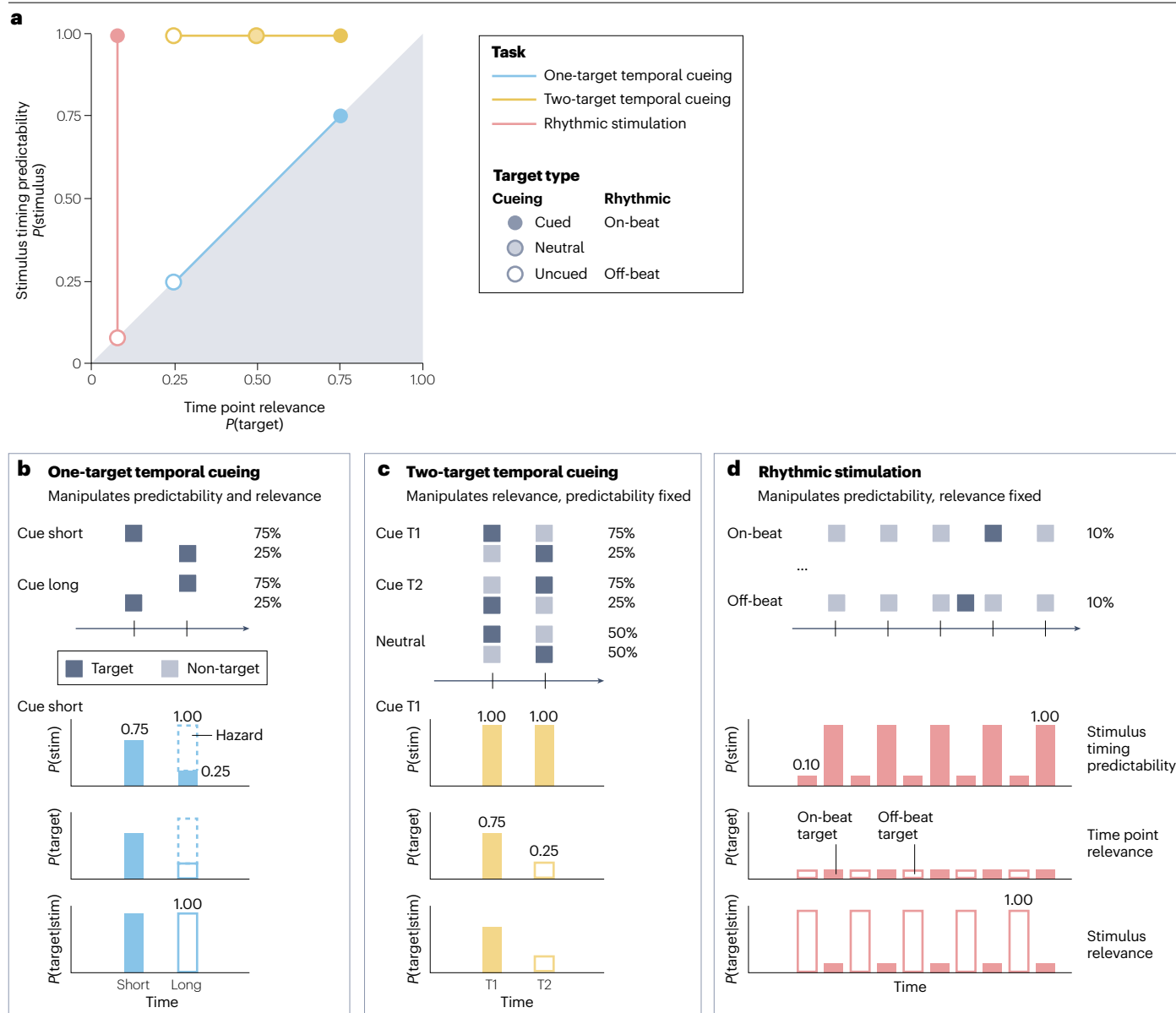
Beyond the scope of this Review, there is also a growing body of work on how temporal attention and expectation affect perception in non-visual sensory modalities<sup>94–97</sup> and interact with a range of behaviours and cognitive processes, from motor preparation<sup>98</sup> to working memory<sup>99–101</sup>.

