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Time for the Fourth Dimension in Attention

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Abstract and Keywords

This chapter takes attention into the fourth dimension by considering research that explores how predictive information in the temporal structure of events can contribute to optimizing perception. The authors review behavioural and neural findings from three lines of investigation in which the temporal regularity and predictability of events are manipulated through rhythms, hazard functions, and cues. The findings highlight the fundamental role temporal expectations play in shaping several aspects of performance, from early perceptual analysis to motor preparation. They also reveal modulation of neural activity by temporal expectations all across the brain. General principles of how temporal expectations are generated and bias information processing are still emerging. The picture so far suggests that there may be multiple sources of temporal expectation, which can bias multiple stages of stimulus analysis depending on the stages of information processing that are critical for task performance. Neural oscillations are likely to provide an important medium through which the anticipated timing of events can regulate neuronal excitability.

Keywords: temporal expectations, temporal orienting, spatial attention, entrainment, active sensing, communication through coherence, neural oscillations

SELECTIVE attention, understood as the processes that focus neural processing in service of current goals and requirements, is inherently and necessarily dynamic. As we navigate along, our receptor surfaces move, events in the environment unfold, and the relationships between our receptors and events change. Ironically perhaps, our core theoretical and computational models of attention are primarily static. They consider mechanisms for selecting relevant or conspicuous target events and inhibiting irrelevant or interfering distraction within freeze-frame instants of experience. As the many chapters in this Handbook attest, tremendous progress has been made in revealing these snapshot mechanisms of attention control and modulation at various levels of organization. However, still largely missing is the consideration of whether and how predictive information in the temporal structure of events can contribute to optimizing perception.

Considering how predictive temporal information can influence perceptual analysis necessitates contemplating new types of modulatory mechanisms. To date, most snapshot mechanisms revealed to enhance perceptual analysis involve regulating and coordinating neuronal excitability according to receptive field properties in anticipation of relevant events. However, we still understand little about whether and how receptive field properties are specifically tuned to temporal intervals within sensory areas. Furthermore, it is unclear how pre-activation of neurons with temporal specificity would preserve temporal estimates. How then can the anticipated timings of relevant events be used to regulate neuronal excitability during perceptual analysis? This chapter reviews the early steps of a burgeoning literature addressing this intriguing and fundamental question.

Early Studies
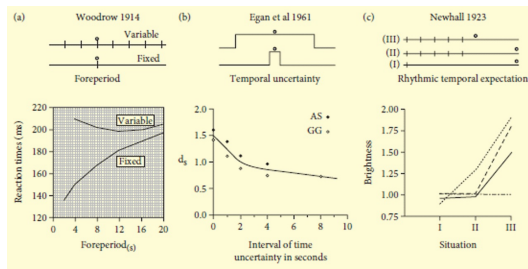
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Figure 24.1 Pioneer investigations on the effect of time in perception and action. (a) Effect of regular and irregular foreperiods on reaction times found by Woodrow (1914: 43). Foreperiod intervals are presented on the X-axis, and reaction times on the Y-axis. The upper curve represents the results with irregular foreperiods, showing consistently high reaction times. The lower line shows faster reaction times with regular foreperiods, which also increase as foreperiods are lengthened (attributed to increasing difficulty to estimate longer intervals accurately). Adapted from Woodrow H., *The Measurement of Attention*, p. 43 © 1914, Whitefish. (b) Results reported by Egan et al. (1961: 774) showing decrements in discriminability (ds) performance as a function of increasing temporal uncertainty. Markers indicate mean values for each observer (AS and GG). Adapted from *Archives of Psychology* 61, Newhall, S. N., Effects of attention on the intensity of cutaneous pressure and on visual brightness pp. 5–75, 1923. (c) Subjective brightness report for each participant in the three experimental conditions ('Situations') presented in Newhall (1923: 60). 'Situations' represent different levels of temporal expectation, from high (III) to low (I). Adapted from, *The Journal of Acoustical Society of America* 33(6), Egan, J. P., Greenberg, G. Z., Schulman, A. I., Interval of Time Uncertainty in Auditory Detection, pp. 771–778 © 1961, Acoustical Society of America.

The role played by the temporal structure of events in guiding perception was not always ignored. The temporal interval between events, known as the foreperiod, has long been acknowledged to be one of the main determinants of response speeds in a variety of (p. 677) tasks (see Teichner 1954; Niemi and Näätänen 1981). According to our reading, Wilhelm Wundt (1874/1904) may have been the first to show that response times are faster in the presence of a warning signal that predicts the occurrence of a target after a constant and predictable interval. He gave participants the task of releasing a key upon hearing the sound of a steel ball hitting a metal plate. They were significantly faster when they had the opportunity to view the release mechanism that dropped the ball. (The foreperiod was manipulated by adjusting the height of the release mechanism.) Extending Wundt's investigation, Woodrow (1914) manipulated the regularity of the interval between a warning signal and a target on a trial-by-trial basis. Response times were faster when intervals were constant and predictable, than when they were variable and unpredictable (Fig. 24.1a). Subsequent investigations showed that though benefits are larger when the nature of the stimulus and response are predetermined, they also occur in choice reaction-time tasks when the identity of the stimulus and the response remain uncertain (Bertelson and Boons 1960). (p. 678)

Benefits carried by temporal prediction in these early tasks were usually interpreted as resulting from increases in the level of readiness of a general type of attention. The degree of preparation was proposed to increase as certainty of the foreperiods increased and as the length of the foreperiod on a particular trial increased (Woodrow 1914; Karlin 1959). An alternative account proposed an additional specific process of temporal 'anticipation', in which the prospective intervals of events are estimated from the time of warning cue (Nickerson 1965; Snodgrass 1969).

Egan et al. (1961) developed a simple and elegant design to explore further the role of temporal un/certainty in perception. They varied temporal expectation parametrically across experimental blocks by presenting an auditory stimulus sometime during the persistence of a light signal of varying duration (e.g. 1 / 2 / 4 / 8 secs in Experiment 1). Detectability deteriorated progressively with the increasing temporal uncertainty associated with increasing interval durations (Fig. 24.1b). Findings were later confirmed and extended in similar experiments in the visual domain by Lowe (1967), Lasley and Cohn (1981), and Westheimer and Ley (1996). Together, these studies suggested that temporal prediction could improve perceptual judgements about target events, and have effects beyond merely speeding response times.

Newhall (1923) introduced the use of rhythms to manipulate temporal expectations. He showed that the brightness perception of a visual stimulus was increased if the stimulus occurred at the next temporal interval of a regular, isochronous rhythm induced by a series of auditory clicks. The three experimental conditions of the experiment involved the visual target occurring 1 sec after a series of five auditory clicks separated by 1-sec intervals (i.e. on

the sixth beat of the rhythm), occurring 4 secs after the train of five auditory clicks, or occurring after a 9-sec interval with no leading rhythm (Fig. 24.1c). As the reader may have noted, not all relevant experimental variables were well controlled in this early experiment. Furthermore, behavioural performance was measured subjectively and compared without statistical methods. Nevertheless, the intent was to manipulate temporal expectations—to 'create three different pre-stimulus situations which differed among other things in that they made the observer aware of the time at which the stimulus would occur' (Newhall 1923: 55).

As is plain to see, these pioneering studies started tapping into some fundamental issues about how temporal predictability and structure of events influence performance. For example, they indicate different ways of manipulating temporal expectations and suggest that there may be multiple points of influence along sensory-motor processing. Inexplicably, somehow, there was insufficient momentum, and investigations into the selective attention based on the timing of events lagged behind those of spatial and object-based attention, leaving the temporal dimension largely out of the established contemporary models. The landscape is changing again. Scholars interested in the selective biasing of information processing have rediscovered, sometimes *de novo*, the importance of temporal expectations in shaping perception. Present-day methods enable a detailed characterization of behavioural consequences of temporal expectations, and are beginning to provide a glimpse into the neural modulatory and control mechanisms. **(p. 679)**

Rhythms

Rhythms provide arguably the most natural and common source of temporal predictions of events. These come from the structure of events in the environment (e.g. cadence of speech, the tempo of music, the breaking of waves) as well as from our means to sample and interact with the environment (e.g. saccadic eye movements, walking, breathing) (see Schroeder et al. 2010).

Jones and her colleagues are modern-day pioneers in investigating how rhythms modulate perceptual excitability over time (Jones 1976; Jones and Boltz 1989; Jones et al. 2002, 2006). Using a similar approach to that initially introduced by Newhall (1923), Jones's tasks typically manipulate the timing of auditory target events relative to a regular isochronic rhythm. The results have consistently shown optimal perceptual discrimination for auditory targets coinciding with the predicted beat of the rhythm, with performance degrading exponentially with increasing leading or lagging intervals between the target and the predicted moment (Jones et al. 2002) (Fig. 24.2a). Rhythmically induced expectations have been found to confer behavioural advantages even when they are not predictive of the timing of the target, suggesting that temporal anticipation triggered by isochronous rhythms may operate through an automatic, exogenous process (for a review see Jones 2010). Using pre-exposure to a rhythm to induce temporal expectations, Sanabria and colleagues have also reported improvements in response times to auditory targets occurring at the beat of the leading isochronous rhythm, even when the rhythm did not reliably predict the timing of the target stimulus (Sanabria et al. 2011). The automatic nature of the benefits conferred by rhythms was supported by a further study by the same group showing that simultaneously performing a demanding working-memory task did not interfere with the effects of rhythmic temporal expectations (de la Rosa et al. 2012).

Perceptual Modulation
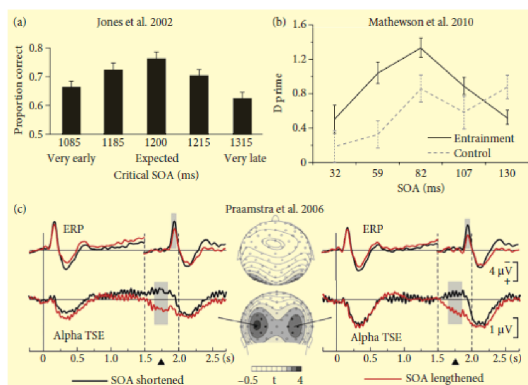
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Figure 24.2 Using rhythms to orient attention in time. (a) Findings from Jones et al. (2002) showing mean proportion correct to discriminate auditory targets as a function of its interval relative to a preceding rhythm. Maximum performance occurs on the expected rhythmic beat interval and falls off systematically as the target occurs increasingly early or late. Adapted from Mari Riess Jones, Heather Moynihan, Noah MacKenzie, and Jennifer Puente, *Psychological Science*, 13(4), pp. 313–319, copyright © 2002 by SAGE Publications. Reprinted by permission of SAGE Publications. (b) Findings reported in Mathewson et al. (2010). Solid line shows the tuning of detection rate for visual targets preceded by predictive rhythms. Performance is maximal for events at the predicted interval and falls off systematically for progressively early or late events. Dashed line shows performance at equivalent intervals in a control condition with no preceding rhythm. Reprinted from Praamstra, P., Kourtis, D., Kwok, H. F., Oostenveld, R., Neurophysiology of implicit timing in serial choice reaction-time performance, *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, 26(20), pp. 5448–5455 © 2006, The Society for Neuroscience. (c) Event-related potentials (ERP) and time course of alpha-band activity (Alpha TSE (temporal spectral evolution)) over occipital electrodes in Praamstra et al. (2006). Alpha-band activity decreases sharply at the time of the expected stimulus (1500 ms) in the short SOA condition, as highlighted by shading in the Alpha TSE plots. This desynchronization in the alpha band was accompanied by an increase in visual evoked activity, as highlighted by shading in the ERP plots. Reprinted from *Cognition*, 115(1), Kyle E. Mathewson, Monica Fabiani, Gabriele Gratton, Diane M. Beck, and Alejandro Lleras, Rescuing stimuli from invisibility: Inducing a momentary release from visual masking with pre-target entrainment, pp. 186–91, Copyright (2010), with permission from Elsevier.

