ORIENTING ATTENTION IN TIME

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1. ABSTRACT

Temporal information is essential for effective perception and action in the dynamic environment in which we exist. However, our ability to use information about time intervals flexibly to direct attention to an expected point in time has until recently been unexplored. Here we report a series of behavioural, neuroimaging and electrophysiological experiments that investigate and define the ability to orient attention in the temporal domain. These studies reveal that we are able to orient attention selectively to different time intervals, enhancing behavioural performance. These effects are mediated by a left-hemisphere dominant frontal-parietal system, which partially overlaps with the networks involved in spatial orienting. The optimisation of behaviour by temporal orienting appears to be achieved via motor-related mechanisms, in contrast to the typical perceptual enhancements produced by spatial attention. From a more general perspective, these findings illustrate the flexibility of attentional functions in the human brain.

2. INTRODUCTION

In our dynamic environment, the time of occurrence of a stimulus is a crucial determinant of our behaviour toward it. In 1914 Woodrow (1) demonstrated that the time interval between a warning signal and a stimulus requiring detection (foreperiod) is one of the main factors influencing the length of reaction time to the stimulus. Since then, studies manipulating foreperiod variability (see (2) for review) have shown that reaction time decreases as a function of certainty about the time of occurrence of stimuli requiring detection (3,4,5) or choice decisions (6,7,8). Also, psychophysical studies have found increased luminance (9), orientation and stereoscopic thresholds (10) when there was uncertainty about the time of stimulus presentation. Performance is improved when stimuli occur at constant and predictable, as opposed to variable, intervals after a warning signal.

Such benefits have been interpreted as suggesting that warning signals can be used as a time cue to start some preparatory/anticipatory adjustments (8) and thereby enhance behavioural performance. Posner and Boies (11) considered such preparatory processes to be part of the alertness component of attention, with the foreperiod between a warning signal and stimulus being likened to a small-scale vigilance situation in which alertness must be developed rapidly and maintained briefly in order to maximise behavioural performance. Indeed, Wilkinson and Haines (12) reported similarities in the brain processes taking place during the foreperiod and those involved in the performance of prolonged vigilance tasks.

The question of the time course of preparation during the foreperiod, i.e. how long it takes such preparatory processes to be built up, has also been

Task schematics for behavioural studies
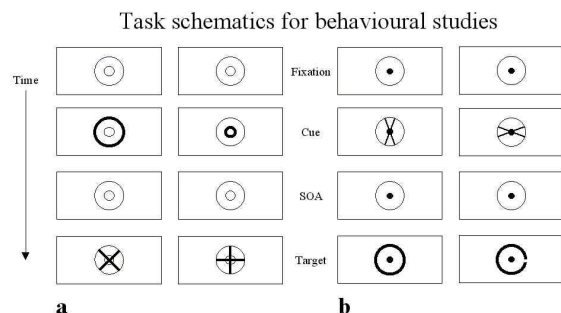
Figure 1. Task schematics for temporal orienting experiments. Subjects maintained their gaze on a central fixation point. A brief cue indicated the probable length of SOA to follow. A target appeared briefly requiring a simple detection or a choice discrimination button-press response. **(a)** In one set of tasks, the cue was the brightening of one of the circles and the target was an upright or rotated cross. **(b)** In another set of tasks, the cue was a narrow or wide cross and the target was the brightening of all or part of the circle.

investigated. Woodrow (1) suggested that at least 2 seconds were needed in order to reach "full attention", and thus obtain the fastest reaction times. More recent studies have shown that the latency of preparation can be shorter than this, with the optimum foreperiod duration being estimated at 1 second (3), 350msec (5), and 100-150msec (8). However, all these studies contain the implicit assumption that there is an absolute optimum foreperiod between warning signal and stimulus, i.e. the reaction time benefits found reflect a rigid process, with a fixed optimal time course (cf. (13)). The possibility that the preparatory processes underlying performance benefits on these tasks could be under flexible cognitive control has so far not been investigated.

Here we report a series of experiments designed to investigate whether we are able to use information about the time interval between a warning signal and a stimulus requiring a response flexibly to optimise behaviour. Firstly, evidence from behavioural experiments in which warning signals (cues) manipulated subjects' expectancies as to when a stimulus would occur is considered. Behavioural performance is shown to be increased when subjects are given information about when a stimulus would appear. Then studies using both neuroimaging and electrophysiological techniques are discussed, which shed some light on the neural underpinnings of this behavioural enhancement by focusing attention within the temporal domain. Finally, direct comparisons are made between the orienting of attention in space and time, revealing that attention is a flexible cognitive process, which can operate at different levels of stimulus analysis.

It is important to note that the notion of focusing attention to a particular time point is distinct both from the "attentional blink", where stimuli compete for resources over a limited time window (14), and also attending to the temporal duration of a stimulus (e.g. (15)). Instead we ask whether the brain is capable of using temporal information to direct attention to a point in time when a stimulus is