## Benefits and costs of temporal attention

Voluntary temporal attention is an appealing research topic in part because it is straightforward to operationalize and manipulate experimentally. In a common temporal cueing protocol, a cue at the start of a trial informs the observer when a target stimulus is likely to appear, enabling the observer to voluntarily attend to that task-relevant time point<sup>6,8,9,11</sup> (Fig. 2b,c). The physical stimuli and task requirements remain constant and only the timing of attention changes, which enables researchers to attribute any changes in behaviour or neural activity that depend on the cue to temporal attention. Further, cueing target timing on a trial-by-trial basis increases confidence that the observer's anticipation of target timing is under voluntary control rather than implicitly learned across trials, which can occur when predictable cue–target intervals are fixed or blocked. I focus on temporal cueing rather than rhythmic expectation (Fig. 2d) because of the difficulty of attributing rhythmic effects to voluntary or involuntary processes. Furthermore, there is evidence for distinct mechanisms involved in rhythm-based versus interval-based expectation<sup>69,102–104</sup>.

Early studies showed that temporal cues speeded reaction times to targets that occurred at anticipated times<sup>6,11,15,26,105</sup>, but





**Fig. 2 | Experimental manipulation of timing predictability and relevance.**

**a**, Predictability × relevance space. For a given time point  $t$ , the probability that any stimulus occurs is plotted against the probability that a task-relevant stimulus (target) occurs. Each point corresponds to an experimental condition, and lines connect conditions compared within an experimental task. Probabilities are therefore conditioned on experimental condition. Along the diagonal, all stimuli are targets. The grey lower triangle is a disallowed area: targets cannot be more probable than stimuli. **b–d**, In cueing tasks (**b**, **c**), a cue at the beginning of the trial instructs the observer when a target stimulus is likely to appear. Note that in the two-target design (**c**), either stimulus can be a target,

but only one is probed for report. In the rhythmic task (**d**), targets appear on-beat or off-beat with equal probability, so the rhythm does not predict target timing. At the top of panels **b–d**, trial sequences are shown; each row is a condition. Percentages indicate how often each type of trial occurs (per cue condition for cueing tasks). At the bottom of panels **b–d**, probabilities of stimulus and target occurrence at each time point are shown for example conditions. Filled bars (target) and unfilled bars (non-target) show the probabilities known to the observer at the start of the trial, just after the cue is presented for cueing tasks. Dashed bars labelled 'hazard' show differences between these initial probabilities and the hazard function.

these effects could have been due either to facilitated perception or increased response preparation<sup>106</sup>. EEG measurements found reliable cue-related changes late (~300 ms after target onset) in target-evoked responses<sup>14,15</sup>, and neuroimaging studies of temporal cueing found

activity in motor-related regions<sup>6,26</sup>, making response preparation the preferred account for those early data.

However, studies using more sensitive perceptual tasks have since found clear evidence that temporal attention and/or expectation

(some studies manipulated them together) influence visual detection and discrimination. Temporal cueing improved accuracy and perceptual sensitivity ( $d'$ ) at cued relative to uncued time points<sup>39,49,89,90,106–115</sup>. In attentional blink tasks, cueing the time of the second target improved accuracy in reporting that target<sup>48,116,117</sup>. However, cued expectation in a detection task speeded reaction times without increasing the estimated rate of evidence accumulation<sup>118</sup>, suggesting that temporal expectation does not always improve the quality of sensory evidence. Temporal cueing also affects neural activity and other physiological measures associated with sensory processing, suggesting

## Box 1

### Neural mechanisms of temporal attention and expectation

Neurophysiological measurements have revealed effects of temporal cues on sensory processing, consistent with an effect on visual perception. Temporal expectation enhances visual evoked responses as early as 100 ms after a target is shown. This finding has been observed in human electroencephalography (EEG) using a difficult perceptual task<sup>109</sup> as well as in monkey inferior temporal cortex when the monkey was trained to expect object images at particular time intervals<sup>203</sup>. In addition, in an EEG study, orientation decoding for a target quickly followed by a distractor was prolonged when the timing of the target was cued by a warning signal<sup>204</sup>, though in a functional magnetic resonance imaging (fMRI) study, warning signals decreased blood-oxygen-level-dependent (BOLD) responses in V1<sup>205</sup>.

Temporal expectation also influences visual cortical activity in advance of a target. Pre-stimulus occipital alpha power decreased in accordance with the timing and location of a spatiotemporal precue<sup>111</sup>. Pre-stimulus alpha phase was also found to depend on a temporal precue<sup>108</sup> as well as fixed temporal predictability<sup>206</sup> (though this has not always been observed<sup>207,208</sup>). Finally, warning signals and their associated hazard functions changed visual cortical activity<sup>209–212</sup> and occipital alpha power<sup>103,104,213</sup> leading up to a target. In all of these studies, the predictability of stimulus timing was manipulated, and the stimulus was always task-relevant. Thus, temporal expectation can affect sensory responses to visual targets and anticipatory responses in visual areas.

