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Research Report

Temporal attention enhances early visual processing: A review and new evidence from event-related potentials

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ABSTRACT

Two fundamental cognitive functions, selective attention and processing of time, have been simultaneously explored in recent studies of temporal orienting of attention. A temporal-orienting procedure may consist of a temporal analogue to the Posner's paradigm, such that symbolic cues indicate the most probable moment for target arrival. Behavioral measures suggest that performance is improved for events appearing at expected vs. unexpected moments. However, there is no agreement on the locus of stimulus processing at which temporal attention operates. Thus, it remains unclear whether early perceptual or just late motor processes can be modulated. This article reviews current ERP research on temporal orienting, with an emphasis on factors that might determine the modulation of temporal orienting at early stages of processing. We conclude that: First, late components (N2 and P300) are consistently modulated by temporal orienting, which suggests attentional preparation of decision and/or motor processes. Second, early components (e.g., N1) seem to be modulated only when the task is highly demanding in perceptual processing. Hence, we conducted an ERP experiment which aimed to observe a modulation of early visual processing by using a perceptually demanding task, such as letter discrimination. The results show, for the first time, that targets appearing at attended moments elicited a larger P1 component than unattended targets. Moreover, temporal attention modulated the amplitude and latency of N2 and P300 components. This suggests that temporal orienting of attention not only modulates late motor processing, but also early visual processing when perceptually demanding tasks are used.

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1. Introduction

Timing is an essential function for intelligent organisms to coherently represent and to act upon the changing elements that structure our dynamic world. Some examples in which perceptual input is organized into temporal patterns are perception of motion, music or speech. Other activities illustrate the involvement of timing to organize motor output

(Rosenbaum and Collyer, 1998), such as performing complex skills as sports, driving or speech production, as well as more basic actions such as reaching objects.

Another function that was presumably crucial in the past to successfully adapt ourselves to the environment is selective attention. Selective attention refers to the plastic ability to prioritize processing of certain stimulus features relevant to the individual's goals, in order to produce efficient behavior.

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Since the seminal work by Posner et al. (1978), many attentional-orienting studies have explored the effects of cueing in advance information concerning target features, such as its location, speed, color, shape, identity, semantic meaning and so on (e.g., Corbetta et al., 1990). They have reported benefits on reaction time (RT) and/or accuracy in a variety of tasks when the target matches the cued feature (valid trials), compared to when such matching does not occur (invalid trials). A simple explanation is that cues allow an extra processing of the relevant target feature during the delay between cue and target (i.e., stimulus onset asynchrony or SOA). This extra processing may consist of a deployment of attentional resources to specific brain areas that code the relevant feature, thus enhancing the speed or the quality of the processes involved in the task.

Relatively recent studies based on physiological measures have discovered a network of brain areas recruited in focusing visual attention to spatial locations (Corbetta and Shulman, 2002). In addition, neuroscientists are interested in exploring how this attentional-orienting mechanism modulates stimulus processing. Thus, an important issue of research is to track the locus of attentional effects underlying behavioral benefits. Research on spatial attention has shown that attending to targets presented at one location leads to increments in both early electrophysiological activity over occipital sites (see Mangun, 1995; Luck et al., 2000, for reviews) and regional cerebral blood flow in extrastriate cortex contralateral to the attended location (Heinze et al., 1994). These data suggest that attention enhances early perceptual processing of targets appearing at cued locations. Moreover, spatial attention has been shown to increase late electrophysiological activity related to decision and motor processes (Mangun, 1995). Taken together, these results indicate that spatial attention improves performance by producing a preparation of both early perceptual and late motor processing related to target stimuli.