Similar patterns of facilitation for events coinciding with regular isochronous rhythms have also been reported in the visual modality. Mathewson and colleagues (2010) used a series of zero, two, four, or eight visual cues presented at a regular pace (12.1 Hz) to entrain rhythmic visual attention. Next came the target event, containing a visual stimulus or a blank followed by metacontrast masking. The target occurred either at the beat, or at increasing leading or lagging intervals (25 or 50 ms). Target detectability, measured by d′, was maximal when the target coincided with the preceding rhythm (Fig. 24.2b). Perceptual facilitation for targets occurring after eight entrainers was substantial compared to a control condition that equated the foreperiod duration for target onset and forward masking effects (i.e. 55% increase in d′). Praamstra and colleagues (2006) recorded EEG during a related task in which a train of regularly presented 11–21 imperative stimuli (at 1.5 or 2.0s stimulus-onset asynchrony (SOA)) was followed by a temporally deviant target (at 1.75s SOA). Response times to deviant targets were slowed relative (p. 680) to the regular stimuli, and electrophysiological recordings showed evidence of anticipatory activity related to the rhythm of the initial stimuli (Fig. 24.2c). Alpha-band desynchronization, linked to anticipation of visual targets (Foxe et al. 1998; Kelly et al. 2006, 2009; Worden et al. 2000; Snyder and Foxe 2010; Bollimunta et al. 2008, 2011; Wyart and Tallon-Baudry 2008; Yamagishi et al. 2008; Mathewson et al. 2009; O'Connell et al. 2009; Gould et al. 2011), was accentuated from the time the target was predicted by the rhythm. Slow preparatory brain activity related to motor preparation in the contingent negative variation (Walter et al. 1964) also developed more steeply toward the end of the interval in the context of faster compared to slower rhythms. Visual event-related potentials (ERPs) evoked by the targets also showed modulation by preceding temporal rhythm, with larger N1 potentials occurring for targets occurring later versus earlier than predicted by the preceding short versus long rhythm respectively.

In our laboratory we have used a complementary approach to investigate the effects of temporal expectation on perceptual processing—manipulating the regularity of the temporal context of target events. Our findings show that temporal expectations combine with spatial expectations to enhance perceptual processing, and implicate ongoing oscillatory brain activity in mediating the effects of temporal expectations.

In one series of studies (see Fig. 24.3), we manipulated the regularity of the timing with which a target (a small disc) moved in discrete jumps across a display containing an occluding band. When the disc moved at a regular, isochronous pace, it was possible to predict exactly when the target would re-emerge after disappearing behind the occluding band. The basic task involved making a fine visual discrimination within the target disc when it re-emerged and executing a speeded detection (go/no-go) or forced-choice response accordingly. In the first study, temporal and spatial predictability of the target were manipulated orthogonally in a factorial design. The disc moved with regular or irregular pace along a linear or erratic trajectory across the display. Temporal and spatial expectations conferred similar benefit to response times. Recordings of event-related potentials showed that the similar behavioural effects of isolated temporal or spatial expectations came about through distinct patterns of neural modulation. Of specific relevance to perceptual modulation, isolated spatial expectations (i.e. under temporal uncertainty) increased the magnitude of visual P1 potentials contralateral to spatially expected targets, in line with spatial orienting effects in spatial cueing tasks (Mangun and Hillyard 1987; Eimer 1994). In contrast,

isolated temporal expectations had no effect on the first visual potential (see also Correa and Nobre 2008). Strikingly, however, temporal expectation greatly potentiated the P1 gain modulation by spatial attention (Fig. 24.3b). Furthermore, amplitude of the contralateral P1 potential correlated significantly with the average response time in go trials across participants. Modulation of later stages of processing (N1, N2, and P3 potentials) by temporal versus spatial expectations occurred in dissociable ways. The findings from this study suggested that temporal expectations combine synergistically with predictive information about other stimulus attributes (in this case location) that can be mapped onto receptive field properties to time the biasing of excitability in a top-down fashion. We are currently exploring the reliability and generalizability of this hypothesis.
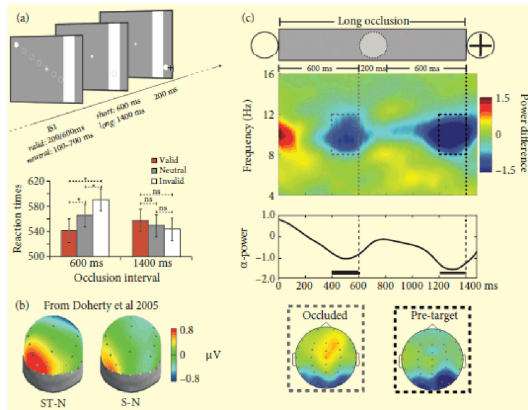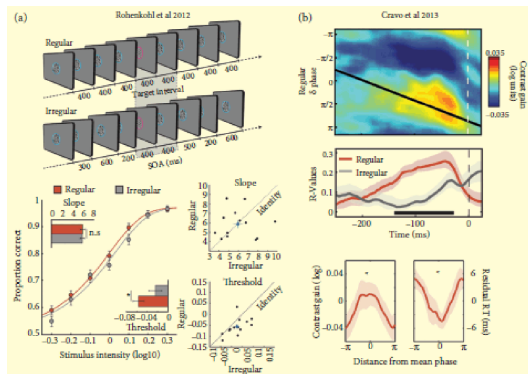

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Figure 24.3 Results from Rohenkohl and Nobre (2011) and Doherty et al. (2005) showing the synergistic effect between temporal and spatial expectations. (a) Schematic of the task used in Rohenkohl and Nobre (2011) based on the original task by Doherty et al. (2005). Bar plot showing reaction times for valid, neutral, and invalid temporal expectation. Note how valid rhythmic temporal expectation shortens reaction times for targets appearing after the short occlusion. Temporal expectations are equated at the long-occlusion interval, and there are no reaction-time differences then. Reprinted from Doherty, J. R., Rao, A., Mesulam, M. M., Nobre, A. C., Synergistic effect of combined temporal and spatial expectations on visual attention, *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, 25(36), pp. 8259–8266 © 2005, The Society for Neuroscience. (b) Topographies presented in Doherty et al. (2005) showing enhanced attentional modulation of early visual P1 potential (between 100 and 130 ms) by combined spatial and temporal expectations (ST-N) relative to spatial expectation alone (S-N). Reprinted from Rohenkohl, G., Nobre, A. C., Alpha oscillations related to anticipatory attention follow temporal expectations, *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, 31(40), pp. 14076–14084 © 2011, The Society for Neuroscience. (c) Time course and topographies of alpha-band activity found in Rohenkohl and Nobre (2011) in regular vs. irregular conditions during the long-occlusion period. The schematic above shows the timings of events: the moment when the disc disappears under the occluding band (0 ms), the moment of the invisible step under the occluding band (600 ms), and the moment when the disc reappears (1400 ms). Temporal expectations developed from a regular rhythmic pattern of stimulation led to time-modulation of alpha-band activity over visual electrodes in anticipation of the target onset.

Using a streamlined and optimized design (Fig. 24.3a), we subsequently replicated the perceptual facilitation conferred by temporal expectations to spatially predicted targets and were able to examine effects of combined spatiotemporal expectations on anticipatory brain activity during the occlusion period (Rohenkohl and Nobre 2011). Analysis of induced oscillatory activity during the period when the target remained (p. 682) (p. 683) occluded showed that alpha-band activity over occipital electrodes became temporally structured in the regular, rhythmic condition. Alpha-band desynchronization followed the time course of temporal expectation induced by the preceding rhythmic pace, being maximal at the predicted times of disc occurrence under the occluding band and of its reappearance after occlusion (Fig. 24.3c). Our findings support the ability of oscillatory activity to mediate changes in neural excitability according to temporal expectations induced by the regular timing of events.

In a related behavioural experiment, we demonstrated that the facilitatory effect of temporal expectations on response times induced by rhythmic apparent motion occurred relatively automatically, and independently of strategic factors (Rohenkohl et al. 2011). The temporal manipulation induced by the regularity of motion (valid, rhythmic versus neutral, arrhythmic conditions) was crossed with a manipulation whereby the colour of the disc acted as a symbolic cue that predicted the timing for target reappearance (valid, 100% predictive versus neutral, non-predictive). In addition to the manipulations of rhythmic and symbolic cueing, we also introduced instructions to attend to the speed (rhythm) or the colour of the disc. The results showed that both rhythmic and symbolic

temporal cues speeded response times, but in dissociable ways. Rhythmic cues facilitated performance regardless of the instructions, but symbolic cues were only effective when participants attended to the symbolic, colour information. These findings indicate that there may be multiple, qualitatively distinct sources of temporal expectations operating upon information processing.

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Figure 24.4 Rhythmic temporal expectation enhances perceptual processing of visual events. (a) Schematic of the task used in Rohenkohl et al. (2012). Stimuli appeared exactly every 400 ms in the regular condition, and appeared between 200 and 600 ms in the irregular condition. Occasional target stimuli were indicated by a pink circumference, and participants discriminated the orientation of a Gabor grating embedded within a Gaussian noise patch. Psychometric functions described performance in regular and irregular temporal expectation conditions as a function of target contrast. Stimulus contrasts were set for each participant using a staircase procedure in an irregular stream of events; Stimulus intensity = 0 corresponds to the contrast value yielding 75% performance threshold. A shift in threshold, but not slope, of the psychometric function indicates that temporal expectation increases the contrast sensitivity for target events. Differences in slope (non-significant) and threshold (significant) are also plotted for regular and irregular temporal conditions in the bar graphs. Scatterplots show the effect of temporal expectation on slope and threshold values for each participant (bluedots indicate the group average). Reprinted from Rohenkohl, G., Cravo, A. M., Wyart, V., and Nobre, A. C., Temporal expectation improves the quality of sensory information, 32(24), pp. 8424–8428 © 2012, The Society for Neuroscience. (b) Results from in Cravo et al. (2013) showing how the entrainment of delta oscillations over visual areas was closely related to a concurrent enhancement of perceptual discrimination to relevant events. Colour map shows the relationship between delta phase and contrast gain in the regular, rhythmic condition. Black line superimposed onto colour map indicates the mean delta phase across participants. R-values line plots show the time course of the correlation between delta phase and contrast gain. Black line along the X-axis (time) indicates when correlation between delta phase and contrast gain was significantly higher in the regular than in the irregular condition (cluster p < 0.05). Lower line plots show contrast gain and residual response times as a function of the distance from mean phase in the pre-target period (–140 to –30 ms) in the regular condition. This figure shows clearly a decrease in contrast gain and increase in reaction times as distance from mean phase increases. Reprinted from Cravo, A. M., Rohenkohl, G., Wyart, V., Nobre, A. C., Temporal expectation enhances contrast sensitivity by phase entrainment of low-frequency oscillations in visual cortex, 33(9), pp. 4002–4010 © 2013, The Society for Neuroscience.