Investigations of physiological mechanisms have begun to distinguish between temporal expectation and temporal attention. Studies of microsaccades (small fixational eye movements) have found that the eyes freeze before an expected target time for visual<sup>40,213–216</sup> as well as non-visual<sup>97,217</sup> targets. When two or more predictable visual targets appear in sequence, temporal attention shifts the timing of this oculomotor freezing around the time of the cued target<sup>40,127</sup>. One study reported a similar pattern in neural activity: anticipatory responses before an expected target time, which were modulated by whether that target was temporally attended<sup>126</sup>. Thus, temporal attention can influence microsaccades and neural activity over and above temporal expectation. Future work should continue to test whether temporal attention and expectation have distinct neural mechanisms.

possible mechanisms for the basic perceptual changes demonstrated psychophysically (Box 1).

Other manipulations have also revealed how predictive temporal information can improve perception. Rhythmic temporal expectation increased contrast sensitivity<sup>65,119</sup>, and expecting a target at a short (versus a long) interval after a warning signal increased spatial acuity, a finding attributed to reduced temporal uncertainty at the short interval<sup>120</sup>. Spatiotemporal regularities improved target detection in visual search<sup>121,122</sup>. And target timing information provided by a countdown could be used to model contrast thresholds for orientation discrimination<sup>123</sup>. These findings build on important early work showing that reducing temporal uncertainty improved perceptual sensitivity in basic visual detection<sup>124</sup> and discrimination<sup>125</sup> tasks.

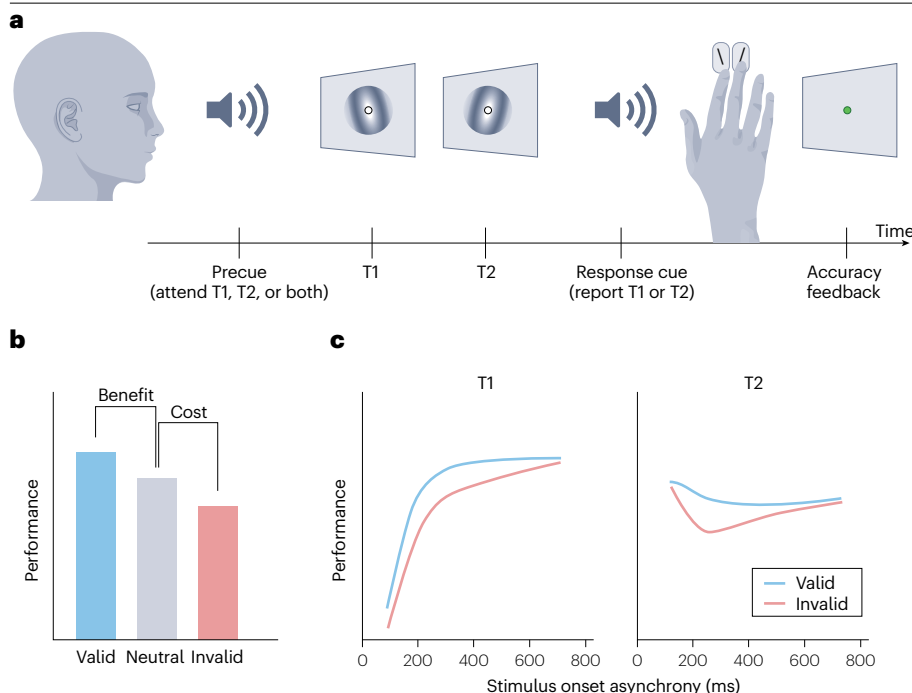
A few studies have disentangled the effects of temporal attention and expectation on perception by presenting two targets sequentially in the same spatial location on each trial, with a cue that informs observers which of the two targets is more likely to be probed for a report at the end of the trial<sup>39,89,90,115</sup> (Figs. 2c, 3a). Because both targets always appear with perfectly predictable timing, expectation is fixed across trials. However, voluntary temporal attention varies from trial to trial with the cue. These two-target temporal cueing studies have shown that voluntary temporal attention affects perceptual sensitivity over and above temporal expectation (Fig. 3b,c).

One question that arises with the two-target design is whether observers prioritize cued targets on the basis of absolute time or temporal order. Eye tracking and neural measurements in this task have shown anticipatory signals that depend on voluntary temporal attention, consistent with attending to an absolute time<sup>40,126,127</sup> (Box 1). An interesting topic for future research is whether observers also use order or can flexibly adjust to rely more on order or time.