Although space has been the predominant dimension in visual attention research, Nobre and colleagues gave an impetus to the study of orienting attention to time. Thus, two fundamental cognitive functions, selective attention and processing of time, were simultaneously explored. They have shown that the moment of target onset could also be a relevant feature, to which attention can be intentionally committed (Coull and Nobre, 1998, see also Kingstone, 1992). The traditional procedure used by Posner's group to study spatial orienting of attention (Posner et al., 1978) was modified as follows. Instead of spatial cues, Coull and Nobre presented symbolic temporal cues to indicate that the target would appear either early (after a short interval of 400 ms) or late (after a long interval of 1600 ms). Then, the SOA was manipulated such that the target actually appeared at the validly cued time interval in 80% of trials. The target appeared at the uncued interval in the remaining 20% of trials. Participants were asked to detect the target onset (a cross) as fast and accurate as possible. Behavioral data revealed validity effects restricted to the short SOA, such that RTs were faster for the early cue-short SOA condition compared to the late cue-short SOA condition. This result has been abundantly replicated (e.g., Naccache et al., 2002, see Nobre, 2001, for a review), and also extended to the long SOA in our laboratory (Correa et al., 2004, see Discussion for details).

Concerning the locus of attentional modulation, neuroimaging research has revealed selective activations in left premotor cortex produced by temporal attention as compared to spatial attention (Coull et al., 2000; Coull and Nobre, 1998). This finding suggests a prevalence of motor over perceptual preparation processes in temporal attention. However, this result has been observed when detection tasks that demand a speeded motor response are used. Therefore, it might be the case that the observed modulation of motor processes is not related to temporal orienting per se, but to the use of a simple detection task.

On the other hand, observing temporal orienting effects on RT in discrimination tasks opened the possibility of a perceptual preparation (Correa et al., 2004; Griffin et al., 2001; Milliken et al., 2003). Thus, attention may facilitate perceptual processes involved in analyzing object features, which are essential to accomplish discrimination tasks. However, the motor account cannot be ruled out, since such results could be merely due to a facilitation of later postperceptual processes, such as decision or motor response execution, which are also demanded in choice-RT discrimination tasks (Nobre, 2001).

More convincing evidence comes from a psychophysical study that showed selective increments in perceptual sensitivity (as indexed by d') with no changes in response criterion (as indexed by beta), produced by the temporal orienting of attention (Correa et al., 2005). Motor explanations were weakened in this case, as the task minimized motor requirements by demanding unspeeded responses, whereas perceptual demands were optimized by asking for accuracy in responding, and principally by using a rapid serial visual presentation procedure in which perception of the target became quite difficult. In spite of the fact that research has correlated d' to perceptual processing in visual cortex (Luck et al., 1994; Ress et al., 2000), one might argue that d' is not a pure index of perceptual processing which can be influenced by postperceptual factors (see, for example, Correa et al., 2005).

In sum, although behavioral findings are suggestive, they are unsatisfactory to confidently claim that temporal attention enhances early perceptual processing. More compelling evidence would be provided if we use a more direct measure of processing. Considering the high temporal resolution of the event-related potential (ERP) methodology, this technique is especially appropriate to explore on-line the dynamic modulations of temporal attention on processing (Doherty et al., 2005).

Hence, the aim of the present work is twofold. We first present a review of the current ERP research on temporal orienting, with special attention being paid to the differential characteristics between experimental procedures that might determine the finding of modulations at early stages of processing. Then, we report an ERP experiment which included key aspects in its design to observe such modulations, according to the conclusions of the review.

1.1. ERP research on temporal orienting of attention: a review

The ERP research on temporal attention is summarized in Table 1.