In a second series of studies, we used a psychophysical approach combined with computational modelling to investigate the consequences of rhythmic temporal expectations on visual perceptual discrimination (Cravo et al. 2013; Rohenkohl et al. 2012a). Participants had to discriminate the orientation of a Gabor grating, presented at one of seven contrast levels and embedded within a patch of Gaussian noise. Targets appeared within foveal streams of Gaussian-noise patches presented in a 'regular', isochronous rhythm (50 ms duration, 400 ms SOA) or in an 'irregular', jittered fashion (50 ms duration, 200/300/400/500/600 ms SOA) (Fig. 24.4a). Importantly, the timing around the target stimulus was equated between the two conditions, with 400 ms SOA between the target and the preceding and subsequent adjacent noise patches. Contrast levels for targets were calibrated to individuals' thresholds, anchored at 75% accuracy and varying 1–3 units above and below in steps of 0.1 on a logarithmic scale. The occurrence of targets was signalled by a coloured annulus around the stimulus patch to prompt a forced-choice response. In our first behavioural investigation (Rohenkohl et al. 2012a), response times were faster in the regular, rhythmic condition. In addition, psychometric functions for the proportion of correct responses estimated for individual participants showed that rhythmic temporal expectation significantly increased the contrast sensitivity for target detection (lowering threshold values). A simple diffusion model (Palmer et al. 2005) indicated that temporal expectation improved the quality of sensory information by enhancing the signal-to-noise contrast of the sensory evidence upon which decisions were made. Our subsequent study combining the same design **(p.**

with EEG recordings replicated these psychophysical and modelling effects, and provided evidence that entrainment of low-frequency oscillatory brain activity to regular stimulus timings may mediate the perceptual benefits (Cravo et al. 2013). Oscillatory activity in the frequency range of the stimulus trains (delta-band activity, 1–4 Hz) became more synchronized in the regular, rhythmic condition over occipital electrodes. Furthermore, delta phase was tightly related to target discriminability, and the optimal delta phase became aligned to target presentation in the regular, rhythmic condition (Fig. 24.4b). Entrainment of delta phase was closely related to increases in contrast gain and the modelling parameter for the sensory accumulation rate. Subsequent visual potentials evoked by target stimuli also became more sensitive to target contrast in the regular, rhythmic condition.

Mathewson and colleagues (2012) conducted a similar experiment using EEG to test whether and how oscillatory brain activity mediated effects of rhythmic temporal expectation. The task was based on their previous study (Mathewson et al. 2010), using rapidly presented streams of stimuli followed by metacontrast masks. In the regular, rhythmic condition, the target followed eight entrainer stimuli appearing at a regular rate (~12 Hz, every 82.3 ms). In the irregular condition, stimulus-onset asynchronies between entrainers varied, but the overall time until target appearance was equated to that of the regular condition. Targets appeared at the time predicted by the regular rhythm or in progressively leading or lagging offsets. As in their previous study, visibility was maximal for targets at the predicted time for the rhythmic condition and fell off with increasing offsets. The effect varied with the degree of regularity in variable entraining rhythms, and was absent in a no-rhythm control condition. Power and phase-locking of oscillatory activity within the frequency of stimulus presentation (~12 Hz, in the alpha band) was significantly higher in the regular rhythmic condition over posterior occipital and parietal electrodes, and phase-locked fluctuations co-varied with fluctuations in visual awareness.

Entrainment of oscillatory activity has also been reported in the auditory domain. Henry and Obleser (2012) found that ability of listeners to detect short gaps within a 3 Hz frequency modulated stimulus clustered around specific preferred phases of the frequency modulation, and was best predicted by the phase of delta-band activity entrained to the temporal structure of the stimulus (see also Will and Berg 2007). Using magnetoencephalogram in rhythmic auditory tasks, Large and colleagues have also proposed that activity in the gamma (Snyder and Large 2005; Fujioka et al. 2009) and beta (Fujioka et al. 2012) band is induced in anticipation of temporally regular events.

Neuronal Mechanisms

By combining laminar recordings of local field potentials (LFPs) and multi-unit recordings in macaques, Lakatos, Schroeder, and colleagues provided some of the first evidence suggesting that entrainment of neuronal activity to external events is an important attentional mechanism—regulating neuronal excitability according to temporal expectation (see also Schroeder, Herrero and Haegens (in chapter 17), this volume). In a set of pioneering studies, Lakatos and colleagues (2008, 2009) recorded neural responses in (p. 686) primary visual (V1) and primary auditory (A1) cortices during performance of an intermodal attention task in which near-rhythmic streams of visual and auditory stimuli were interdigitated. On average, the interval between successive stimuli in each modality was 650 ms (500–800 ms range, 1.5 Hz, in the delta frequency), and the two stimulus streams remained 180º out of phase over trials. As expected, current-source density and multi-unit responses in V1 were significantly enhanced when the visual stream was task-relevant compared with when the auditory stream was relevant. In addition, they also discovered that low-frequency oscillations became entrained to the carrier rhythm of the task-relevant, attended stimuli and that higher frequency gamma-band activity became coupled to these delta oscillations. Single-trial analysis of the influence of delta-phase on event-related responses showed visual responses to be systematically related to the pre-stimulus delta phase. Based on their findings and previous literature, the authors proposed a mechanism by which task-relevant events are capable of resetting ongoing oscillatory activity. In contexts containing rhythmic events, entrainment of low frequency oscillatory activity plays an active part in regulating neuronal excitability through hierarchical cross-frequency coupling that leads to increases in response gains and amplification of neuronal responses to task-relevant stimuli (Lakatos et al. 2008, 2009; Schroeder and Lakatos 2009b; see also Lakatos et al. 2005; Canolty et al. 2006). In the absence of a rhythmic context, when attention needs to be sustained tonically over time, low-frequency oscillations may be suppressed (e.g. see Fries et al. 2001).

A recent study by Lakatos and colleagues (2013) further suggests how temporal entrainment of low-frequency

activity aids differentiation between competing stimuli occurring at similar times. Macaques were cued to attend to one of two competing auditory streams of different frequency content that differed in their rate of presentation (1.6 vs. 1.8 Hz). As in the intermodal studies, low-frequency oscillation became entrained to the attended auditory stream. However, the phase of entrainment depended on the tone frequency, with counter phase entrainment to attended versus unattended tones. The result was amplification and sharpening of neuronal responses to relevant tones at attended time points.

Working Hypotheses and Open Questions

Together, findings in humans and in macaques support recent proposals that entrainment of neural excitability to environmental rhythms is a fundamental aspect of successful perceptual selection. Entrainment of brain activity to sensory input may be a pervasive mechanism across animal species. For example, it has been observed in the optic tectum in the larvae of zebra fish (Sumbre et al. 2008), in retinal ganglion cells of salamanders (Schwartz and Berry 2008), as well as in sensory areas in humans (Herrmann 2001; Williams et al. 2004; Mathewson et al. 2012; Cravo et al. 2013; Nozaradan et al. 2011).

However, a major open question is whether specific frequency bands play privileged roles in regulating neural excitability according to the rhythmic temporal structure of events. So far, the results suggest entrainment of neural activity to the pace of external events, but there may be constraints according to intrinsic brain rhythms and (p. 687) entrainment within different frequency ranges may have different modulatory consequences. Schroeder and Lakatos (2009a, 2009b; Schroeder et al. 2010) suggest a primary role for endogenous low-frequency delta and theta rhythms in guiding active sensing of environmental stimuli. Active sensing mechanisms may, in turn, be shaped by or aligned to motor sampling mechanisms, such as the rates of saccades (Bosman et al. 2009) or speech prosody (Ghazanfar et al. 2013). Separately, entrainment of alpha-band activity, which has been particularly implicated in mediating visual excitability, has been proposed as a mechanism for selective temporal attention based on rhythms (Mathewson et al. 2009; Jensen et al. 2012; Hanslmayr et al. 2011). Future studies varying entrainment rhythms systematically will be needed in order to explore this basic and important issue.

The sources and extent of neural modulation by rhythmic context also remain to be characterized. The endeavour may prove challenging, as the temporal correlations inherent in tasks manipulating stimulus rhythms complicate the use of hemodynamic imaging methods with low temporal resolution, such as functional magnetic-resonance imaging (fMRI), which provide good spatial sampling across the brain. Furthermore, hemodynamic measures may not be sensitive to mechanisms relying on changes in timing or synchronization of brain activity. Besle and colleagues (2011) were able to observe large-scale entrainment of brain areas by using intracranial electrocortical recordings in human epilepsy patients. They used an adaptation of the intermodal attention task used by Lakatos (2008, 2009). Modulation of low-frequency activity entrained to the stimulation was not confined to primary visual areas, but instead occurred over a large number of brain areas, including higher order cortices implicated in control functions. The authors noted considerable overlap in the network of modulated areas with those implicated in cued temporal orienting tasks (Coull and Nobre 1998; see below). This large-scale rhythmic entrainment of brain areas may occur locally and become coordinated across brain areas through bootstrapping. Alternatively, there may be a centralized mechanism, which in turn coordinates oscillatory entrainment. A combination of both local and central mechanisms is also possible.

Studies are also beginning to explore the role temporal expectations play in organizing and facilitating higher order cognitive functions involving rhythmic patterns of stimulation, such as music (e.g. Gordon et al. 2011; Nozaradan et al. 2011; Large and Snyder 2009; Tillmann 2012), language (e.g. Ghazanfar et al. 2013; Hoch et al. 2013; Astheimer and Sanders 2009, 2011, 2012; Schmidt-Kassow and Kotz 2009; Power et al. 2012; Kotz et al. 2009), and sensory-motor coordination (Fujioka et al. 2012). As investigations progress, it will be interesting to investigate temporal expectations that occur in the context of complex, non-isochronous rhythms (Chapin et al. 2010; Large et al. 2002). Initial studies have started to reveal interesting effects of temporal sequences involving non-isochronous repeating patterns of intervals on implicit learning (Olson and Chun 2001; O'Reilly et al. 2008a). Interestingly, a striking interaction was also noted between implicit learning of a repeating sequence of temporal intervals and a sequence of stimulus locations in facilitating response times in a serial reaction-time task (O'Reilly et al. 2008a)— echoing the synergistic effects noted between temporal and spatial expectations in the visual task by Doherty and colleagues (2005), and (p. 688) between temporal expectations and task-relevant tone frequencies in the

auditory task by Lakatos and colleagues (2013). Whereas no implicit learning of temporal sequences was observed when the stimulus location was uncertain, temporal sequences amplified the implicit learning of spatial sequences enormously.

Hazards

Predictable temporal structure of events is not confined to rhythmic contexts. Any reoccurring episode may contain temporal predictions about the sequence and timing of its events. The conditional probability of an event occurring at a specified time given that it has not yet occurred is known as the 'hazard function' (Luce 1986).