Voluntary temporal attention does not simply enhance behavioural performance (similar to the effects of arousal); rather, it mediates a selective process that prioritizes some moments in time over others. Observers seem unable to sustain attention (or some aspect of visual processing) maximally across short time intervals, even when they are instructed to do so<sup>39,89,90,108</sup>. Such tradeoffs show that attention is selective in time<sup>39,89</sup>. Selectivity has been considered a hallmark of attention<sup>16,44,45</sup>, and the selectivity of temporal attention mirrors that of spatial attention. In both domains, attentional cueing leads to selective processing even in sparse displays of just two items (separated in either space<sup>128–130</sup> or time<sup>39,89,90</sup>).

#### Limited resources across time

Perceptual tradeoffs, particularly under minimal stimulus conditions, imply limited resources for processing visual stimuli across time. A psychophysical study showed that the effects of voluntary temporal attention on perceptual sensitivity peak when stimuli are separated by about 250 ms and dissipate at very short (100 ms) as well as at longer intervals<sup>89</sup>. When stimuli were separated by as long as 800 ms, performance was high, and temporal cueing had no effect (Fig. 3c). Whatever the limited resource is, it seems to be limited on a timescale of a few hundred milliseconds. This timescale matches that of the attentional blink and of temporal crowding<sup>131</sup> but is longer than the intervals classically associated with masking<sup>132</sup>. This timescale is also consistent with the timescale of saccadic eye movements: 2–3 Hz (ref. 133). Speech rates across languages are around 4–5 Hz, and the amplitude spectra of music peak around 2 Hz (ref. 134). Such observations raise the question of whether the similarities in timescales across domains are incidental or whether they reflect some core underlying timescale of information processing in the human brain.



**Fig. 3 | Visual temporal attention selectively affects perception.** **a**, In each trial, two targets are presented in sequence, and observers are instructed via a precue to attend to the first, to the second or to both targets. The task of the observers is to discriminate the orientation of the target probed by the response cue at the end of the trial. The precue informs them which target will be probed with 75% validity. In valid trials, observers are asked to report the same target they were instructed to attend and in invalid trials observers must report the target that was not attended. In neutral trials, the precue is uninformative and the response cue probes each target with equal probability. **b**, Characteristic performance accuracy averaged across two targets for a 250-ms stimulus onset asynchrony shows that voluntary temporal attention is selective: manipulating temporal attention leads to both perceptual benefits at attended times and costs at unattended times. **c**, Characteristic performance accuracy as a function of the stimulus onset asynchrony. Temporal attention affects perceptual sensitivity only at intermediate stimulus onset asynchronies. Thus, temporal attention governs perceptual tradeoffs across subsecond time intervals. Part **a** and **c** adapted from ref. <sup>89</sup>, Springer Nature Limited.

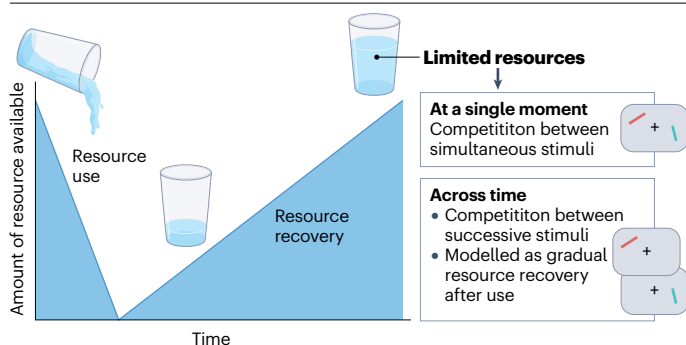
The term ‘limited resources’ has commonly been used to express the general notion of biological constraints that prevent humans from fully processing all sensory information at all times<sup>16,17,135</sup>. Indeed, there are probably many biological constraints. In the spatial domain, limited resources have been proposed at multiple loci, including competition between stimuli that fall within the same receptive fields of ventral stream neurons<sup>17,136–138</sup>, competition between the two brain hemispheres<sup>139,140</sup>, competition for working-memory representation<sup>141,142</sup> and bioenergetic constraints<sup>143</sup>. Limits at the level of cognitive control have been proposed to arise from overlapping task-related representations<sup>144</sup>. Some of these possibilities could apply to the time domain as well. Competition within visual receptive fields might apply if a neuron’s temporal receptive field<sup>145,146</sup> integrates over long enough time windows that responses to successive stimuli nonlinearly interact<sup>147,148</sup>. Following this logic, classic notions of biased attentional competition between simultaneously presented stimuli could be extended to capture the impact of attention on competition between sequentially presented stimuli, effectively implementing biased competition across time. However, some constraints in the spatial domain are not relevant for time: for example, competition between hemispheres is not expected to limit sequential stimulus processing. Other kinds of constraint, such as interference between feedforward and feedback activity<sup>149</sup> or constraints that lead to slow, serial processing of sequential stimuli<sup>150–152</sup>, might be specific to the time domain.