Table 1

Manuscript	Task	Conditions	Exp.	ERP component	T. window	Amplitude	Latency	Interpretation
Miniussi et al. (1999)	Temporal cueing Onset detection 80% validity	Valid vs. Invalid at short SOA	1	P1	60–140	–	–	Temporal attention seems not to involve perceptual preparation Breaches in expected stimulus associations Temporal attention synchronizes and prepares motor processes (decisions/responses)
				N1	100–200	–	–	
				N2 (occipital)	200–300	↑ Invalid	–	
				P300	250–500	↑ Valid (over midline and posterior areas)	↓ Valid	
Griffin et al. (2002)	Temporal cueing Feature detection Peripheral targets (Exp. 1: bilateral Exp. 2 unilateral) 75% validity	Attended vs. Unattended non-target arrays at short SOA	1	P1	80–120	–	–	Different mechanisms for spatial and temporal attention Perceptual preparation by temporal attention Unclear
				N1 (bilateral)	120–200	↑ Attended	–	
				N2 (occipital)	240–320	↑ Attended	–	
			2	P300	250–500	↑ Attended	↓ Unattended	Decision processes and preparation for responses
				P1	80–120	–	–	
				N1	120–200	–	–	
				N2	250–300	↑ Unattended ($P = 0.058$)	–	
Lange et al. (2003)	Auditory stimuli Temporal cueing (between-blocks) Intensity discrimination 50% validity	Attended vs. Unattended standards at both SOAs	1	P300	250–500	–	↓ Attended	Related to go/nogo tasks (response inhibition) or to temporal deviant stimuli Motor preparation Modulation of early perceptual processing (gating process) Response to infrequent stimuli, novelty detection Amount of information delivered
				N1 (frontal)	100–140	↑ Attended	–	
				N2 (target vs. standard)	225–275	↑ Target	–	
				P300	300–370	↑ Attended	–	
Correa et al. (2005)	Temporal cueing (between-blocks) Discrimination 75% validity	Valid vs. Invalid at short SOA	1	P1	130–170	↑ Valid	–	Enhancement of early visual processing – Conflict detection Synchronization and preparation of decisions/responses
				N1	250–290	–	–	
				N2	360–400	↑ Invalid	↓ Valid	
				P300	500–540	↑ Invalid	↓ Valid	
Doherty et al. (2005)	Motion cueing Feature detection (50% go/nogo) Peripheral target	Temporal vs. Neutral expectancy	1	P1	110–130	–	–	Lack of retinotopic representation of time Visual or post-visual processing (time perception) Temporal uncertainty Enhancement of late decision and motor processes
				N1 (central-occipital)	170–190	↓ Temporal	–	
				N2 (central-parietal)	220–330	↑ Neutral	–	
				P300	500–600	–	↓ Temporal	
Correa and Nobre (in preparation)	Motion cueing Feature detection (80% go/nogo); -Peripheral target; -50% validity	Valid (50%) vs. Early-Invalid (25%)	1	P1	80–120	–	–	No perceptual demands in this task – Temporal uncertainty or conflict detection Synchronization and preparation of decisions/responses
				N1	160–220	↑ Valid (right hemisphere)	–	
				N2	230–270	↑ Invalid	↓ Valid	
				P300	350–450	↑ Valid	↓ Valid ($P = 0.06$)	

Note. The manuscripts are organised by rows. Each column includes information about the ‘task’, ‘conditions’ (those included in the ERP analysis, which showed significant behavioural effects). ‘Exp’ refers to the experiment number in the manuscript. Then, the ‘ERP component’ and the temporal window (‘T. Window’) used in the analysis are specified. Finally, the table shows the results on ‘amplitude’ and ‘latency’ measures and their ‘interpretation’, as proposed by the authors.

To our knowledge, the first ERP experiment that studied temporal orienting was carried out by [Miniussi et al. \(1999\)](#). The task was very similar to that used by [Coull and Nobre \(1998\)](#); see above), that is, symbolic central cues indicated when the target would appear, with a probability of 0.80. The target to be detected was an abrupt onset of a cross symbol. Event-related potentials evoked by valid vs. invalid targets were compared at the short SOA. One important aspect was that all stimuli were presented foveally.

The major result was a modulation of the P300 latency, such that it peaked earlier for valid targets. This result is not usually reported in spatial attention research, so it seems characteristic of temporal attention. The authors suggested that temporal information may be used to synchronize and/or prepare motor processes, or sharpen processes linked to decisions or responses (p. 1516). The P300 amplitude was larger for valid targets, though the effect was significant only with additional analyses over midline and posterior areas. The N2 component was not considered a priori in the analysis. However, it showed to be influenced by temporal attention, such that invalid targets elicited a larger N2 over occipital sites. Miniussi et al. related this unexpected effect to the N2 component typically found in go/nogo tasks, so it was linked to a response inhibition process. However, the N2 in go/nogo experiments shows a scalp distribution which is more anterior than the observed for the temporal attention manipulation. Then, the authors proposed that the N2 effect could rather index the result of breaches in the expected stimulus associations that guide responses ([Nobre et al., 1999](#)).