expected in order to optimise behaviour, or rather whether the temporal alertness effects mentioned earlier reflect a fixed process that cannot come under conscious control.
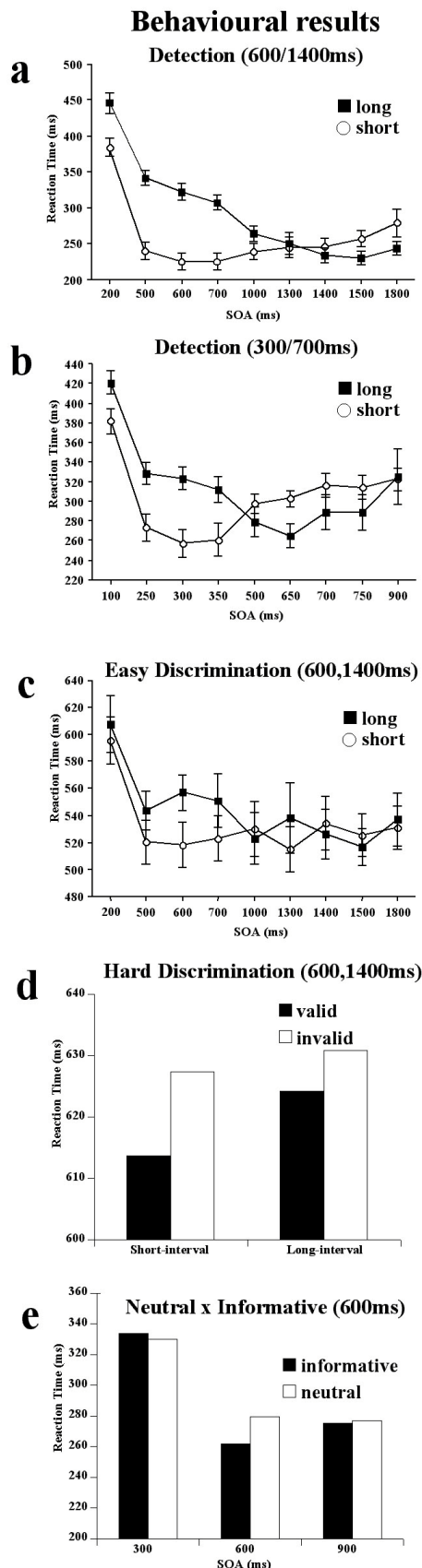
3. TEMPORAL ORIENTING

3.1. Behavioural studies

We developed tasks in which the warning signal (cue) provided information about when a stimulus would occur (see Figure 1), in an analogous fashion to the way subjects are cued as to where a stimulus will appear in studies of the spatial orienting of attention (16). Subjects were cued to expect target stimuli after a particular time interval (short or long). The cues predicted the correct time of stimulus onset on the large majority of trials (75-80%, valid cue), but occasionally predicted the time interval incorrectly (invalid cue). Cue and target stimuli were always presented foveally, so there was no spatial information available to guide detection or discrimination of targets. In this way we investigated whether we could use temporal information to enhance behavioural performance.

3.1.1. Experiment 1

In experiment 1 subjects (n=18) were cued to expect a target stimulus after either a short (600ms) or long (1400ms) interval (Figure 1a). The background visual display consisted of a composite cue with an inner and outer circle (0.1° and 0.7° visual angle respectively). The trial commenced with the brief (150ms) brightening of one of these circles, cueing the subject to expect either a short (600ms) or long (1400ms) delay between cue and target onset (stimulus onset asynchrony, SOA). The target stimulus consisted of either an upright cross (+) or a cross rotated through 45 degrees (x). Target stimuli appeared overlaid on the composite cue stimulus for 50ms. There were 9 possible SOAs: 200, 500, 600, 700, 1000, 1300, 1400, 1500 and 1800ms. The cues predicted the correct interval on 80% of trials. On invalid trials, the target appeared at one of the 8 remaining SOAs. Subjects were required to respond as quickly as possible as soon as they detected the target stimulus, while avoiding mistakes. No target discrimination was required. Reaction times to target stimuli occurring at both valid and the various invalid time points were measured in order to examine how predictive information about when target stimuli would appear affected behavioural performance.

The results from this experiment (Figure 2a) demonstrate our ability to use information about predicted time intervals to enhance behavioural performance. Reaction times were decreased to targets appearing after an expected time interval. A comparison of targets that appeared at 600ms revealed a 100ms benefit in reaction time when subjects expected the target at this time interval compared to when their temporal expectation was invalid (expected target at the long interval). Behavioural facilitation also occurred for stimuli occurring 100ms from the expected time point (500 and 700ms SOAs), with this perhaps being related to the limits of accuracy of time estimation. As quickly as 200ms after cue onset there was a behavioural advantage of attending to the short interval,

Behavioural results

a Detection (600/1400ms)

b Detection (300/700ms)

c Easy Discrimination (600,1400ms)

d Hard Discrimination (600,1400ms)

e Neutral x Informative (600ms)

Figure 2. (**a**) Mean reaction times and standard errors for targets in behavioural experiment 1, separated according to when subjects were cued to expect the target. The results showed main effects of cue validity (F(1,22)=91.90, p=0.0001) and SOA (F(8,176)=73.94, p=0.0001), and an interaction between cue validity and SOA (F(8,176)=19.16, p=0.0001). (**b**) Mean reaction times and standard errors for targets in behavioural experiment 2, separated according to when subjects were cued to expect the target. The results showed a main effect of SOA (F(8,64)=15.68, p=0.0001) and an interaction between cue validity and SOA (F(8,64)=8.50, p=0.0001). (**c**) Mean reaction times and standard errors for targets in behavioural experiment 3, separated according to when subjects were cued to expect the target. The results showed a trend for cue validity (F(1,8)=5.01, p=0.056) and a main effect of SOA (F(8,64)=13.07, p=0.0001). (**d**) Mean reaction times for targets at the short and long interval in behavioural experiment 4, separated according to the factor of cue validity. The results showed a main effect of cue validity (F(1,11)=13.89, p=0.003) and a trend toward an interaction between cue validity and SOA (F(1,11)=3.55, p=0.086). (**e**) Mean reaction times for targets appearing after 300, 600 and 900ms in behavioural experiment 5, separated according to whether the cue was neutral or informative. Informative cues predicted target appearance at 600ms (valid trials). The results showed a main effect of SOA (F(4,40)=55.01, p=0.0001) and an interaction between cue validity and SOA (F(4,40)=2.63, p=0.048).

illustrating that the preparatory processes initiated by the cue develop over time and start very soon after the cue. The different reaction time functions after the short and long cues indicate that the processes giving rise to such behavioural benefits are under flexible control, rather than having a fixed time course.