Although voluntary temporal attention differs in important ways from the attentional blink, both phenomena involve prioritization of stimuli at one moment in time accompanied by impairments of stimuli at other moments, across similar time intervals. Thus, although the mechanisms of voluntary temporal attention might differ from the mechanisms underlying the attentional blink, this literature offers theories of limited resources that could underlie the basic difficulty in reporting two sequential targets – the same difficulty that makes

it useful to selectively attend in time. Explanations of the attentional blink generally involve delayed or suppressed attentional enhancement of the second target<sup>59</sup>, failure to encode the second target into working memory<sup>153</sup> or both<sup>154,155</sup>. There is little evidence for neural changes at the earliest stages of visual processing (<150 ms)<sup>155</sup> (although one study showed that early neural representations of the second target predicted second target accuracy<sup>156</sup>).

Theories of the attentional blink have primarily proposed limitations at later, post-sensory processing stages, including constraints on working-memory encoding<sup>154,157</sup> and on activating a global workspace<sup>158–160</sup>. Similar central bottlenecks have been proposed to underlie the ‘psychological refractory period’<sup>150,151,161,162</sup>, in which responses to the second of two sequential targets are slowed when the two targets are separated by less than 500 ms (refs. <sup>150,163–165</sup>). One theory proposed that rather than a central bottleneck, successive episodes of target-driven attentional enhancement cannot occur too close together owing to a refractory period in the locus coeruleus and noradrenaline system that is involved in phasic alerting<sup>84</sup>. This account might predict that voluntary temporal attention would change pupil size<sup>166</sup>, but so far this prediction has not been confirmed<sup>167</sup>. At first glance, proposals for limited resources at a later, more central stage of processing seem at odds with findings that voluntary temporal attention and expectation affect early sensory responses and anticipatory responses in sensory areas. One possible resolution is that when stimulus timing is predictable, limited resources could be strategically allocated by modulating responses at the sensory level. Such sensory modulation would bias what stimulus information reaches the limited processing stage.

One way to conceptualize a limited resource across time is as a continuous resource that is used and then gradually recovers as time passes (Fig. 4). An alternative possibility is a discrete resource, which would be fully occupied for some duration and then become



**Fig. 4 | Limited resources across time.** Performance reductions when processing sequential visual stimuli indicate that limited resources are available for perception and/or attention across time. Like water poured out of a glass that is then gradually refilled, once resources are used, they take time to become available again (blue area on graph), according to continuous resource models.

fully available again after a delay (as in a bottleneck). In either case, the key idea is that neural resource use takes time and resource recovery is not instantaneous. Thus, accounts of dynamic attention have emphasized how stimulus processing extends across time and interacts with ongoing attentional modulation<sup>168</sup>. However, the temporal dimension of resource limitation is not obvious from conceptions of limited resources developed for spatial attention (which describe how resources are allocated across space at a single moment)<sup>17,137,169</sup>. An interesting open question is whether some limited resources are fundamentally spatiotemporal (for example, owing to competition within spatiotemporal receptive fields). Important tasks for future research will be to continue to develop proposals for limited resources across time, make them concrete at a computational level, and link them to behaviour and to neural mechanisms.

## Computational models of temporal attention

Mathematical and computational models have various advantages over verbal theories: they are precise, they make quantitative predictions and they can facilitate the development and communication of theoretical ideas. Even if two scientists disagree about the definition of voluntary temporal attention, they can agree on which model better fits the data.

Computational models of visual attention differ in how they incorporate attentional dynamics (Table 2). The major classes include: static models; models with dynamic components but no attentional dynamics; models with reactive attentional dynamics but no ability to prioritize upcoming time points; and models of voluntary temporal attention.

Many models of visual attention are static, with no time-varying components. Several of these models implement interactions between attention and normalization<sup>169–174</sup> (for a review with mathematical detail, see ref. 175). Normalization produces competitive interactions between neighbouring neural populations via divisive suppression<sup>176,177</sup>. The consequence is larger responses to parts of an image that vary across space (such as an edge) and smaller responses to uniform parts of an image. One of the most successful static attention models is the normalization model of attention (developed in ref. 169), in which attention modulates the gain of stimulus input to neurons before normalization. In this way, attention biases the competitive

interactions within a neural neighbourhood to favour an attended stimulus. This model can account for a wide range of behavioural and neural data<sup>169,178–180</sup>. However, it has no time-varying components, so it cannot handle dynamic sensory input or attentional dynamics.