Most psychophysical or cognitive tasks have temporal predictions embedded within their task structure (see Griffin and Nobre 2005). In warning-signal tasks, conditional probabilities of target events increase with the passage of time, and can become sharply tuned to specific moments when the foreperiod before the target is fixed. The importance of foreperiod duration and regularity has been acknowledged since the classic warning-period studies (Woodrow 1914; reviewed in Niemi and Näätänen 1981). In tasks with variable foreperiods, the sequence of intervals across trials may also influence response times (Woodrow 1914), and the resulting response time is dictated by a combination of foreperiod sequence effects and hazard rates (e.g. Los and Agter 2005). In the earlier literature, foreperiod effects were often treated as reflecting general mechanisms for non-specific preparation for the target (e.g. Bertelson 1967; Niemi and Näätänen 1981), and sometimes linked to effects of general alertness (Posner and Boies 1971). More recently, active and selective mechanisms of temporal anticipation are increasingly acknowledged to contribute to foreperiod effects (see Nobre et al. 2007).

Perceptual Modulation

Hazard rates have been shown to influence many types of behaviour. Proactive anticipation of target timings is clearly evident in smooth-pursuit tasks, in which eye position often leads a temporally anticipated change in target trajectory (e.g. de Hemptinne et al. 2007, 2010; Barnes and Asselman 1991). Anticipatory saccades (Kingstone and Klein 1993) and manual responses (Nickerson 1965) are also common in simple detection tasks using constant, predictable intervals. Regular, predictable timings for target appearance can also affect perceptual judgements: improving thresholds for luminance, orientation, and stereoscopic discriminations (Lasley and Cohn 1981; Westheimer and Ley 1996); increasing accuracy for discriminating targets under high perceptual demands Rolke and Hofmann 2007; reviewed in Rolke and Ulrich 2010); and attenuating attentional blink (Shen and Alain 2012).

Sophisticated psychophysical experiments combined with computational modelling are beginning to be carried out to characterize the effects of hazard rates on different stages of information processing. At this stage, it is worth bearing in mind that multiple (p. 689) levels of influence may occur and differentially influence performance depending on the perceptual, mnemonic, and motoric demands in the task. Using an unspeeded task and modelling of processing parameters according to the 'theory of visual attention' (TVA) (Bundesen 1990; Bundesen et al. 2011) (see also Bundesen and Habekost (in chapter 37), this volume), Vangkilde and colleagues (2012) found that hazard-rate manipulations primarily affected the speed of encoding items into visual short-term memory, rather than the temporal threshold for perception (but see also Seifried et al. 2010; Bausenhart et al. 2008, 2010). Using a fixed-foreperiod manipulation as well as a temporal cueing paradigm (see below) combined with a type of drift-diffusion model (Ratcliff and Rouder 1998), Jepma and colleagues (2012) concluded that temporal expectation affected the duration of non-decision processes, such as target encoding or response preparation, but had little effect on the rate of evidence accumulation or on setting the response threshold (see also Seibold et al. 2011). These results are qualitatively different from our results using rhythms to manipulate temporal expectations (Cravo et al. 2013; Rohenkohl et al. 2012a, 2012b). These interesting discrepancies call for additional rigorous and systematic studies using computational models to compare the effects of temporal expectations induced by different procedures (e.g. rhythmic contexts vs. hazard rates) and under differing perceptual, mnemonic, and motor demands. For now, it is safe to conclude that manipulations of hazard rates, like rhythmic contexts, exert strong and reliable influences over information processing in tasks emphasizing perceptual discrimination or speeded responses.

Neuronal Mechanisms

Hazard rates have been shown to influence activity across multiple brain areas. Single-unit and local field potential studies in animal models have revealed modulations in striate and extrastriate visual cortices (Ghose and Bearl 2010; Ghose and Maunsell 2002; Shuler and Bear 2006); parietal area LIP (Janssen and Shadlen 2005; Premereur et al. 2012), motor and premotor cortices (Riehle et al. 1997; Lucchetti and Bon 2001; Heinen and Liu 1997; Renoult et al. 2006); striatal and prefrontal cortices (Jin et al. 2009; Tsujimoto and Sawaguchi 2005; Roesch and Olson 2005); and subcortical reward-related areas (Hollerman and Schultz 1998; Fiorillo et al. 2003; Bermudez et al. 2012). Non-invasive studies in humans have also indicated modulation across large networks of brain areas, including sensory and motor areas, depending on task parameters (e.g. Bueti et al. 2010; Schubotz and von Cramon 2001; Cui et al. 2009; Coull and Nobre 2008; Cravo et al. 2011b; Schoffelen et al. 2005). Findings using single-unit recordings in sensory cortices and in sensorimotor areas implicated in the control of attention are of particular interest to understanding how temporal expectations can contribute to attentional modulation of perception.

Sensory areas
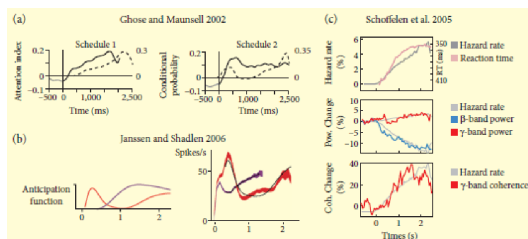
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Figure 24.5 Effect of hazard rates on neural activity related to perception and action. (a) Findings from Ghose and Maunsell (2002) showing that activity in V4 (solid line) follows the conditional probability distribution (dashed line) of target occurrence in a spatial attention task. Reprinted by permission from Macmillan Publishers Ltd: *Nature*, 419 (6907), Geoffrey M. Ghose and John H. R. Maunsell, Attentional modulation in visual cortex depends on task timing, pp. 616–620, copyright 2002, Macmillan Publishers Ltd. (b) Findings from Janssen and Shadlen (2006). Two distinct 'anticipation functions' for target appearance, and LIP responses corresponding to the anticipation functions in a delayed-saccade task. Reprinted by permission from Macmillan Publishers Ltd: *Nature Neuroscience*, 8(2), Peter Janssen and Michael N Shadlen, A representation of the hazard rate of elapsed time in macaque area LIP, pp. 234–241, copyright 2005, Macmillan Publishers Ltd. (c) Results reported by Schoffelen et al. (2005). Top panel shows hazard rate (grey line) with the resulting reaction times (pink line). Note the inverted reaction-time axis at the right. Middle panel shows the time course of power change in gamma (red) and beta (blue) band. Grey lines represent scaled copies of the hazard rate. Bottom panel shows that the time course of corticospinal coherence in the gamma-band (40 to 70 Hz) also follows the hazard rate. From *Science*, 308 (5718), Wendy Winckler, Simon R. Myers, Daniel J. Richter, Robert C. Onofrio, Gavin J. McDonald, Ronald E. Bontrop, Gilean A. T. McVean, Stacey B. Gabriel, David Reich, Peter Donnelly, and David Altshuler, Comparison of Fine-Scale Recombination Rates in Humans and Chimpanzees, pp. 111–113 (c) 2005, The American Association for the Advancement of Science. Reprinted with permission from AAAS.

Ghose and Maunsell (2002) were the first to note modulation of neuronal activity in a visual area by temporal expectation. They observed that the top-down anticipatory effects of spatial attention on the firing rates of neurones in visual area V4 followed the hazard rate predicting the timing of the change in a target stimulus that the monkey had **(p. 690)** to report (Fig. 24.5a). They demonstrated convincingly the modulation of the spatial attention effect by temporal expectations by introducing bimodal hazard rates, which yielded a bimodal amplification pattern of the spatial attention effects. These results, like those in the human ERP study by Doherty and colleagues (2005) manipulating temporal and spatial expectations, point to the ability of temporal expectations to tune modulation of neuronal activity based on other receptive-field properties.

More recently, Ghose and Bearl (2010) measured neuronal activity in visual area MT in a task requiring detection of a very brief motion pulse in one of two locations. The probability of the pulse occurring at each location (with 0.95 to 0.98 certainty) alternated in a square-wave function of a constant period (0.5 Hz or 1.33 Hz in different conditions). In addition, the direction and duration of the motion **(p. 691)** pulse were kept constant, so that it was also possible to predict the nature of the anticipated stimulus. Behavioural performance was strongly correlated to the spatial and temporal probability of pulse appearance, with animals displaying near optimal spatiotemporal integration when pulses were likely (see also Ghose 2006). Reverse-correlation analysis showed dynamic modulation of receptive field properties in MT over a sub-second timescale according to changing spatiotemporal

expectations. Again, these findings indicate strong interactions between temporal and spatial expectations.

A recent study by Lima and colleagues (2011) demonstrates that temporal expectation can modulate sensory processing as early as in primary visual cortex (V1). A simple detection task was used, requiring monkeys to release a lever upon a change in the colour of the fixation point. Task-irrelevant visual stimuli were presented to drive and measure changes in visual excitability according to temporal expectations. Temporal expectations were manipulated in different ways over three experimental protocols. One experiment in particular introduced a clear hazard-rate manipulation (Experiment 2, block protocol), in which the probability for the imperative stimulus appearing at one of two intervals (1600 or 3600 ms) was changed between experimental blocks (Fig. 24.6a). Targets occurred at the probable interval on 85% of trials. Power and coherence of gamma-band activity increased during the foreperiod and was modulated by the hazard rates (see also Liang et al. 2005). Increases in gamma-band activity were paralleled by decreases in alpha-band activity. Gamma and alpha modulation developed significantly earlier in blocks in which targets were expected early (Fig. 24.6a). Changes of oscillatory activity were not confined to the spatially attended location. Instead, comparable effects on gamma-band activity occurred for stimuli at attended, foveal, as well as for unattended, peripheral locations.

Jaramillo and Zador (2011) studied the neuronal mechanisms of temporal expectations in primary auditory cortex (A1) of rats. Auditory targets occurred embedded in tone sequences at one of two interval periods (300–450 or 1350–1500 ms). Temporal expectation was manipulated in a blocked manner, so that targets appeared early or late on 85% of trials in 'expect-early' or 'expect-late' blocks respectively. Behavioural results revealed temporal expectation improved both reaction times and accuracy. Temporal expectations also modulated local field potentials and firing rates in primary auditory cortex, and these effects correlated with the behavioural performance on a trial-by-trial basis (Fig. 24.6b). Reversible lesions of the auditory cortex diminished the behavioural effect, confirming its causal involvement in using temporal predictions to enhance performance. Together, these results indicate that modulation of early sensory areas can mediate behavioural advantages conferred by temporal expectations.

Sensorimotor and motor areas
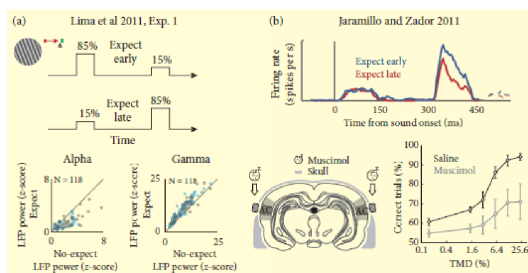
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Figure 24.6 Effects of hazard rates on early sensory areas. (a) Schematic of the task used in Lima et al. (2011). In a block design, monkeys were required to respond to a small change in the fixation point. During expect-early blocks, the fixation point change occurred for most of the cases (85%) early in the trial, at 1600 ms. Only rarely (15% of the cases, catch trials) did the change occur late in the trial, at 3600 ms. In expect-late blocks, the probabilities of fixation point change were reversed. Scatterplots comparing LFP power in the alpha and gamma band on expected versus unexpected stimuli in V1 (Lima et al. 2011). Note how there is a decrease in alpha and an increase in gamma power for high compared with low temporal expectation. Reprinted by permission from Macmillan Publishers Ltd: *Nature Neuroscience*, 14(2), Santiago Jaramillo and Anthony M. Zador, The auditory cortex mediates the perceptual effects of acoustic temporal expectation, pp. 246–251, copyright 2011, Macmillan Publishers Ltd. (b) Findings from Jaramillo and Zador (2011). Similarly to the protocol used in Lima et al. (2011), here rats were rewarded for discriminating target sounds presented at 350 or 450 ms in expect-early blocks and 1350 or 1500 ms during late blocks. Responses of a single neuron in A1 show increased spiking rate in anticipation of the target under early (blue) compared to late (red) temporal expectations when the stimulus parameters were equated. Note how the greatest difference in evoked activity is seen for the tone that immediately preceded the early target (450 ms). Bottom panel shows the results of the inactivation experiments presented by Jaramillo and Zador (2011), showing that bilateral inactivation of A1 reliably impaired the performance in the task. Reprinted from Lima, B., Singer, W., Neuenschwander, S., Gamma responses correlate with temporal expectation in monkey primary visual cortex, 31(44), pp. 15919–15931 © 2011, The Society for Neuroscience.