The advantage of being validly cued to expect the target after the long interval was much smaller than the advantage of being validly cued to expect the target after the short interval. A reason for this may be the fact that as the SOA increases, the probability of the stimulus appearing increases; i.e. the flow of time itself provides predictive information (cf. (17)). Subjects may have re-oriented their attention to the long interval if they were expecting the target after the short interval, and it did not appear (cf. (18)). Subjects therefore may be able to prepare for targets at long intervals regardless of whether they were cued to expect the target after the short or long interval. An alternative explanation would be that temporal orienting mechanisms dissipate after the first relevant time interval, and thus cannot affect targets at the long interval. However, the reaction times remain fast at the longer SOAs, suggesting a maintenance rather than a dissipation of attentional resources.

3.1.2. Experiment 2

Additional behavioural experiments have extended the investigation of selective temporal orienting by testing the roles contributed by specific SOAs, perceptual discriminations, and response requirements. Experiment 2 investigated more closely the time course of

our ability to direct attention to temporal intervals, by decreasing the range of time intervals at which the target stimulus could appear. It is possible that the short time interval in Experiment 1 (600ms) was the inherently optimal foreperiod for behavioural facilitation in this type of task. The result might therefore be a spurious occurrence, rather than reflect cognitive control of orienting attention to time intervals. We therefore tested subjects (n=9) using the same task but a different time frame (300 and 700ms). The stimuli and procedures were equivalent, except for the range of time intervals. The 9 possible SOAs were: 100, 250, 300, 350, 500, 650, 700, 750 and 900ms. Subjects were cued to expect either a short (300ms) or long (700ms) delay between cue onset and appearance of the target.

The pattern of results from this experiment (Figure 2b) were broadly similar to those of Experiment 1. Valid cueing produced reaction time benefits, with these effects being larger when subjects were cued to the short interval. The results showed that attentional resources can be allocated over time periods as short as 300ms, with benefits already present even 100ms after the cue. Behavioural advantages of attending to a specific time interval can thus occur over multiple time frames. Optimal behaviour is under flexible control according to the predictable stimulus contingencies, and is not fixed inherently at one given foreperiod (cf. (13)). There may be some constraints at very short or very long intervals. It will be interesting to observe whether such behavioural effects could be found for even shorter SOAs.

3.1.3. Experiment 3

The previous two experiments demonstrated decreased reaction times with selective temporal attention. This effect could be due to facilitated perception of stimuli occurring at the attended point in time, modulation of the motor response, or a more general mechanism, possibly involving a combination of the two. Experiment 3 manipulated motor variables associated with the task by asking subjects (n=9) to perform an easy perceptual discrimination between two target stimuli and make a choice response, as opposed to simply detecting them. The stimuli and procedures were the same as for Experiment 1, except that subjects were instructed to respond to one target stimulus (x or +) using the index finger of their right hand, and the other stimulus using the middle finger of their right hand. The requirement of a choice response probes whether the behavioural advantages are tied to a particular stimulus-response pair (specific motor preparation), or whether they reflect a more general attentional mechanism.

Again, results were broadly similar (Figure 2c). There was a behavioural benefit of valid cueing in this experiment, which was focused over the short interval. The behavioural effects were not as strong as those seen in Experiments 1 and 2, which may have resulted from variability in this particular small subject group, or reflected some contribution of specific motor preparation to the effects seen in the previous experiments. Choice reaction times were also generally longer than those for simple detection (Figures 2a and 2b), a well known phenomenon in the

alertness literature (e.g. (6)). Overall, the results showed that behavioural advantages from cueing information remain even when there is uncertainty as to the type of response to be given. Manipulating response demands does not completely abolish the effects of temporal orienting. This suggests that the processes underlying the orienting of attention in the temporal domain are not solely linked to preparation of a specific motor response. However, there may be some aspect of motor preparation or response timing involved in the effects seen, as the advantages of being cued to expect the target after the short or long interval are not as strong as in the detection experiments. Direct experimental comparisons between detection and discrimination procedures in the same subject group should yield additional interesting information.

3.1.4. Experiment 4

Experiment 4 manipulated perceptual variables within the time orienting task, by requiring subjects to make a difficult perceptual discrimination. The perceptual manipulation was used in order to test whether the requirement for more effortful visual analysis could contribute to the effect of temporal orienting. Subjects (n=12) made choice responses according to whether a small gap was present or not in the target stimulus (Figure 1b). The visual display of the task was slightly different to the tasks used in the previous experiments, and only two time intervals were used for target presentation. The background stimulus consisted of a circle (1.7° diameter) surrounding a small fixation point. The cue was either a narrow or wide cross (upper angle of 30° or 60° respectively) presented briefly (100ms) inside the circle. The narrow or wide cross cued the subject to expect the target after either a short (600ms) or long (1400ms) interval, with 80% validity. At one of the two intervals, the circle brightened for 100ms. Inside the circle a small gap could be present. Subjects made speeded choice responses using the index or middle finger to indicate whether the gap was present or absent. There were 10% invalid trials and 10% catch trials where no target stimulus was presented. The size of the gap was automatically adjusted by computer between blocks to maintain performance between 75-95% accuracy.

The behavioural advantage for targets at correctly predicted time intervals was maintained with a difficult perceptual discrimination (Figure 2d). As with the previous discrimination experiment, the effects were modest and the average reaction times were longer than those seen in the earlier detection experiments. The difficult perceptual discrimination diminished but did not eliminate the effect of temporal orienting. The opportunity for additional perceptual aspects of attention did not appear to increase the attentional effects. This supports the interpretation that the effects of temporal orienting may be biased toward the post-perceptual aspects of stimulus processing. However, one cannot rule out modulations at the perceptual level based on these reaction-time results alone.