The first step toward a model of dynamic perception and attention is incorporating time-varying stimulus input. This functionality requires a model with dynamic components, such that stimulus dynamics drive model dynamics. Two prominent attention modelling frameworks, competitive interaction theory<sup>175,181,182</sup> and the theory of visual attention<sup>183–185</sup>, have dynamic components for visual processing without modelling attentional dynamics themselves. Competitive interaction theory<sup>175,181,182</sup> implements normalization consistent with static normalization models. However, this model is dynamic and can handle time-varying stimuli. The role of attention in the model is to modulate the rate of stimulus encoding into working memory, enabling the model to predict how spatial attention influences reaction times and interacts with masking. The model has also been adapted to capture salience representations in the frontal eye field<sup>186</sup>. Generally, in applications of this theory to spatial attention, attention has been modelled as varying across space but being static in time, though in one instance, attention was modelled to function as a gate that opened earlier or later depending on spatial attention<sup>182</sup>. The second modelling framework, the theory of visual attention<sup>183–185</sup>, describes how the probability of categorizing a stimulus varies across time, which in turn depends on the rate of working-memory encoding. This model captures many results relating to spatial attention<sup>183–185</sup> and some temporal phenomena<sup>187</sup>. As in competitive interaction theory, the model implements spatial attention via different encoding rates at attended versus unattended locations. Although attention is not time-varying in this model, it has been adapted to model the effects of a fixed hazard rate on letter identification<sup>188–190</sup>.

Models that specify the dynamics of attention in response to a target stimulus, or reactive attentional dynamics, provide a step forward by including time-varying attention. The attentional dynamics for these models depend on whether a stimulus is task-relevant (unlike involuntary attention, which is usually understood to be purely stimulus-driven<sup>16</sup>). These models explain behavioural data from tasks in which observers must first detect an unpredictable target and then report subsequent stimuli presented within a rapid visual stream. They formalize the notion that attention and working-memory encoding are episodic (empirical support reviewed in ref. 168). An early model of reactive dynamic attention is the attention gating model<sup>145,191,192</sup>. The model describes a time-varying attentional function that gates items into working memory, with each instantiation of the gating function termed an attentional episode. This model could explain both which stimuli were reported from a rapid visual stream and in which order. An influential model of the attentional blink called the simultaneous type/serial token model also models reactive attentional dynamics that determine the gain of stimulus input to working memory<sup>154,193–195</sup>. Attention is enhanced by the appearance of a target and suppressed during working-memory encoding, which generates the attentional blink; the periods of enhancement constitute attentional episodes. This model can explain the basic attentional blink phenomenon along with several variations<sup>154</sup>.

Finally, models of voluntary temporal attention include proactive attentional dynamics, or the dynamics of attending to a point in time that the observer knows in advance will be relevant for their task. The normalization model of dynamic attention describes how neural population responses depend on time-varying sensory input



and time-varying attention within a recurrent neural network<sup>89</sup>. It generalizes the normalization model of attention<sup>169</sup> into the time domain, so it inherits that static model's ability to explain a wide variety of behavioural and neural data from spatial and feature-based attention tasks<sup>169,178,179</sup>. The role of attention in the dynamic model is to dynamically modulate the gain of sensory responses. Importantly, this model implements voluntary temporal attention by increasing gain at anticipated task-relevant time points and implements involuntary attentional dynamics via a recurrent circuit that changes gain in a stimulus-driven fashion<sup>89</sup>.

To explain limited resources over a timescale of a few hundred milliseconds<sup>39,89,90</sup>, the normalization model of dynamic attention includes a constraint on the availability of voluntary attentional gain over short timescales<sup>89</sup>. Voluntary attentional gain is modelled as a limited resource that takes time to recover to baseline levels once used (Fig. 4). As a consequence, fewer resources are available to distribute when targets are separated by shorter time intervals, and the model strategically allocates gain to the most relevant target, mediating perceptual tradeoffs between the targets. When the targets are distant enough in time for resources to fully recover, maximum attentional gain can be allocated to both targets and there are no tradeoffs. Fitting this model to psychophysical data produced an estimate for the recovery time of attentional gain of about 900 ms (600–1,000-ms confidence interval)<sup>89</sup>. This finding provides a quantitative estimate of the timescale over which limited resources operate and can be governed by voluntary temporal attention. This interval is shorter than the rhythmic interval at which observers are best able to extract a visual rhythmic pattern and predict the timing of an upcoming target (about 1.4 s)<sup>196</sup>, and therefore suggests a further distinction between rhythmic expectation and voluntary temporal attention<sup>29,102,103</sup>. In the future, it will be important to determine the generality of the timescale identified for voluntary temporal attention across other stimuli and tasks and to empirically test the limited gain mechanism underlying tradeoffs in the model. As a testable theory of voluntary temporal attention and its selectivity in time, the normalization model of dynamic attention offers a further step toward a theoretical understanding of the mechanisms and limits of dynamic attention.