As a general conclusion, given that attentional modulations were found in late but not in early ERP components, they naturally interpreted that temporal attention seemed not to involve a perceptual preparation. Rather, temporal attention enhanced potentials related to motor processing. However, the authors did not draw strong conclusions from that null effect and recognize a potential lack of sensitivity in their task. Importantly, it might be that attention was not needed in their task to further optimize visual processing, as all the stimuli were presented at an area already optimized (i.e., the fovea). Moreover, the abrupt onset of the target did not imply a considerable perceptual demand to accomplish the detection task.

Hence, two subsequent experiments were conducted to test these issues ([Griffin et al., 2002](#)). The main changes were the use of peripheral targets and a 'feature detection' task. This task was also a simple-RT task, but unlike onset detection, the feature detection task involved a finer perceptual analysis because the target was defined by more complex visual features. The target was a pattern of concentric squares with one of its inner squares missing. Event-related potentials evoked by attended (i.e., attend short SOA) vs. unattended (i.e., attend long SOA) standard non-target arrays were compared at the short SOA, to avoid additional effects produced by targets.

Importantly, Experiment 1 showed an increased N1 in the attended condition over bilateral occipital electrodes. Experiment 2, however, did not replicate this early effect. One difference was the use of unilateral targets in Experiment 2, instead of the bilateral targets presented in Experiment 1. This finding was interpreted as a modulation of early visual

processing by temporal attention. However, the diffuse (non-lateralized) enhancement, and the lack of effects on P1, led them to argue that the modulation had a different nature to the typical observed for spatial attention.

Concerning late components, Experiment 2 replicated with more success the previous study ([Miniussi et al., 1999](#)), such as the N2 enhancement at the unattended condition and the earlier P300 peak at the attended condition. A novel interpretation was provided for the N2 effect, which was produced by stimuli appearing at unexpected moments (i.e., temporal deviant stimuli, [Loveless, 1986](#)).

To conclude, a modulation of early processing by temporal attention was observed in Experiment 1, in which a feature detection task and bilateral peripheral targets were used. This finding led us to assume that a high requirement of perceptual processing could be a key factor in order to observe such modulation.

A different approach was taken to investigate temporal orienting in the following study ([Lange et al., 2003](#)). The authors explored temporal attention in the auditory modality. Their logic was that the use of auditory stimuli could increase the sensitivity of the task to measure early modulations, as the auditory is superior to the visual modality in temporal processing efficiency (e.g., [Repp and Penel, 2002](#)). Lange et al. adapted the paradigm introduced by [Hillyard et al. \(1973\)](#) to the temporal domain. Two consecutive auditory stimuli delimited both the short and the long SOA. The second stimulus was the target in 20% of trials and the standard in the 80% remaining. The target was defined by a louder sound intensity. Participants were to discriminate and respond to infrequent deviant stimuli (target). As in [Griffin et al.'s \(2002\)](#) study, standard stimuli served as the event to which potentials were linked. Two novel features of this experiment were: (a) that temporal expectancy was manipulated between blocks, instead of trial-by-trial (i.e., participants attended to the short or to the long interval in alternating blocks), and (b) that the task required a perceptual discrimination of stimuli (i.e., sounds of different intensity). Unlike endogenous cueing procedures, there was a cue validity of 0.50, i.e., the same proportion for attended and unattended standard stimuli.

The most important result was that the typical auditory evoked potential, the frontal N1, showed to be larger for attended standard relative to unattended standard stimuli. This was also true for the P300 component. ERPs to deviant-targets vs. standard-non targets were also compared, and a larger N2 for deviant-targets was found. The authors interpreted the auditory N1 effect as evidence supporting that temporal attention improves early perceptual processing in a similar way to spatial attention. On the basis on the superiority of audition over vision in temporal processing, they speculated that temporal attention could affect earlier levels of stimulus processing in the auditory modality.