3.1.5. Experiment 5

Experiment 5 investigated whether the effects of temporal orienting reflected mainly benefits or costs. Reaction times in 11 subjects were compared when cues

were predictive or neutral regarding the time interval of the target. The stimuli and procedures were based on Experiment 1, but with the following modifications. The informative cue (150ms duration) predicted (80% validity) target appearance after 600ms. On invalid trials targets appeared at one of four alternative SOAs: 300, 450, 750 or 900ms (5% probability each). When the cue was neutral the target appeared at one of 21 SOAs: 100, 150, 200, 250, 300, 350, 400, 450, 500, 550, 600, 650, 700, 750, 800, 850, 900, 950, 1000, 1050, 1100ms (5% probability each, except for extreme SOAs where the probability was 2.5%). The task consisted of simple detection of the target stimulus (50ms duration).

The results of this experiment (Figure 2e) indicate that the behavioural advantages conferred by attending to a particular point in time are best conceptualised in terms of behavioural benefits of valid cueing, rather than costs of invalid cueing. The effect can also be thought to correlate with the absolute probability of target occurrence at a given interval, since the absolute probability differed only between valid (80%) and neutral (5%) trials, but not between invalid (5%) and neutral (5%) trials at comparable intervals. The behavioural advantages of valid cueing were evident as mainly decreased reaction times to validly cued targets at 600ms, as opposed to targets preceded by neutral cues. There was no increase in reaction times to invalid as opposed to neutral trials. In fact, the invalid trials with targets at 750ms actually showed decreased reaction times compared to neutral trials. This could be due to a number of factors. Firstly, as mentioned earlier, the conditional probability of the target appearing increases with longer SOAs (17). This is unlikely to be the sole explanation, since no reaction time advantage was found for the targets following predictive cues at 900ms. These targets have the highest conditional probability in informative trials, which is higher than the conditional probability of targets at equivalent intervals during neutral cueing. Alternatively, the temporal information in the predictive trials may have spilled over into the adjacent interval, due to limits of time estimation. Facilitation of reaction times to targets in nearby intervals is a consistent pattern in these experiments (see Figure 2).

3.1.6. Behavioural conclusions

Together, the behavioural experiments have shown that predictive (probabilistic) information about the time interval of target appearance can be used to optimise behavioural performance. Reaction times to detect or discriminate a target are facilitated by valid temporal cueing, at multiple time frames. The effect survives manipulation of specific SOAs, response requirements and perceptual judgements. There are many additional parameters that remain to be tested behaviourally, such as the limits of the time frames that afford temporal orienting, the minimum difference required between possible intervals, the effect of stimulus modalities, etc. Another aspect for investigation is the neural mechanisms for selective temporal orienting. The studies so far have shown that the effect does not depend upon specific motor programming, and can survive difficult perceptual thresholds. However, neither response nor perceptual

variables can be excluded from participating in temporal orienting. Additional behavioural experimentation may help shed light upon the levels at which temporal orienting can exert its effect upon target processing. For example, measurements of different types of perceptual thresholds may indicate whether and which perceptual levels may be affected. However, teasing apart what may be multiple effects of temporal orienting with behavioural manipulations alone can prove to be very difficult, since response variables are influenced by rate-limiting steps and bottlenecks of cognitive processes, which may interfere with the readout of some levels of stimulus processing. Event-related potentials were therefore used, to provide a measure of on-line information processing during visual temporal orienting experiments.

3.2. Event-related potentials

Event-related potentials (ERPs) have provided an important means of investigating attentional processing in the human brain, giving a more complete picture of stimulus processing than behavioural measures alone. Their high temporal resolution provides information about the on-line modulation of brain activity by attention, and about the level of stimulus processing at which attention acts. They also provide a measure of stimulus processing without any requirement for the subject to attend or respond to that stimulus, thus allowing comparison of the processing of both attended and unattended stimuli during conditions of focused selective attention.

Miniussi *et al* (19) used ERPs to investigate the selective orienting of attention to time intervals. The mechanisms involved in *orienting* attention in the temporal domain were reflected by ERPs elicited by the cues. The mechanisms for *modulation* of stimulus processing by temporal attention were reflected in ERPs elicited by predicted and unpredicted target stimuli. The task used was similar to Experiment 4 (see Figure 1b). Cues were narrow or wide crosses (100ms duration) that predicted the appearance of the target after a short (600ms) or long (1400ms) SOA. The target consisted of the brightening of the circle surrounding the cue for 100ms. The cues had 80% validity, with 10% invalid and 10% catch trials. The EEG was recorded continuously from 54 electrode sites positioned according to the 10-20 International System (20).

A behavioural benefit of temporal attention was found (Figure 3a), similar to those seen in the purely behavioural experiments. Subjects were significantly faster to detect valid than invalid targets after the short interval. Analysis of ERPs elicited by the cueing stimuli (during the cue-target interval) revealed dynamic brain activity linked to orienting attention in time. Differential processing of cues predicting short and long intervals modulated the CNV (contingent negative variation) component (see (21)). The CNV is a slow negative voltage change occurring between two stimuli, with the first stimulus being a warning signal and the second stimulus requiring a response. It has been linked to expectancies and motor preparation (see (22,23,24,25)). The CNV was significantly accentuated when subjects expected targets at the short