Parietal area LIP has been strongly implicated in regulating control of spatial attention (see Bisley and Goldberg

2010; Gottlieb 2007; see also Gottlieb (in chapter 12), this volume). This area may provide a nexus for integrating signals from different perceptual modalities, reward prediction, motor intention, and task set. These qualities, combined (p. 692) with its involvement in sensorimotor integration for oculomotor control, place LIP in a strong position to influence ongoing perceptual analysis. Janssen and Shadlen (2005) showed that firing rates in LIP neurons vary systematically with hazard-rate functions in anticipation of 'go' stimuli prompting saccade in a delayed saccade task (Fig. 24.5b). More recently, Janssen and colleagues have started investigating the effects of temporal expectation on local field potentials and induced oscillations during visually guided and memory-guided saccade tasks and during passive visual fixation (Premereur et al. 2012). They found that gamma-band activity encoded the location of the saccade, but decreased during the foreperiod before the saccade. In contrast, alpha- and beta-band activity were less sensitive to saccade location but increased with temporal probability (p. 693) during the foreperiod. Interestingly, significant time-locked local field potentials and multi-unit responses also occurred at the anticipated time of the go stimulus, even when this stimulus was omitted.

Schoffelen and colleagues (2005) showed strong effects of hazard rates at the end of the information-processing pathway. They examined the effects of hazard-rate manipulations on motor excitability in a simple reaction-time task, measuring the temporal evolution of coherence between motor cortex and spinal cord neurons. Both reaction times and the strength of cortico–spinal coherence in the gamma-band followed the hazard-rate function (Fig. 24.5c). A study of ours in humans using a simple reaction-time task and EEG recordings also showed co-variation of response times and motor excitability with the hazard rates (Cravo et al. 2011b).

Working Hypotheses and Open Questions

How modulations by temporal expectations in sensorimotor areas, like LIP, relate to those in sensory areas, like V4, MT, V1, or A1, is unknown. Principles of organization in modulatory mechanisms of temporal expectation still remain to be revealed. At this point it is unclear whether coordination of modulatory mechanisms across large networks of regions is required to bring about behavioural benefits; whether central sources of temporal expectation are required to drive these effects; or whether localized mechanisms occurring at stages of processing that are most relevant for task performance are sufficient. In order to tease apart the degree and direction of influence among different brain areas across different frequency bands and firing rates, it will be important to use similar measures of spiking and oscillatory neuronal activity across different sites and under varying task parameters. Studies using simultaneous recordings across sites (Buschman and Miller 2009; Bosman et al. 2012; Zhou and Desimone 2011) will be particularly useful. For example, one interesting puzzle to solve is the observation that alpha-band activity in LIP increases in anticipation of the imperative signal (Premereur et al. 2012), whereas alpha becomes desynchronized in V1 (Lima et al. 2011; see also Rohenkohl and Nobre 2011).

It will also be important to understand whether influences of temporal expectations driven by rhythms and hazard rates are supported by co-extensive mechanisms. Some of the mechanisms proposed to support increases in sensory excitability in rhythmic context do not translate onto hazard-rate contexts in a trivial way. Activity in lower-frequency, delta and theta, bands is often suppressed in perceptual tasks that may be subject to hazard-rate effects. Furthermore, it is difficult to conceive how up-regulation of a specific frequency band, and cross-frequency coupling to that carrier frequency, can account for facilitatory effects of complex manipulations of hazard rates, such as bimodal (Ghose and Maunsell 2002; Janssen and Shadlen 2005) or alternating (Ghose and Bearl 2010) distributions of stimulus intervals. It is possible that common underlying mechanisms for regulation of neuronal excitability account for effects in predictable rhythmic and hazard-rated contexts. For example, these could rely on dynamic combinations of oscillatory activity across different frequencies. However, it is also prudent to entertain the possibility of multiple, dissociable sources of influences related to the temporal expectations. (p. 694)

Cues

The early foreperiod studies, as well as the more recent work on rhythms and hazard rates, left open the question about whether temporal expectations are under flexible, voluntary control. One possible interpretation was that increases in preparatory processes with the passage and predictability of time occur automatically and outside voluntary control. Another, more interesting possibility was that foreknowledge about predicted or relevant time intervals could be used to orient attention voluntarily and flexibly to a point in time in order to optimize behaviour.

Coull and Nobre (1998) adapted the spatial orienting task developed by Posner (1978, 1980) in order to investigate whether it was possible to orient attention voluntarily to temporal instants, analogously to our ability to orient attention to spatial locations, objects, or features (Fig. 24.7a). Symbolic cues were introduced to predict the time interval after which a target stimulus would appear. In this first experiment, predictive temporal cues (80% validity) were crossed factorially with predictive spatial cues (80% validity). Targets could appear at one of two intervals (300 or 1500 ms) and at one of two locations (left or right peripheral locations), and required a simple detection response. Relative to a neutral-cue condition, both temporal and spatial valid cues conferred significant behavioural advantages. In fact, behavioural benefits for temporal cues were larger than those for spatial cues. Because of changes in the hazard rates over time, targets are always 100% certain to occur at the long interval if they have not already occurred earlier. Accordingly, temporal cues led to equivalent performance at the long-interval condition, independently of whether the cue was valid (long-interval cued) or invalid (short-interval cued). This study opened up the investigation of voluntary orienting of attention based on the predicted timing of events.
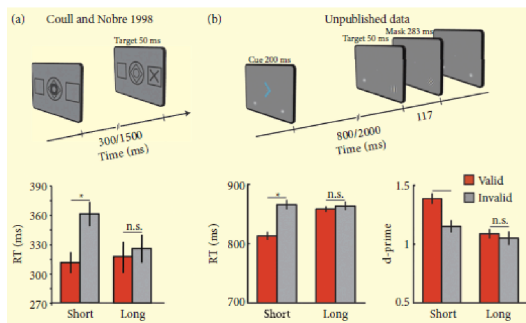
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Figure 24.7 Behavioural effects of temporal cueing. (a) Schematic of the temporal orienting task, and interaction between temporal cues (valid × invalid) and cue-target interval (short × long) obtained in Coull and Nobre (1998). Temporal orienting cues significantly diminished response times to targets appearing at the short interval. (b) Results of an ongoing study using symbolic temporal orienting cues in a perceptually demanding task requiring participants to discriminate a peripheral target (low contrast) followed by a backward pattern mask. The cues in this task were 100% spatially predictive, according to the direction of the arrow, and 80% temporally predictive, according to its colour. The results indicate that under these conditions, temporal orienting not only speeds response times, but also improves perceptual discrimination. In line with the manipulations of conditional temporal probability, effects of temporal orienting in (a) and (b) are confined for targets occurring at the short interval. Reprinted from Coull, J. T., Nobre, A. C., Where and when to pay attention: the neural systems for directing attention to spatial locations and to time intervals as revealed by both PET and fMRI, 18(18), pp. 7426–7435 © 1998, The Society for Neuroscience.

Several behavioural studies have replicated and extended the effects of temporal orienting. In our laboratory, effects were shown with peripheral and foveal targets; in simple detection and in discrimination tasks; using predictive and instructive cues; using cues of different shapes; and over different interval ranges (see Griffin et al. 2001, 2002; Miniussi et al. 1999). In a related experiment, Correa and colleagues (2004) demonstrated that the benefits of temporal cues were not dependent on effects of foreperiod duration or sequence. All of our early experiments emphasized response speed and used tasks with relatively low perceptual demands. Using event-related potentials in these types of task, we found that the substantial benefits of temporal orienting were supported by a set of mechanisms that was qualitatively different from the modulatory mechanisms described for spatial orienting. In the absence of spatial certainty or spatial cueing, the early visual P1 potential was unaffected by temporal orienting. The most reliable modulatory effects were the attenuation of a frontally distributed N2 potential followed by an earlier rise and peak of the late positive centro-parietal 'P3' potential, as well as an increase in its amplitude (Griffin et al. 2002; Miniussi et al. 1999). This pattern of effects is similar to that which we observed in experiments using rhythmic apparent motion to manipulate (p. 695) temporal expectation in the absence of spatial certainty (Doherty et al. 2005; Correa and Nobre 2008; see above). Using a series of foveal temporal cueing tasks of this type, Zanto and colleagues (2011) replicated the behavioural and neural effects of temporal orienting under detection, discrimination, and go/no-go conditions. Interestingly, they found that these effects were highly sensitive to ageing; proactive voluntary use of temporal cues was not observed in groups of elderly (62–82-year-old) participants.

Perceptual Modulation

Studies using visual tasks with higher perceptual demands suggest that it may be possible for cued temporal orienting to influence early stages of visual perceptual processing. For example, Correa and colleagues (2005) found that valid temporal cues (p. 696) enhanced perceptual sensitivity (d') measures for detecting a target letter embedded within a stream of letters under rapid serial visual presentation (RSVP) conditions. Using a shape discrimination task, this group also reported modulation of the early visual P1 potential (Correa et al. 2006). However, some caution is required in interpreting these findings, since cues predicting short versus long intervals were also blocked, making this experiment a combination of a cueing and a blocked hazard-function manipulation.

Jepma and colleagues (2012) used computational modelling to reveal the information processing parameters influenced by predictive temporal cueing (400 or 1400 ms, 75% validity) to foveal visual targets requiring a simple, speeded detection response. Responses were significantly speeded to validly cued targets; the effects were pronounced at the short foreperiod and for dimmer targets. Model fitting indicated that temporal orienting affected the duration of processes such as stimulus encoding and/or motor preparation, which are unrelated to the critical decision-related variables: rate of evidence accumulation or setting of the decision threshold. These results argue against early perceptual modulation by temporal cueing in simple visual tasks, and are consistent with the authors' findings using a fixed-foreperiod manipulation of the hazard rate during a lexical-decision task (Jepma et al. 2012; Experiment 1, see above). They are, however, qualitatively different from our results using a rhythmic manipulation of temporal expectation in a perceptually demanding psychophysical task sensitive to changes in contrast sensitivity (see above Cravo et al. 2013: Rohenkohl et al. 2012a). We have pointed out (Rohenkohl et al. 2012b) that there may be multiple reasons for the difference in results; for example, rhythmic temporal expectations may be more potent at influencing early visual excitability and/or effects of temporal expectations may differentially reflect bottlenecks in perceptual analysis or response parameters depending on the demands of the task.