The models featured in this section capture several major efforts to model dynamic attention and how attention influences visual dynamics

(for further models in this domain see refs. 98,197–200). They vary in whether and how they support time-varying stimuli and time-varying attention; in the functional role of attention; and in the type and timing of attentional dynamics (Table 2). Perhaps not surprisingly, given the diversity of phenomena that have been related to dynamic attention, each model has been applied to explain behavioural data from different types of experiment. However, a benefit of computational models is that they make predictions that can be tested experimentally. An important future research direction will be to determine and assess such predictions, testing how well different models generalize across stimuli and tasks. Doing so will ideally lead to convergence on modelling frameworks that predict and explain a wide array of behavioural and neural data.

Other theoretical treatments of dynamic attention that are not formulated mathematically can still integrate large bodies of literature. For instance, the unified diachronic account of attentional selectivity<sup>168</sup> posits that voluntary attention (including voluntary temporal attention) enhances early perceptual processing, which in turn speeds decision processes that trigger the initiation of transient attentional enhancement (an attentional episode<sup>88,154,168,192</sup>) following the appearance of a target. Thus, this account also connects voluntary temporal attention and reactive attentional dynamics, but not in a mathematical formalization.

Summary and future directions

Voluntary temporal attention enables the prioritization of visual information at moments in time that are most relevant for one's behavioural goals. Anticipating these relevant moments requires exploiting the predictable temporal structure of upcoming events<sup>8</sup> and interactions with the environment to develop temporal expectations about how the visual world will unfold. Experimental manipulation of the task relevance of specific time points has shown that temporal attention increases response speed and perceptual sensitivity<sup>39,89,90,106–108,110</sup>. Improvements in perceptual sensitivity at attended times are accompanied by impairments at unattended times within several hundred milliseconds, demonstrating that temporal attention is selective in time<sup>39,89</sup>. Several modelling frameworks capture aspects of dynamic perception and attention<sup>45,154,175,187,197</sup>, and one model captures voluntary temporal attention to task-relevant points in time<sup>89</sup>.

Table 2 | Models of visual attention and attentional dynamics

	Time-varying attention	What attention influences	Attentional limits across time	Reason for limits
Static models				
Normalization model of attention <sup>169</sup>	No	Sensory gain	Not applicable	Not applicable
Dynamic models				
Competitive interaction theory <sup>175,181,182</sup>	Rarely implemented	Rate of working-memory encoding	None	Not applicable
Theory of visual attention (TVA) <sup>183,184,187</sup>	No	Rate of working-memory encoding	None	Not applicable
Attention gating model (AGM) <sup>45,191,192</sup>	Yes, reactive	Gating into working memory	Attentional episodes	Limited working memory
Episodic simultaneous type/serial token (eSTST) <sup>154,195</sup>	Yes, reactive	Input gain	Attentional episodes/Involuntary suppression of working-memory encoding	Limited working memory
Normalization model of dynamic attention <sup>89</sup>	Yes, voluntary and involuntary	Sensory gain	Limited availability of attentional gain	None proposed

## Box 2

### Considering unitary attention

The fractionation of attention into types — temporal attention, spatial attention, feature-based attention and object-based attention — naturally leads one to wonder whether and when a unitary construct of attention is valuable<sup>45,46</sup>. Because it is a psychological construct, there might not be a single answer as to what attention is or is not<sup>41,42</sup>. However, different formulations of attention have more parsimony and power to explain experimental observations. At times it is useful to split the concept of attention into categories and subcategories and at other times it is useful to conceptualize attention as a unitary construct.

A growing body of research has shown that temporal and spatial attention affect perception in common ways. For example, temporal anticipation (broadly defined) and spatial attention both affect orientation discrimination, contrast sensitivity and acuity<sup>16,39,65,89,90,113,115,120,129,179,218,219</sup>. However, there are many empirical gaps in the temporal domain and few studies have performed direct comparisons between temporal and other types of attention for the same observers and tasks. One study directly compared temporal and spatial cueing and found that temporal cueing improved temporal integration of two successive images, whereas spatial cueing improved both integration and segregation<sup>220</sup>. Other findings also suggest a difference in the speed with which temporal and other types of attention can be voluntarily allocated. Whereas spatial attention takes 300 ms (refs. 31–34) and feature-based attention 500 ms (ref. 47) to be fully allocated, performance improvements can occur as early as 100–150 ms after a temporal cue<sup>48,49</sup>. These differences in allocation speed suggest differences in the control mechanisms for different types of attention.