a Behavioural Results
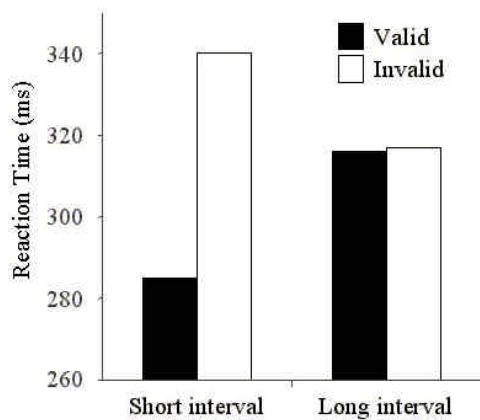
b ERPs to Cues
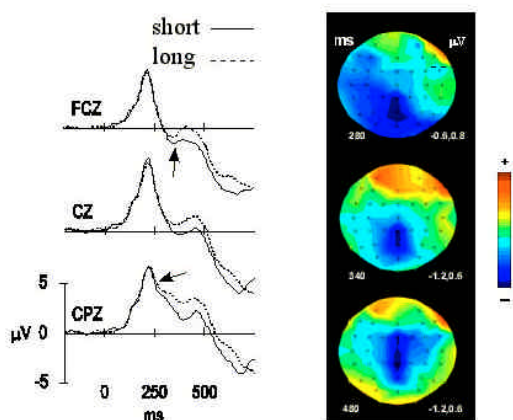
c ERPs to Targets (short interval)
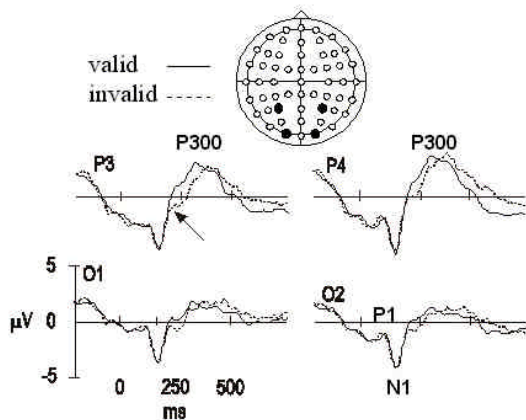
Figure 3. Behavioural and ERP results from Miniussi *et al* (19). **(a)** Mean reaction times for targets at the short and long interval separated according to the factor of cue validity. The results showed that valid targets were detected faster at the short intervals. **(b)** Grand-averaged ERPs evoked by cues at representative midline electrode sites. Positive polarity is plotted upward in this and all subsequent figures. ERPs to cues predicting either a short or long interval show a significant modulation starting around 280ms, and included modulation of the CNV component. The distribution of the CNV effect between 280 and 480ms is shown on the scalp topography. The colour scale (coloured bar on the right) shows the range of possible voltage values in the topographies. The voltage range for the topographies is presented below each map. **(c)** Grand-averaged ERPs elicited by targets at the short interval are shown for the electrodes shaded black in the electrode montage. There was no modulation of visual evoked potentials P1 and N1 at posterior electrodes, but there was modulation of the latency and amplitude of the P300 potential at parietal and central sites.

interval, starting around 280ms (Figure 3b). The greater negativity when subjects attended to the short interval can thus be interpreted as an index of expectancy for an upcoming stimulus, with subjects expecting the target to appear, and demand a response, very soon. This suggests that orienting attention in time modulates brain processes linked to motor preparation and expectancies. This effect is markedly distinct from those seen during the cue-target interval in studies of spatial attention (e.g. (26,27,28)). During visual spatial orienting lateralised posterior and then anterior potentials are modulated according to the predicted location of the stimulus. The striking difference in ERP modulations in tasks of temporal and spatial orienting suggests that these two forms of selective expectancies may affect behavioural processing via very different mechanisms.

Analysis of ERPs elicited by the target stimuli revealed the modulatory effect of temporal attention on stimulus processing (Figure 3c). Unlike studies of spatial attention (see (29,30)), temporal orienting did not enhance the early visual-evoked potentials (VEPs). Temporal attention did have a modulatory effect on brain activity after the visual components. Differences were observed in the amplitude of the N2 potential, and the amplitude and latency of the P300 potential. These potentials have been linked to expectancies, decisions, and motor preparation (e.g. (29,31,32)). Latency changes in the P300 have not been previously observed in studies of spatial attention, and may represent a novel mechanism of behavioural enhancement by temporal attention. P300 latency changes may reflect the anticipation or sharper temporal tuning of decision- or response-related variables afforded by the predictive temporal cues. The absence of VEP modulation and emphasis on modulation of later, response-related potentials suggests that temporal orienting exerts its effects via different mechanisms than spatial orienting. However, one important confound remains, which constrains the interpretation of the results. Unlike most spatial attention studies, this task used bright transient foveal stimuli. The

processing of foveal stimuli may already be optimised by the visual system, so there may be no need to enhance resources further, thus explaining the absence of early VEP modulation. Temporal orienting may therefore affect stimulus processing by different, or additional, mechanisms to the early perceptual modulation seen in studies of spatial attention.

Although yielding information about the modulatory mechanisms of temporal orienting, ERPs are not particularly useful in identifying the neural system controlling the orienting of attention toward specific time intervals, due to their poor spatial resolution. Brain imaging techniques such as PET (positron emission tomography) and fMRI (functional magnetic resonance imaging) afford a much more detailed analysis of the neuroanatomical substrates of temporal orienting, and are now considered.

3.3. Brain Imaging

An experiment using event-related fMRI revealed the brain areas that participate in temporal orienting, and their sensitivity to trial validity and SOA (33). The task used was a simplified version of Experiment 1 (see Figure 1a). Inner or outer circular cues (100ms duration) predicted (80% validity) either a short (600ms) or long (1400ms) cue-target SOA. The target (50ms duration) was an upright cross and required a speeded detection response by pressing a button with the right index finger. The results supported the modulation of brain activity linked to motor preparation and attention during temporal orienting.

The comparison between invalid and valid trials isolated brain activity linked to attentional variables. Sensory and motor variables are well controlled. During invalid trials, temporal expectations are breached and attention is shifted from one time point to another. Invalid trials preferentially activated inferior parietal, inferior premotor and prefrontal areas in the left hemisphere predominantly, as well as orbitofrontal cortex bilaterally (see (34)). Activations in similar left-hemisphere parietal and premotor areas have been found during studies of motor preparation (35,36). Furthermore, patients with left parietal lesions have deficits in a motor orienting task, in which the cue predicts the type of motor response to the stimulus, rather than its spatial location (35). The role of the left parietal cortex in motor control and attention is also emphasised by the incidence of motor apraxic deficits after lesions to this brain area (37). This suggests that orienting attention in time is closely linked with motor preparation and motor attention.