Studies of temporal cueing in the auditory modality, combined with ERP recordings, have consistently suggested modulation of early perceptual analysis. Valid temporal cues have been reported to enhance the auditory N1 potential, linked to perceptual analysis in auditory cortex (Lange et al. 2006; Lange and Röder 2006; Lampar and Lange 2011; Sanders and Astheimer 2008; reviewed in Lange and Röder 2010). Similar auditory modulation has also been observed in an audio-tactile cross-modal study of temporal cueing (Lange and Röder 2006). However, again, strong conclusions must remain curbed. Most auditory cueing tasks also contain conflated blocked manipulations of hazard rate, in which cues predicting short or long intervals occur with higher probability in separate blocks (Lange et al. 2003, 2006; Sanders and Astheimer 2008). No enhancement of the auditory N1 was observed in a predictive temporal cueing experiment using equiprobable short and long foreperiods within blocks and a target-discrimination task (Lampar and Lange 2011, Experiment 1), though significant N1 modulation was observed when cues were instructive (rather than predictive) and signalled which target interval was relevant for task performance (Experiment 2). Furthermore, to strengthen conclusions about the role of temporal cueing in modulating early auditory analysis, it will be necessary to measure effects (p. 697) even earlier, during the first stages of sensory processing in primary auditory cortex, which has been shown to be modulated by spatial attention (mid-latency potentials; see Woldorff et al. 1987).

The ability of predictive temporal cues to enhance perceptual analysis is also suggested by their strong influence on visibility of second targets in attentional blink tasks. Identification of a second target (T2) presented in a stream presented under RSVP conditions is usually significantly compromised when it follows a previous target (T1) within a brief temporal window (Raymond et al. 1992). However, cues predicting short intervals between the successive targets greatly diminish this effect in both vision (Martens and Johnson 2005) and audition (Shen and Alain 2011). Influences of temporal cueing have also been noted in tasks tapping into higher levels of stimulus analysis, such as unconscious categorical or semantic priming in RSVP tasks (Naccache et al. 2002; Kiefer and Brendel 2006; Fabre et al. 2007) or spatial Stroop tasks (Correa et al. 2010).

We are yet to characterize the gamut of mechanisms by which cued temporal expectations may influence different stages of stimulus analysis. Whether early, perceptual or later, motor-preparation stages are affected may heavily depend on whether, at one extreme, perceptual limits dictate variability in performance or whether, on the other extreme, perceptual requirements are trivial but instead motor preparation and selection limit performance. In addition, predictions about other properties of the anticipated stimulus, such as its location or constituent features, may also interact with temporal orienting effects (see Nobre et al. 2012). We are currently investigating some of these issues in the laboratory. In an ongoing study (unpublished observations), we observe strong effects of trial-by-trial temporal cueing when combined with spatial cues on perceptual sensitivity to discriminate the orientation of

masked peripheral visual targets (Fig. 24.7b).

To complete the picture, it will also be important to compare and contrast effects under similar tasks between different modalities. It is highly probable, for example, that temporal orienting impacts visual and auditory processing differently (Nobre 2010). Vision and audition have complementary levels of spatial and temporal acuity, and it is reasonable to propose that these modalities have evolved to sense the organization and changes of events along these dimensions differentially. Audition is characterized by high temporal sensitivity and acuity, and temporal parameters of stimuli are coded from the earliest, subcortical processing stages (Viemeister and Plack 1993; Poeppel 2003; Theunissen 2003; Theunissen et al. 2000; King and Nelken 2009). This sense may therefore contain earlier substrates for and greater sensitivity to temporal expectations.

Neuronal Mechanisms

To the best of our knowledge, only two studies have used intracranial recordings to investigate how neuronal activity is modulated by temporal cues used to (p. 698) orient attention flexibly, in a trial-by-trial manner. The first study was by Anderson and Sheinberg (2008), recording from the inferior temporal visual area IT. Two visual pictures appeared in succession, separated by an interval of one or two seconds (Fig. 24.8a). The first picture acted as a predictive temporal cue (80% validity) and the second picture, which could be presented at different levels of contrast, prompted the execution of a previously associated left or right button-press response. Similar to speeded discrimination studies in humans, macaques showed evidence of using temporally predictive cues in a flexible manner. They were significantly faster in validly cued trials, especially at the short foreperiod and for dimmer stimuli. Spiking rates in IT neurons were also significantly enhanced for validly cued target pictures appearing at the short foreperiod compared to invalidly cued targets appearing at the same time. Increases in anticipatory beta-band power also occurred during heightened temporal expectation, and there was greater coherence between neuronal firing elicited by the target and both low (~4 Hz) and higher (beta and gamma band, 32–40 Hz) frequencies of the underlying field potential.

Lima and colleagues (2011, see above) also included a temporal cueing condition in their investigation of temporal expectations in primary visual cortex (Experiment 3, cue protocol). Cues appeared early (1000 ms) or late (3000 ms) into the trial, and indicated the appearance of the target 800 ms later on the majority of trials. However, on 10% of trials, cues appeared early (1000 ms) but were only followed by targets 2800 ms later. Modulations of gamma-band and alpha-band activity were similar to those observed in the blocked modulation of hazard rates (Experiment 1, sequence protocol), except that no gamma-band enhancement was observed in anticipation of the target when no stimulus was present within the receptive field of the recorded neuron. Gamma-band modulation was dependent on there being a stimulus present to drive the gamma response (Fig. 24.8b), suggesting that a covert change in the excitability state in visual cortex only becomes manifest once the cortical circuit is activated by the stimulus. In contrast, anticipatory desynchronization of alpha-band activity occurred in the presence or absence of a stimulus in the receptive field.

Of course, there are striking differences between these two studies, which make it difficult to extract overall patterns of neuronal modulation by cued temporal expectations. Recordings are made from different visual areas, using different cueing manipulations. Whereas stimuli driving neuronal responses being investigated are task-relevant and associated with responses and rewards in the study by Anderson and Sheinberg (2008), the stimuli are unrelated to the task in the study by Lima and colleagues (2011).
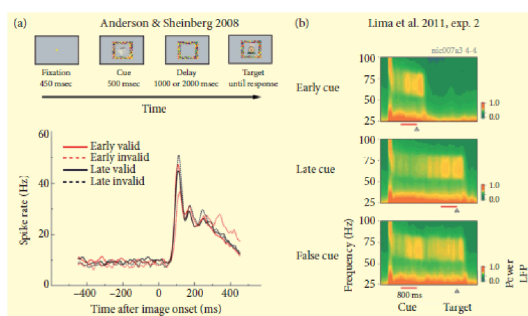
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Figure 24.8 Perceptual effects of temporal cueing. (a) Schematic of the task used in Anderson and Sheinberg (2008). In this study, a first image of an object cued a temporal delay before a second target image appeared (1000 or 2000 ms later). Cue validity was 80%. As in human behavioural studies, effects of temporal orienting were confined to the early foreperiod condition. Spiking rates were significantly elevated for predicted, attended targets (Early Valid, solid red line) compared to unexpected, invalidly cued targets at the same time (Early Invalid, dashed red line). Reprinted from Neuropsychologia, 46(4), Britt Anderson and David L. Sheinberg, Effects of temporal context and temporal expectancy on neural activity in inferior temporal cortex, pp. 947–57, Copyright (2008), with permission from Elsevier. (b) Results in the second experiment reported by Lima et al. (2011) using symbolic cues. Here, a slight increase of fixation point luminance predicted that a change in fixation colour (target) would occur 800 ms later. In the Early and Late Cue conditions, the onset of the cue occurred either early or late in the trial, at 1000 ms or at 3000 ms respectively, and the target occurred at the predicted time, 800 ms later (at 1800 or 3800 ms). In the remaining 10% of the cases (false-cue condition), the cue appeared early in the trial (at 1000 ms), but the fixation point colour change was delayed until the end of the trial (3800 ms). Gamma power was highest preceding target presentation. Interestingly, note how under the false-cue condition, gamma oscillations transiently ceased when the target was not presented at the interval indicated by the cue, then gradually increased again toward the end of the trial. Reprinted from Lima, B., Singer, W., and Neuenschwander, S., Gamma responses correlate with temporal expectation in monkey primary visual cortex, 31(44), pp. 15919–31 © 2011, The Society for Neuroscience.

More studies will be required, therefore, for defining the set of cellular modulatory mechanisms of temporal cueing. It would be straightforward to introduce predictive temporal cues into future single-unit and field-potential studies of perception and attention in macaques. Such manipulation would likely yield hugely informative data that would shed light not only on the putative mechanisms of cued temporal expectations, but also on the characteristics of the other perceptual and attentional mechanisms under study, with which temporal expectations may interact. (p. 699)
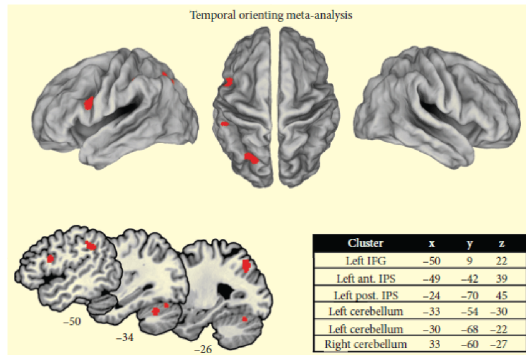
Control networks

Brain-imaging studies using hemodynamic methods (positron emission tomography (PET) and fMRI) have implicated the left posterior parietal cortex along the intraparietal sulcus (IPS) and in the anterior inferior parietal lobule, as well as the inferior premotor cortex, in the control of temporal orienting (Cotti et al. 2011; Davranche et al. (p. 700) 2011; Coull et al. 2000, 2001, 2013; Coull and Nobre 1998). This frontoparietal network appears to reflect a qualitatively distinct sensorimotor circuit compared to that involved in oculomotor control, which has been strongly implicated in the control of spatial orienting. Its left-hemispheric dominance and more inferior location suggest that it may comprise inferior parietal and frontal areas related with preparation and control of manual responses for reaching and grasping (see Krams et al. 1998; Rushworth et al. 1997). Timing is of particular importance to manual dexterity, and frontoparietal circuits for manual control may therefore contain fine-scale temporal computations that can support temporal orienting of attention. Accordingly, it has been suggested that temporal orienting may rely on manual control circuits in an analogous way to how spatial orienting relies on the oculomotor circuitry (see O'Reilly et al. 2008b).

The reliability of the involvement of this network in temporal orienting, and especially of the left parietal cortex, is increasingly clear. The pattern of parietal activations across temporal cueing, and related, tasks is plotted in a meta-analysis we produced for this chapter (Fig. 24.9). The analysis includes eight studies, and plots activations induced by the main or simple effect of temporal orienting. The resulting pattern confirms the reliability of activations in left IPS, anterior inferior parietal lobule, and premotor cortex. In addition, reliable activations are also observed in the cerebellum (see also O'Reilly et al. 2008b), although unfortunately cerebellar activations have not been systematically reported or discussed across studies.