Distinct control mechanisms for temporal attention are also supported by neural studies<sup>6</sup>. For example, activity in the left inferior parietal cortex is consistently found in temporal cueing tasks<sup>6,110,221–223</sup>. Neural activity anticipating a task-relevant time has also been observed in the cerebellum<sup>224</sup>, a structure that is causally involved in generating improvements in both reaction time<sup>225</sup> and perceptual sensitivity<sup>226</sup> with interval-based temporal expectation.

Existing data indicate that in many but not all cases, temporal and spatial attention have similar effects on behaviour and can interact to improve visual processing at a behaviourally relevant place and time<sup>63,107</sup>. However, the brain networks involved in temporal and spatial attention differ<sup>6,201</sup>, and given the relative paucity of research on visual temporal attention, it is still far from clear when it is useful to think of temporal and spatial attention as separate processes and when as two aspects of a unitary process of attention (Box 2).

There are rich opportunities for future research into temporal attention. Basic questions about how voluntary temporal attention influences different aspects of visual perception — from lower-level visual abilities like contrast sensitivity and acuity to higher-level ones like object and scene processing — are ripe to address with psychophysical studies. As our understanding of how humans temporally attend to the simplest kinds of dynamic display grows, stimuli and tasks with greater

Joint manipulations of different types of attention could shed light on whether those attentional manipulations depend on distinct or shared mechanisms<sup>227</sup> and further probe the usefulness of attention as a unitary construct. Joint manipulations of temporal and spatial attention or expectation have found combined effects of predictive information about space and time<sup>11,36,63,107,228,229</sup>, with better performance using both temporal and spatial predictability than either one alone. Combined effects of temporal expectation and spatial or feature-based attention have also been demonstrated at the neural level<sup>63,210–212,230</sup>, with interactive effects interpreted as a potentiation of other types of attention by temporal attention. However, temporal expectation changed V1 neuronal responses even at task-irrelevant spatial locations<sup>209</sup>, indicating that effects of temporal expectation are not strictly gated by other types of attention. As it has not always been possible to distinguish attention and expectation in these studies, it will be important to do so in future experiments by manipulating them independently.

Going forwards, it might be useful to distinguish between common computational principles and common neural mechanisms. Many neural mechanisms, operating on different aspects of visual information and at multiple levels of neural processing, might interact to prioritize some visual information at the expense of other information. Experiments that carefully manipulate the task relevance of specific points in time (alone or in combination with other visual dimensions) and in a variety of task contexts will be required to parse out the shared and distinct mechanisms of different types of attention. At the same time, distinct neural mechanisms can be consistent with shared computational principles at a higher level of abstraction. For example, it seems that temporal and other types of attention regulate competition among stimulus representations for limited processing resources in a way that has, in some cases, been captured by normalization models. At an even more abstract psychological level, a large number of experimental observations are consistent with the notion that attention is selective<sup>16,45</sup>.

dynamic complexity can facilitate an understanding of how attention dynamically interacts with the rich temporal structure of natural vision and behaviour, including temporal structure that depends on eye and body movements. Likewise, the neural mechanisms that control the allocation of temporal attention and alter perception and behaviour at attended times still require investigation.

A recognition of the distinct operations involved in predicting the timing of an upcoming stimulus (temporal expectation) and prioritizing that time as task-relevant (temporal attention) will facilitate experimental designs that independently manipulate these two processes to discover their shared and distinct behavioural effects and neural mechanisms. Maintaining this conceptual distinction has already revealed the selectivity of voluntary temporal attention<sup>39,89</sup>, which accords with phenomena like the attentional blink. Such observations raise questions about the computational and neural sources of limited resources

across time. On the behavioural front, experimental designs that disentangle temporal attention and expectation will enable investigations to determine their coordinated and separate effects on perception. On the neural front, more work is needed to relate anticipatory changes in advance of a target to changes in sensory responses following a target, to understand how temporal attention and expectation affect neural responses throughout the visual hierarchy, and to relate these changes in neural activity to perception and behaviour.

Finally, there is considerable opportunity for the development of theories and models of dynamic perception and attention. Most models of vision and visual attention are static, but there are efforts to expand such models into the dynamic realm<sup>45,89,154,175,187,197</sup>. Modelling attention as one or more latent variables to predict behaviour and neural activity will also help to inform us when it is useful to model attention as unitary or as multiple types. A virtuous cycle of empirical and modelling work will advance the understanding of visual attention as a dynamic phenomenon, working towards a major goal of movie-computable vision models that can handle both stimulus and task inputs<sup>202</sup>. Such models might one day enable prediction of the ebb and flow of human attention in a world in which change is always expected.

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## Competing interests

The authors declare no competing interests.

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