The comparison between valid trials with long and short SOAs emphasised brain activations linked to timing, anticipation, and motor readiness. Long-interval trials enhanced activation in the medial premotor cortex in the region of the anterior supplementary motor area (SMA), left putamen and the thalamus bilaterally. These brain regions have a well-known role in the timing and readiness of motor responses (e.g. (25,38)). Their modulation during temporal orienting suggests the ability to affect variables related to motor readiness to optimise behavioural responding, as suggested by the ERP experiment (19).

Further fractionation of the processes that can be involved in orienting attention in time came from comparing brain activation during the two types of invalid trials. Trials in which a target is expected at the short interval but does not appear may permit subjects to re-orient attention voluntarily to the later time point, thus emphasising top-down, endogenous control mechanisms. Contrastingly, targets that appear sooner than expected may automatically grab attention, thus emphasising bottom-up, exogenous shifts of temporal attention. Indeed, brain activation differed in the two types of trial, supporting the existence of endogenous and exogenous control of temporal orienting. Endogenous temporal orienting involved activations in right frontal cortex (including dorsolateral and ventrolateral areas), and left superior parietal lobule. These prefrontal activations are coherent with the notion of a higher order, "top down" attentional mechanism being involved in endogenous shifts. Exogenous shifts were associated with increased activation in visual extrastriate cortex, consistent with the notion of a "bottom up" attentional mechanism being involved in exogenous shifts of temporal attention, being subserved by sensory association cortex.

In conclusion, the brain system for temporal orienting appears to involve a left-hemisphere dominant frontal-parietal network, which also interacts with areas related to motor attention and motor readiness. The brain-imaging results thus support the suggestion from the ERP experiments that modulation of motor-related variables plays an important role in temporal orienting. Activity is also co-ordinated with other areas subserving specific aspects of temporal orienting, such as prefrontal control and visual areas. Studies of temporal orienting have not yet been conducted on neurological patients, but we would predict that patients with lesions to left parietal-frontal areas would show significant deficits in orienting attention to time intervals. Patients with lesions in areas related to motor preparation, such as basal ganglia and SMA are also likely to show impairments. It will be interesting to test different groups of patients on these tasks.

4. COMPARISON OF SPATIAL AND TEMPORAL ORIENTING

To test whether there exists a single attentional system, or rather different subsystems depending on the information available to guide selection, we directly compared temporal orienting with visual spatial orienting. Visual spatial orienting is the most well studied type of selective attention and therefore provides a useful framework for comparison. The neural system for visual spatial orienting has been investigated by both brain imaging (e.g. (39,40,41)) and neuropsychological studies (see (42) for review). Convergent findings from these experiments have suggested a large-scale frontal-parietal network of brain regions that support spatial attention. ERP studies have suggested that spatial attention acts by modulating early visual processing in extrastriate areas (see (29,30,43)).

a Task

b Behavioural Results

c Brain Activations
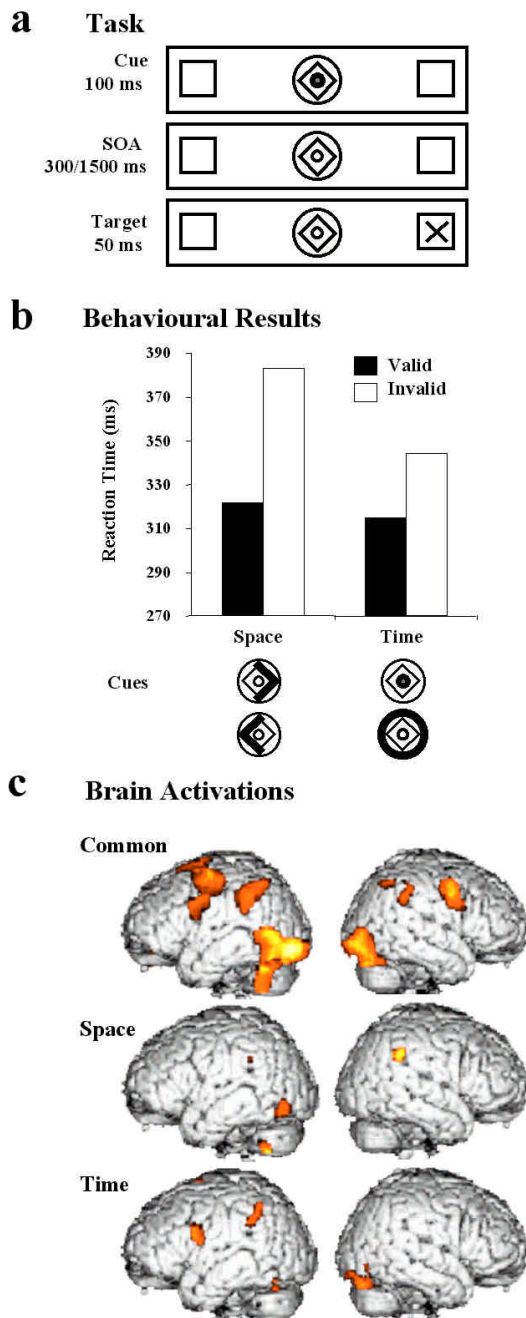
Figure 4. Task and results from Coull and Nobre (44). **(a)** The central symbolic cue predicted (80% validity) either the location or time interval of target appearance (see text). **(b)** Mean reaction times to valid and invalid targets in the spatial and temporal orienting conditions. Valid targets were detected more quickly in both the spatial and temporal orienting conditions. **(c)** PET brain activations superimposed upon a representative brain volume with standardised anatomy, from left and right lateral perspectives. The top row shows common areas activated in both the orienting conditions. The next two rows show selective parietal and frontal activations for spatial and temporal orienting respectively.