Left parietal cortex is arguably the most reliable site of activation, and tends to be preferentially involved in temporal orienting compared to other types of orienting. Its activation strength is higher when conditions of temporal cueing are contrasted to spatial cueing (Coull and Nobre 1998) and when conditions of temporal cueing are contrasted to cueing of the motor effector for responding (Cotti et al. 2011). In the latter experiment, partial overlap was observed between parietal areas involved in temporal orienting and in preparing to use manual (vs. saccadic) responses, supporting a possible functional overlap between temporal orienting and manual preparation (Cotti et al. 2011; O'Reilly et al. 2008b). Left intraparietal activation is observed in tasks requiring unspeeded difficult perceptual discriminations as well as in tasks requiring speeded motor responses (Davranche et al. 2011). Furthermore, by comparing functional connectivity between tasks, Davranche and colleagues found that parietal

cortex was more strongly correlated with extrastriate visual cortex in the perceptually demanding task and with premotor cortex in the speeded motor task. Consistent parietal activations have also been noted in tasks in which temporal expectations about event timings are induced by predictions based on stimulus motion (Assmus et al. 2003, 2005; Coull et al. 2008b; O'Reilly et al. 2008b).

In contrast, patterns of brain activation in temporal cueing tasks differ from those in tasks that require participants explicitly to estimate and produce temporal intervals in order to make judgements about the timing of stimuli or execute timed responses (Coull et al. 2004, 2013). Explicit timing tasks of this sort have been reported to engage right frontostriatal networks, as well as auditory cortex (see Coull and Nobre 2008; Nobre and O'Reilly 2004).

Cluster	x	y	z
Left IFG	−50	9	22
Left ant. IPS	−49	−42	39
Left post. IPS	−24	−70	45
Left cerebellum	−33	−54	−30
Left cerebellum	−30	−68	−22
Right cerebellum	33	−60	−27

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Figure 24.9 Activation likelihood estimation (ALE—GingerALE 2.0 software) maps for temporal orienting studies. Eight studies were included in the meta-analysis (Coull and Nobre 1998—Exp. 1 and 2; Coull et al. 2000, 2001, 2012a, 2012b; Cotti et al. 2011; Davranche et al. 2012). Values are significant at FDR q < 0.05, minimum cluster size > 200 mm^3. **(p. 722)**

Coull and colleagues have interpreted the pattern of results across studies, sensibly and parsimoniously, as implicating the left parietal cortex as an important source of **(p. 701)** temporal expectations in cueing tasks (Coull et al. 2008a, 2011; Coull and Nobre 2008). However, it is still worth bearing in mind possible alternatives. fMRI studies so far have not isolated neural activations specifically triggered by cues, nor shown direct influence of cue-related parietal activations on activations along the information processing stream and behaviour. The closest we get to this is the recent study by Davranche and colleagues (2011). A competing possible explanation is that parietal involvement in temporal cueing tasks reflects modulation of target-related processes. Multiple candidate functions remain in play, since similar posterior parietal areas have been implicated in accumulation of sensory evidence (Gold and Shadlen 2007; Yang and Shadlen 2007; Gould et al. 2012), limitations in perceptual detection or working-memory capacity (Marois and Ivanoff 2005; Tosoni et al. 2004; Heekenren et al. 2004), and motor preparation (Krams et al. 1998; Rushworth et al. 1997).

The limitations of the fMRI methodology pose particular problems when trying to pinpoint the specific functional contributions of parietal and other putative areas to top-down control of temporal orienting. Hemodynamic measures are slow and therefore susceptible to effects of differential temporal correlations among task events. Temporal cueing, by its very nature, requires systematic manipulations of temporal correlations. The rapid pace, and differential correlations among events in temporal cueing tasks greatly complicate the dissecting out of activations specifically related to top-down control versus target-related analysis. Complementary problems in spatial resolution **(p. 702)** plague studies using electroencephalography or event-related potentials. We are currently using magnetoencephalography with the goal of investigating the time course of involvement of parietal and other brain areas during temporal orienting based on trial-by-trial cues.

Temporal cueing studies using event-related potentials have consistently shown modulation of the contingent negative variation (CNV) (Walter et al. 1964) during selective temporal anticipation of target events (e.g. Zanto et al. 2011; Miniussi et al. 1999; Los and Heslenfeld 2005; Capizzi et al. 2013). The time course of the CNV follows that of cued temporal expectation. The potential develops more sharply in anticipation of target events at shorter intervals, building up to a common maximum level at the anticipated time of the target event. Similar CNV modulation is observed in explicit timing tasks, for example, in which participants have to judge the duration of a target stimulus relative to a standard (Macar et al. 2004; Pfeuty et al. 2005). It is difficult to conclude whether the CNV modulation in cued temporal orienting tasks and in explicit timing tasks taps into a common timing mechanism

used both for orienting and for timing, or whether temporal orienting is used to optimize perceptual and decision-making processes in explicit timing tasks. This common pattern of CNV build-up mirrors the gradual and systematic increases in neuronal firing rates in parietal (Janssen and Shadlen 2005; Leon and Shadlen 2003), motor (Renoult et al. 2006; Riehle et al. 1997), premotor (Akkal et al. 2004; Lucchetti and Bon 2001), and prefrontal (Niki and Watanabe 1979) regions in motor and timing tasks. Most likely, CNV modulation in temporal cueing tasks reflects proactive preparation and/or synchronization processes linked to sensorimotor integration and motor preparation; which can occur independently of perceptual modulation (Nobre and Coull 2010; Nobre and O'Reilly 2004; Nobre 2001).

Not many human temporal cueing studies have reported anticipatory effects related to optimization of perceptual analysis. However, this may simply reflect the use of tasks with low perceptual demands and the lack of analysis of induced oscillatory activity in earlier studies (e.g. Miniussi et al. 1999). More recently, Zanto and colleagues (2011) found enhanced alpha-band desynchronization when young adults anticipated targets at shorter versus longer intervals (see also Babiloni et al. 2004). These findings are similar to what is observed with rhythmic modulation of temporal expectations for visual stimuli (Praamstra et al. 2006; Rohenkohl and Nobre 2011), and in intracranial recordings during temporal cueing or blocked foreperiod manipulations in the macaque (Lima et al. 2011). More reports of anticipatory modulatory mechanisms are expected as more studies get under way.

Working Hypotheses and Open Questions

The growing literature on temporal cueing has already made some significant contributions to our understanding of attentional biasing. Going beyond the literatures on (p. 703) foreperiod, rhythms, and hazard rates, cueing studies show that temporal anticipation of events is under flexible and voluntary control. The effects are robust and occur across a variety of task settings and in different modalities.

Investigations of neural modulatory mechanisms are still relatively few. We lack a full picture, and it is likely that more temporal modulatory mechanisms will be discovered. But we have already learned that similar benefits of spatial and temporal orienting observed at the behavioural level can result from markedly different underlying neural mechanisms (Griffin et al. 2002). Cueing studies will be particularly useful in determining whether there are dedicated networks for top-down control of temporal expectations, and for separating these from mechanisms at the sites of modulation. It is a real possibility that the flexible deployment of temporal expectations relies on flexible temporal organization of activity within networks of brain areas participating in the task. Assuming there are dedicated networks for top-down control, these may be difficult to isolate because of methodological difficulties. Convergence across tasks and across methods, including imaging (magnetoencephalography) and interference (transcranial magnetic stimulation) methods with high temporal resolution, will be essential.

So far, studies in different modalities suggest that we are not heading toward an equivalence of modulatory mechanisms. Instead, temporal biases may influence different stages of information processing, and in different ways across the senses. Temporal biases may also interact differently with other biases about other stimulus attributes or action intentions. The initial findings remind us that our senses are not redundant, but most likely evolved to provide complementary sources of information about the external environment.

Conclusions and Open Questions

Types of temporal biases

We have discussed three types of temporal biases, but now we have to admit that this subdivision is somewhat arbitrary, possibly acting as a placeholder for subsequent, better-informed categorizations. We have focused on temporal biases concerned with short temporal intervals that frame the timing of cognitive functions (sub-second to seconds). These operate within slower fluctuations that may alter the cognitive and emotional state in our system, such as those related to circadian rhythms. There may also be much faster temporal regulatory mechanisms that fine-tune perceptual or motor processing beyond the scope of our awareness.

Within the 'interval timing' stretch we discussed, behavioural modulations—'foreperiod effects'—can arise from the length, regularity, sequence, contextual conditional probability, cued probability, and cued relevance of an event.

At the moment it is unclear how many underlying types of temporal biases may carry these effects. Behavioural performance may also be affected by temporally non-specific transient (p. 704) changes in alertness (Posner and Boies 1971; Petersen and Posner 2012; Posner and Petersen 1990), which may interact with selective temporal biases (as well as other types of biases) to modulate their effects (see Nobre et al. 2012). We have proposed three major classes of selective temporal biases, guided by the subdivisions and distinctions in the literature, combined with our synthesis and analyses of the various findings. Refining our understanding of the number and nature of the essential temporal biasing mechanisms that adapt our perception on a moment-to-moment basis should remain a priority area for research.

Looking back at the effects of temporal expectations produced by rhythms, hazards, and cues, we can note many similarities. All types of manipulations lead to modulations of anticipatory CNV potentials, at least in tasks that require speeded responses (Praamstra et al. 2006; Cravo et al. 2011b; Miniussi et al. 1999; Hackley et al. 2007; Los and Heslenfeld 2005; Muller-Gethmann et al. 2003). Temporal expectations also tune desynchronization of alpha-band activity in anticipation of targets in a variety of tasks manipulating rhythms, hazards, and cueing (Rohenkohl and Nobre 2011; Praamstra et al. 2006; Lima et al. 2011). This effect, however, is not apparent in all rhythmic tasks (e.g. Cravo et al. 2013; Lakatos et al. 2008), and has not been well investigated in human studies using temporal cues. Modulations of event-related potentials triggered by targets are also similar in rhythmic and cued attention tasks (e.g. Correa and Nobre 2008; Doherty et al. 2005; Griffin et al. 2002; Miniussi et al. 1999).

But there are also some differences. For example, in audition, regular rhythms were found to attenuate the N1 potential elicited by targets falling on the predicted beat (Lange 2009, 2010), while temporally predictive cues (presented in a blocked fashion) lead to enhancement of the auditory N1 potential (Lange and Röder 2006; Lange et al. 2003, 2006). By directly comparing cued versus rhythmic temporal expectations in a visual task, we showed that benefits were functionally dissociable. In a rhythmic motion task, additive performance benefits were provided by temporal predictions based on the colour (cueing) or the pace (rhythm) of the moving disc (Rohenkohl et al. 2011). Furthermore, effects of rhythmic expectations were independent of strategic factors, whereas effects of cueing were dependent upon instructions to attend to the colour cues. We concluded that rhythmic cues triggered an automatic, exogenous type of temporal orienting, while symbolic cues relied on an endogenous mechanism; and proposed an analogy to the distinction made between exogenous vs. endogenous orienting of spatial attention (Posner 1980; Posner and Boies 1971). De la Rosa and colleagues (2012) also found effects of rhythmic temporal orienting to be independent of cognitive control. A concurrent working-memory task interferes with performance benefits conferred by temporal cueing but not with benefits from temporal rhythms. Similarly, sequential effects are unaffected by concurrent working memory tasks that disrupt temporal cueing (Capizzi et al. 2012, 2013). Deficits in patients with lesions in the left vs. right frontal lobes also suggest functional dissociations among temporal effects related to rhythms, hazards, and cues (Trivino et al. 2010). Right frontal lesions were found to disrupt temporal cueing selectively, and left frontal lesions to disrupt benefits from rhythms and constant foreperiods. Sequential effects remained unaffected by either type of lesion. (p. 705)

Different sources and mechanisms contributing to temporal expectations may contribute to discrepancies noted in performance benefits in different studies. For example, stronger and more automatic effects of temporal rhythm may make it easier to modulate early levels of stimulus analysis, such as those related to contrast sensitivity and accumulation of perceptual evidence for subsequent decision-making (Cravo et al. 2013; Rohenkohl et al. 2012a, 2012b). However, in order to understand the contributions of temporal expectations generated by different task manipulations, it will be necessary to compare these using stimulus parameters and task demands that are otherwise controlled.