In addition, as will be explained below, task demands and the way by which expectancy was manipulated could have been decisive in observing such early effects. Thus, the task gained sensitivity through demanding a perceptual discrimination and using a blocked manipulation of temporal expectancy.

The last set of studies ([Correa and Nobre, in preparation](#); [Doherty et al., 2005](#)) largely differed from previous studies in

the cueing procedure. In the latter, expectancy was induced by presenting symbolic explicit cues. In the former, expectancy was induced implicitly by showing a dynamic stimulus that followed predictable patterns of movement. The task consisted of a 'ball' that moved across the screen, in discrete steps from left to right before disappearing under an occluding band placed at the right hand-side of the screen. Once the ball reappeared, participants were to press a key when they detected a small dot in its center (i.e., the target). They withheld response when the target was not present. The target appeared in 50% of trials (Doherty et al., 2005), or in 80% of trials (Correa and Nobre, in preparation).

The pace of movement was manipulated to induce neutral expectancy (a random/unpredictable pace) or temporal expectancy (a regular/predictable pace), which allowed participants to predict the moment of the ball's reappearance. The temporal expectancy condition included a single expectancy, such that the speed of movement was the same for all trials (i.e., 550 ms per step). Behavioral results replicated studies that used the traditional Posner's paradigm, that is, RTs were faster in the temporal expectancy condition. Moreover, Doherty et al. found that temporal attention attenuated N1 and N2 amplitudes. The attenuation of N1 had not been reported so far and could indicate a modulation of visual processing, or even postvisual processing (e.g., time perception). Finally, the modulation of P300 latency reported in previous studies was replicated with this paradigm.

The subsequent study aimed to extend such results to a broader range of temporal expectancies, by including a variety of predictable speeds of movement (Correa and Nobre, in preparation). Another difference was that the attentional manipulation was not based on patterns of movement before the occlusion. Instead, both the attention and non-attention conditions were equated in perceptual input, but they differed in the time for which the ball was occluded. Thus, the temporal expectancy condition was divided into valid, early-invalid (earlier than expected targets) and late-invalid trials, depending on whether the ball virtually 'moved' during the occlusion at the same speed, faster or slower than before the occlusion, respectively. As occurred with other temporal-orienting paradigms, analyses focused on the early-valid vs. early-invalid comparison (i.e., the short SOA). They revealed an earlier and smaller N2 component in valid relative to early-invalid trials. The latency modulation of N2 by temporal attention had not been observed previously. N2 was additionally considered as reflecting conflict detection (van Veen and Carter, 2002, see Discussion for details). The P300, replicating previous research, was significantly larger, and tended to appear earlier ($P < 0.06$) in the valid condition.

Broadly, this new procedure to study temporal orienting replicated the main behavioral and ERP findings obtained with the traditional Posner's task (e.g., Miniussi et al., 1999), which suggests that both procedures could be engaging analogous cognitive processes. However, this novel approach seems more naturalistic and simulates more accurately our dynamic real world.

Concerning our main question, the Doherty et al. study provided additional evidence to the modulation of early processing as reflected by the N1 component. Given the low visibility of the target, the task can be considered as even more

perceptually demanding than the feature detection task described above. Thereby, the presence of the target was not a salient feature, since it was peripherally presented, and had a small size and low color contrast. In fact, participants frequently reported high uncertainty on whether they saw the target. In contrast, when the target was undoubtedly visible in the following experiment (Correa and Nobre, in preparation), the early effects vanished. This circumstance further emphasizes the necessity of high perceptual demands to obtain such early effects.

1.2. Conclusions

In summary, the following conclusions can be drawn from the present review. First, late components, such as N2 and P300, are consistently modulated by the temporal orienting of attention. The latency modulation (particularly of the P300) seems to be an idiosyncratic feature of temporal attention, and fits well with the function of synchronizing processes with the expected moment of occurrence of relevant events. Therefore, the reviewed studies provide converging support to the motor account. As mentioned earlier, there is a tight link between temporal and motor processing (Rosenbaum and Collyer, 1998).