The studies of temporal orienting discussed above suggest that different brain systems and mechanisms may be at play. However, the interpretations are hindered by the lack of direct comparisons and by the use of foveal stimuli. Further experiments were thus conducted to compare temporal and spatial orienting in the same subjects using identical peripheral stimuli. Brain-imaging studies were used to reveal the networks of brain areas engaged, and ERP studies to reveal the mechanisms.

4.1. Brain imaging

Coull and Nobre (44) used both PET and fMRI to compare directly the neural systems involved in temporal and spatial orienting of attention. It was of interest to see whether there was a general system for allocating attentional resources, independent of stimulus dimension, or whether there are functionally specialised brain regions involved in directing attention to spatial or temporal aspects of the environment.

The task (Figure 4a) manipulated subjects' expectations of where and when a peripheral target stimulus would occur. The use of peripheral, as opposed to foveal, targets afforded a direct comparison between the spatial and temporal orienting of attention. Symbolic central stimuli oriented subjects either to a spatial location (left, right) or temporal interval (300, 1500ms). The central stimulus consisted of a diamond and two concentric circles. Cueing involved the brightening (100ms) of part of this compound stimulus. During spatial orienting, the left or right side of the diamond brightened to indicate that the target was likely to appear in the left or right peripheral box respectively. During temporal orienting the brightening of the inner circle indicated that the target would appear after the short interval (300ms) and the brightening of the outer circle represented target appearance after the long interval (1500ms). The cues had 80% validity, and subjects responded by pressing a button with their right index finger.

Behavioural advantages of valid cueing were found for both spatially and temporally informative cues (Figure 4b), These results show that the benefits of orienting attention to time are not restricted to foveal stimuli. There was considerable overlap between the activations seen in the spatial and temporal orienting tasks in frontal and parietal regions compared to a low-level resting baseline (Figure 4c). This is consistent with the suggestion of a large scale frontal-parietal attentional network (e.g. (41,45,46)), and extends this view by showing that these areas may represent a general network for attentional orienting, not restricted to the spatial domain.

However, when identifying areas specifically involved in focused spatial and temporal attentional orienting (removing sensory and motor activations), there was a hemispheric lateralisation within this common frontal-parietal system. There was a preferential activation of the right posterior parietal cortex by spatial orienting, consistent with previous brain imaging studies(39,40,41,46)) and neuropsychological evidence (see

a Task

b Behavioural Results

c ERPs to Bilateral Arrays
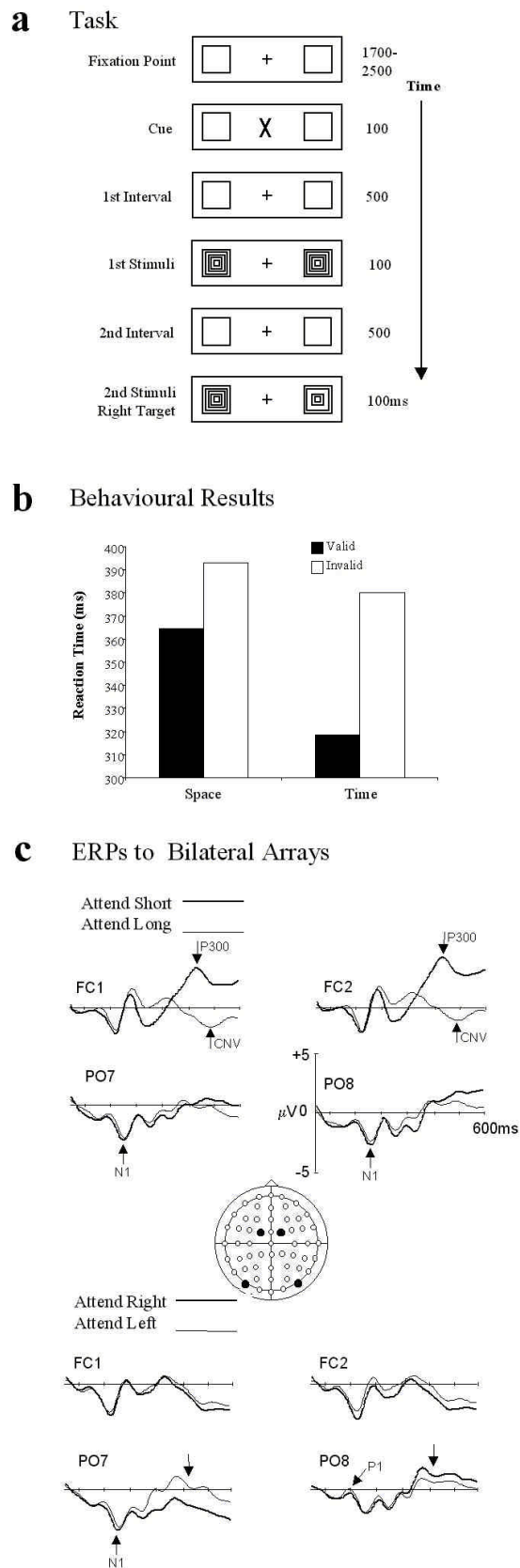
Figure 5. Task and results from Griffin *et al* (47). **(a)** The cue predicted either the spatial location (spatial orienting) or time interval (temporal orienting) of target appearance. The cue was followed by two bilateral stimulus arrays. The target was presented at one of the two spatial locations at one of the two time intervals. **(b)** Mean reaction times to valid and invalid targets in the spatial and temporal orienting conditions. Valid targets were detected more quickly in both the spatial and temporal orienting conditions. For temporal orienting the effect was most pronounced at the short interval (not shown). **(c)** Grand averaged ERPs to the bilateral arrays in the temporal orienting (upper panel) and spatial orienting (lower panel) conditions, at representative electrode sites (shaded black on montage). The ERPs showed distinct patterns of modulation by spatial and temporal orienting. Temporal orienting modulated the N1 component at posterior electrodes bilaterally, and the P300 component at central electrode sites. Spatial orienting modulated the P1 and N1 potentials at lateral posterior electrodes.