Interactions between temporal and other biases

When manipulated separately, effects of temporal expectations often appear to be independent from those of spatial expectations (Griffin et al. 2002; MacKay and Juola 2007; Bruchmann et al. 2011; Lange et al. 2006). Cueing temporal intervals also yielded additive effects to cueing the motor effector for responding to a target in a task eliminating specific spatial expectations about the stimulus or the action to be performed (Cotti et al. 2011). In contrast, strong interactions are observed when expectations about timing of events are combined with other selective expectations. In our first rhythmic manipulation of temporal and spatial expectations, we noted a striking interaction between these two sources of biases on early stages of analysis (Doherty et al. 2005). In the absence

of spatial certainty, rhythmic temporal expectations had no effect on the visual P1 potential. In contrast, temporal expectations greatly magnified the effect of spatial attention on P1 amplitude. The synergy between temporal and spatial expectations was not observed at the behavioural level, in which additive effects were obtained; but this may be because the bottleneck for performance in that particular task may not have been early perceptual analysis. We are currently investigating whether synergistic effects of temporal and spatial expectations become manifest in tasks requiring fine perceptual discriminations under perceptually challenging conditions (see also Milliken et al. 2003, discrimination task). Strong interactions have also been observed between learning temporal and spatial/motor sequences, even when the sequences in the different dimensions are completely orthogonal (O'Reilly et al. 2008a).

These kinds of observations suggest an intuitive way by which temporal expectations may help guide selective perception. It is difficult to imagine how isolated temporal expectations can modulate sensory processing in a proactive and anticipatory manner. Overall changes in sensory excitability by temporal expectations may be possible, in the form of a transient alerting-like mechanism. However, on its own this kind of mechanism would not only be metabolically costly, it would also be highly non-selective, magnifying processing of any and all events, targets and distractors alike, at predicted relevant moments. However, by interacting with other receptive-field properties, temporal expectations can adjust proactive anticipatory biases over time in order to optimize the state of excitability of relevant items at the right time. Temporal modulation of spatial-attention biases has been noted in single-unit studies in the macaque (Ghose (p. 706) and Bearl 2010; Ghose and Maunsell 2002) and in human EEG studies (Rohenkohl and Nobre 2011; van Ede et al. 2011). Effects of temporal expectation in non-spatial attention tasks are also suggestive of interactions between temporal and feature-based expectations (Lakatos et al. 2013; White et al. 2010). Enhanced preparation of specific movements and associated neural activity has long been noted in motor tasks (e.g. Riehle et al. 1997; Lucchetti and Bon 2001; Heinen and Liu 1997; Schoffelen et al. 2005; Cravo et al. 2011a).

Stepping back, the idea that temporal expectations combine with foreknowledge about other attributes makes obvious sense. We struggle to conceive or understand the nature of time in isolation—indeed some scholars negate its very existence (e.g. Rovelli 2007). In cognition, encoding and sensing of timing may be intrinsically bound to events and their constituent properties. Expectations are about events and not about timings or spatial locations in isolation. Events in turn are situated in time and space, and contain spatiotemporal structure. It will be interesting to continue to explore the synergies between temporal expectations and expectations about other attributes of task relevant events, such as their locations or features, as well as expectations about decisions and actions to be taken in response to these events. Looking at interactions among different types of biasing signals will enrich the study of attention in general, and not only the study of temporal expectations.

Proposed mechanisms

There is still a difficult puzzle to solve: how are temporal expectations coded in the brain in the first place so that they can interact with other biases, or change neuronal excitability in their own right? It is early days to attempt any definitive answer, but it is probably worth airing briefly different types of mechanisms that have been envisaged so far.

One common starting point is to consider whether temporal expectations rely on the same or similar mechanisms that might be in place for explicit timing functions in the brain—whatever those turn out to be (for discussion see Coull and Nobre 2008). If we had a clear understanding of the neural systems and mechanisms responsible for explicit timing functions, it would be possible to design experiments to measure or manipulate activity in these areas during tasks manipulating temporal expectations. However, in its current state, the timing literature provides little guidance. There is still no accepted view on the networks and mechanisms that support perception of temporal intervals. Traditional proposals for the existence of an internal clock (Gibbon et al. 1984; Treisman 1963), for keeping time and enabling retrieval and comparison of stored time intervals, still frame much of contemporary research. Dedicated timing networks have been proposed to involve frontostriatal circuits (Buhusi and Meck 2005; Coull et al. 2004, 2011). The cerebellum has also been suggested to participate specifically in the timing of events (Ivry and Spencer 2004). In contrast, other researchers propose that timing functions occur in a much more widely distributed fashion, as a common property of many or all neural systems (Mauk and Buonomano 2004; Nobre and O'Reilly 2004). Distortions in (p. 707) temporal perception that are highly specific to events occurring within

specific sensory modalities and in specific locations (e.g. Morrone et al. 2005; Johnston et al. 2006) suggest the involvement of highly localized mechanisms for time perception. These could support timing functions in isolation, or interact with centralized timing mechanisms to bring about highly specific effects (Coull et al. 2011).

Within timing systems, be they centralized or distributed, temporal intervals have been proposed to rely on periodic or oscillatory neural activity (e.g. Buhusi and Meck 2005; Miall 1989; Treisman 1963). Others have noted that temporal intervals and regularities within a given context may also be encoded through time-dependent neuronal properties and short-term plasticity mechanisms embedded within neuronal assemblies (Buonomano and Maass 2009; Karmarkar and Buonomano 2007; Crowe et al. 2010). If such state-dependent dynamics and plasticity exist, timing signals could be intrinsic to information processing systems, and these could contribute to optimizing neural processing at anticipated relevant events.

Our current review of the emerging literature on temporal expectations clearly suggests that oscillatory brain activity may provide an important medium for the coding and integration of temporal expectations in the brain. The most developed theoretical proposal so far is that of 'active sensing' based on rhythmic sensory sampling of the environment (see above Lakatos et al. 2008, 2009, 2013; Zion Golumbic et al. 2013; Schroeder et al. 2010; Schroeder and Lakatos 2009b). This proposal combines classic ideas about the importance of motor control and intention in guiding perception (Liberman and Mattingly 1985; Rizzolatti et al. 1987, 1994: Schubotz 2007) with the appreciation that many of our effector systems display rhythmic activity within frequencies similar to our intrinsic low-frequency oscillations (Schroeder et al. 2010; Bosman et al. 2009). It suggests that low-frequency oscillations become entrained to the timing of rhythmic sensory input, occurring naturally within the environment or as a result of rhythmic sampling. This entrainment regulates neuronal excitability so that it is maximal at the predicted times of relevant events, and may also serve to coordinate rhythmic changes of neuronal excitability across different brain areas involved in a given task (see Buzsáki 2006). Because of the ebbing and flowing of neuronal excitability, higher frequency oscillations related to stimulus processing or anticipation become nested within the periods of higher excitability. This process can be repeated, regulating neuronal excitability at multiple temporal scales. Mounting evidence from human and animal studies supports the viability of such a mechanism in the context of regular, rhythmic stimulation (e.g. Cravo et al. 2013; Rohenkohl et al. 2012a; Lakatos et al. 2008, 2009, 2013; Mathewson et al. 2010; Henry and Obleser 2012; de Graaf et al. 2013). Recent work further points to the ability of such mechanisms to enhance selectively signals related to task-relevant events, sharpening the contrast between target and distractor processing (Lakatos et al. 2013).

However, it remains unclear whether and how this kind of rhythmic nesting mechanism can be generalized to conditions in which more complicated hazard functions predict event onsets (e.g. Ghose and Maunsell 2002; Janssen and Shadlen 2005), or during predicted sequences of events (e.g. Olson and Chun 2001; O'Reilly et al. 2008a). (p. 708) In principle, it is possible that elemental rhythmic entrainment mechanisms can become combined to generate more complex temporal predictions, in a Fourier-like fashion. The biological plausibility of such a mechanism would have to be ascertained. Conversely, or additionally, short-term plasticity mechanisms working upon temporal dynamics of neuronal assemblies could reinforce temporal states of relevant events within given contexts (Buonomano and Maass 2009). To test whether summation of oscillatory activity at different frequencies and/or reinforcement of dynamical states contribute to complex temporal expectation functions, it may be worth investigating modulation of oscillatory activity within temporal prediction contexts that vary systematically from isochronous rhythms to complex predictable temporal sequences of events.

Alpha-band activity has also been consistently linked to anticipatory states in perceptual tasks in visual (Worden et al. 2000; Thut et al. 2006; van Dijk et al. 2008; Ergenoglu et al. 2004; Hanslmayr et al. 2007; Romei et al. 2010; Gould et al. 2011) and also other modalities (van Ede et al. 2011; Haegens et al. 2011, 2012). Different theoretical accounts have been suggested for how alpha-band regulates the excitability for sensory events. For example, Jensen and colleagues have suggested that alpha-band activity reflects activity in an inhibitory circuit, such that cortical uptake of sensory processing is mainly limited to the periodic windows of alpha-band desynchronization (Jensen et al. 2012; see also Ray and Cole 1985; Klimesch et al. 2007; Pfurtscheller and Lopes da Silva 1999; Pfurtscheller et al. 1994, 1996). Others have suggested that alpha desynchronization may also contribute to the organization and support of awareness and maintenance of sensory representations in short-term memory (Jensen et al. 2012; Palva and Palva 2007). As we have reviewed, the timing of alpha-band activity in anticipation of sensory stimuli is often modulated by temporal expectations, with effects noted in rhythmic (Rohenkohl and Nobre 2011; Praamstra et al. 2006; Mathewson et al. 2012), hazard-rate (van Ede et al. 2011; Lima et al. 2011), and

temporal cueing (Lima et al. 2011; Zanto et al. 2011) tasks. Modulation in the anticipatory alpha-band activity, however, does not always co-occur with modulation of lower frequency bands suggestive of entrainment to the timing of task-relevant events (Cravo et al. 2013; Besle et al. 2011; Lakatos et al. 2008). It will be important, therefore, to test the extent to which modulations of oscillations in alpha and in lower-frequency (delta and theta) bands express common versus dissociable mechanisms for adjusting and coordinating neural excitability according to temporal expectations.

Fries and colleagues have recently proposed that alignment of phase coherence among distinct populations of neurons involved in a task is of central importance for the selection and integration of relevant events during perception (Bosman et al. 2012; Fries 2009). Modulation of neural activity according to the predicted timings of events, either through rhythmic entrainment or through other mechanisms, is likely to play a significant role in modulating the efficacy of neuronal communication through their coherence. It will be of great interest to introduce manipulations of temporal expectation into large-scale multi-site recording studies of selective attention (e.g. Bosman et al. 2012). **(p. 709)**

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