On the other hand, the modulation of early perceptual processing by temporal attention is not a well-known phenomenon to date. Thus, several studies have failed to find the effect, whereas some others have succeeded to find it. Furthermore, when the attentional effect is observed, it is not consistently reflected in a particular modulation of ERPs, leading to either N1 enhancement or N1 attenuation.

Although such a discrepancy might be due to methodological differences between experimental procedures, it could be due to more theoretical reasons such as the different way by which temporal and spatial attention modulates processing (Nobre, 2001). This could be a consequence of the differential nature of representations of space and time in the brain. Whereas space is accurately represented in retinotopic maps within the visual system, time implies a rather different way of representation, which might include the cerebellum and basal ganglia and cortical structures located in frontal-parietal areas (see Ivry and Spencer, 2004, for a review). Being that true, we might expect that temporal attention experiments scarcely show influences at perceptual levels of visual processing, as it actually happens.

Despite the discrepancy in procedures, one can find a common aspect in studies that have reported perceptual modulations. Specifically, high demands in perceptual processing appeared to be a key factor. Hence, we propose that temporal attention not only modulates late motor processing, but also early visual processing when perceptually demanding tasks are used.

1.3. The present ERP experiment: a shape discrimination task with temporal expectancies blocked

According to the conclusions drawn from the review, the present study aimed to find a modulation of visual processing by using a perceptually demanding task. The task consisted of letter discrimination (between 'X' and 'O'), which demands

more perceptual processing than detection tasks, as a more detailed analysis of the visual features is required. There was a difficulty, however, since the use of choice-RT discrimination tasks produces smaller temporal-orienting effects than simple-RT detection tasks when temporal expectancy is manipulated on a trial-by-trial basis (Griffin et al., 2001). Nevertheless, other behavioral studies have reported robust temporal-orienting effects in discrimination tasks when temporal expectancy was blocked (Milliken et al., 2003). In a subsequent study, we directly compared detection and discrimination tasks, and further examined the effects of blocking expectancy in the discrimination task (Correa et al., 2004). The results revealed larger effects for the detection task relative to the discrimination task. The analysis of the discrimination task revealed that the size of attentional effects was larger when temporal expectancy was manipulated between blocks, rather than within-blocks. We proposed that the on-line generation of temporal expectancy involves controlled processing (e.g., underlying time estimation processes), which could be impaired by demanding tasks. Thus, the effects were reduced in choice-RT compared to simple-RT detection tasks because the former task demanded more central resources to maintain in working memory a more complex and arbitrary stimulus-response association (see also Correa et al., 2005, for further evidence). Moreover, this explanation accounted for the effect of blocking expectancy in discrimination tasks. Demands to generate temporal expectancy were reduced when expectancy did not change during a block of trials (i.e., between blocks manipulation), thus producing larger effects than when expectancy was manipulated within-blocks.

Consequently, the present experiment combined a shape discrimination task with the manipulation of temporal expectancy between blocks. Given that such features increased the sensitivity of our procedure, we expected to observe an early modulation of ERP components linked to visual processing, such as P1 and N1, produced by temporal attention. According to previous research, a modulation of late components (N2 and P300) was also expected.

2. Results

2.1. Behavioral results

Data from the 12 participants who contributed to ERP results were used for behavioral analyses. Trials with correct responses faster than 200 ms or slower than 1000 ms, anticipations (i.e., responses before target presentation), misses, responses in catch trials and incorrect responses were excluded from the RT analysis. Less than 5% of the trials were rejected.

Mean RTs were submitted to a repeated-measures ANOVA with expectancy (early/late) and SOA (450/950/1450 ms) as factors. Crucially, the interaction between expectancy and SOA was significant, $F(2,22) = 37.5$, $P < 0.001$. As can be seen in Fig. 1, valid trials were significantly faster than invalid trials at both the short SOA, $F(1,11) = 44.73$, $P < 0.001$ and the long SOA, $F(1,11) = 11.75$, $P < 0.01$. However, validity effects seemed to be larger at the short SOA (50 ms) than at the long SOA (36 ms).