(42) for review). Temporal orienting was associated with preferential activation of the left parietal and inferior premotor cortex, as seen by Coull *et al* (33) (see section 3.3 for discussion). This shows that within the core frontal-parietal network that supports attentional orienting, differential involvement of specialised areas is also possible, depending on the type of information available to guide orienting. In addition to the cortical activations, the cerebellum was also engaged in the orienting tasks. Some cerebellar regions were active in both tasks, whereas others were selective for spatial or temporal orienting. The cerebellum has been increasingly implicated in cognitive functions such as attention. However, its role in attentional orienting requires further clarification.

4.2. Event-related potentials

A study by Griffin *et al* (47) compared the neural correlates of focusing visual attention to spatial locations and temporal intervals, using ERPs to measure real-time modulatory effects of spatial and temporal attention on stimulus processing. Of specific interest was whether selective spatial and temporal orienting acted at the same or different level(s) of stimulus analysis. To achieve this a symbolic central cue generated either a spatial or temporal expectancy, then ERPs to identical target stimuli in the two conditions were analysed.

Two task conditions using identical stimuli were performed by subjects in separate sessions. The task (Figure 5a) used symbolic central cues consisting of a narrow or wide cross (upper angle of 30° or 60° respectively), which were flashed for 100ms. There was a 500ms interval following the cue, after which two peripheral patterns of concentric squares simultaneously appeared, one on either side. These were presented for 100ms. There was then another 500ms interval, followed by two more patterns of squares flashed simultaneously for 100ms. The target consisted of a pattern with one of its inner concentric squares missing, and occurred at one of the two locations, at one of the two time intervals. In the temporal

orienting condition, the appearance of the narrow or wide cross cued subjects to expect the target after the first interval (short, 600ms from cue onset) or second interval (long, 1200ms from cue onset). No information was given about probable target location (left, right). The spatial orienting condition used exactly the same stimuli and timing, except the narrow or wide cross cued the subjects to expect the target at either the left or right location, with no information being given about probable target interval. In both conditions the cues had 75% validity.

Behaviourally, valid cueing produced significant reaction-time benefits in both the spatial and temporal orienting conditions (Figure 5b). Consistent with previous temporal attention experiments (e.g. (19)), benefits only occurred when targets appeared at the short interval in the temporal orienting condition.

ERPs were analysed to identical, non-target bilateral stimulus arrays occurring after the first interval. These highly controlled conditions ensured that there were no attributes in the stimulus array that could automatically "grab" attention selectively, making it possible to isolate purely endogenous attentional mechanisms (see (48,49)). The ERP analysis revealed that the optimisation of behaviour by spatial and temporal orienting is achieved via different attentional mechanisms (Figure 5c).

Spatial attention modulated the amplitude of visual-evoked components P1 and N1. This is consistent with previous studies of spatial attention (e.g. (29)), and confirms the ability of spatial attention to modulate early stages of stimulus processing.

Temporal orienting involved a different pattern of modulation to spatial orienting, with the early perceptual P1 component being unaffected. The N1 component was modulated by temporal attention, but with a different and non-lateralised scalp distribution. The N1 modulation by temporal attention demonstrated here, something not found by Miniussi *et al* (19), suggests that temporal attention can modulate visual processing, though in a different, and more diffuse, manner than spatial orienting.

The later effects of temporal attention were similar to those seen by Miniussi *et al* (19), that is, modulation of the N2 and P300 components. N2 modulation has been interpreted as reflecting response inhibition (32, 50), and found in response to stimuli occurring at unexpected times (51). P300 modulation is also thought to reflect response preparation and functional decision processes (29), or the occurrence of unexpected stimuli (31). These later effects of temporal orienting can thus be seen to be linked to decisions and responses, and are distinct from those seen during spatial orienting. It can therefore be seen both that the behavioural advantages of spatial and temporal orienting are due to distinct modulatory effects upon stimulus processing, and, more generally, that attention is a flexible cognitive process that can operate at both early (perceptual) and late (response-related) levels of stimulus analysis depending on the nature of the information available.

5. SUMMARY AND CONCLUSIONS

In conclusion, we have shown that we can use predictive information about time intervals to direct our attention to a predicted point in time, and enhance behavioural performance. Temporal orienting appears to be under flexible control, with behavioural advantages being seen for stimuli occurring over multiple time frames. Temporal orienting involves processes linked to motor readiness and expectancies, and generally modulates response-related stages of stimulus processing. The neuroanatomical substrates of temporal orienting include a frontal-parietal network of areas with a left hemisphere bias, as well as co-ordinated activity in areas related to motor attention and readiness. One important domain for further exploration is whether overt and speeded motor responses are required to observe the effects of temporal orienting. Tasks in which no on-line responses are required to temporally expected stimuli are needed to address this concern. In addition, it will be interesting to test whether the patterns of brain activation depend specifically on the type of motor response required (e.g., comparing button presses, eye movements and verbal responses).

The comparison of temporal and spatial orienting reveals that there is not a single mechanism of action or a ubiquitous attentional system in the brain. Rather, the information available for selection, and the demands of the task dictate which functionally specialised brain areas will support the optimisation of behaviour by attentional orienting. Such behavioural enhancement by predictive information may be achieved by different modulatory effects on stimulus processing, from perceptual to motor-related effects, depending on the nature of the task. This illustrates the flexibility of attentional functions in the human brain. Further fractionation of the neural systems and brain mechanisms that support the orienting of attention will shed light into the gamut of potential ways in which behavioural performance can be enhanced.

6. ACKNOWLEDGEMENTS

7. REFERENCES

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