The purpose of including the medium SOA intervals was to examine the linearity of temporal-orienting effects (i.e., whether the orienting of attention produces effects on RT that depend on the difference between the expected temporal interval and the actual temporal interval). In particular, the analyses revealed that both early and late expectancies followed a linear trend, $F(1,11) = 44.99$, $P < 0.001$, $F(1,11) = 19.01$, $P < 0.001$, respectively. The quadratic trend was far from significance for the early expectancy, $F < 1$ and was marginally significant for the late expectancy ($P < 0.07$).

The global accuracy in the discrimination task was of 96% correct. The analysis of accuracy was in line with RT results, although it did not reveal significant effects.

2.2. Electrophysiological results

Data from 7 participants were rejected from analyses due to excessive artifacts during the recording.

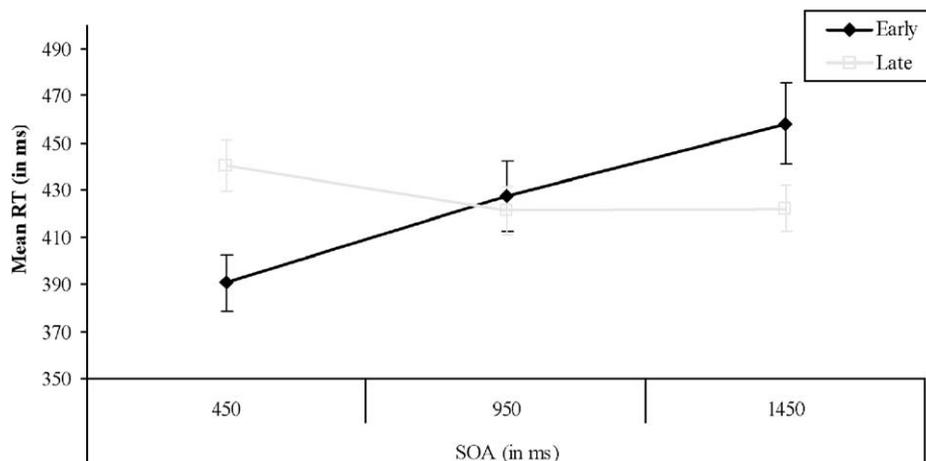


Fig. 1 – Mean RTs as a function of temporal expectancy (early or late) and SOA. Note that at the short SOA the early expectancy condition is valid (late expectancy is invalid), whereas at the long SOA the late expectancy is valid (early expectancy is invalid).

2.2.1. ERPs evoked by temporal cues

Fig. 2A represents ERP waveforms, evoked by valid-early and valid-late cues, recorded at occipital and central electrodes.

The occipital electrode (lower panel A) showed the typical response to visual stimulation. In particular, the P1/N1 component was produced by both early and late cues, by targets appearing at the short SOA when the cue was (valid) early, and by targets appearing at the long SOA when the cue was (valid) late.

The central electrode (upper panel A) showed a positive deflection peaking at around 260 ms. Then, a negative deflection appeared with an earlier onset and a shorter duration for the early cue compared to the late cue. Moreover, this negativity was larger for early vs. late cues during an interval that included the early-target onset (i.e., 450 ms after cue onset). In contrast, the negativity appeared larger for late vs. early cues during an interval that included the late-target onset (i.e., 1450 ms after cue onset). In other words, this negative potential seemed to be time-locked to the expected target onset, which suggests a link to the contingent negative variation (CNV) component (Walter et al., 1964). Afterwards, positive waves related to the P300 component were observed in response to respective early and late targets.

These visual impressions were statistically tested by a 2 (expectancy: early/late) \times 3 (hemisphere: left/midline/right) repeated-measures ANOVA, using a subset of the voltage values used for depicting Fig. 2. Specifically, we used shorter epochs for analysis [–200, 800] ms, and given that such epochs were longer than the shortest SOA (450 ms), trials with targets appearing at the short SOA (regardless its validity) were rejected to exclude activity related to targets. Note that Fig. 2 does not exactly represent the specific subset of the analyzed data. However, the graphical representation of such a subset closely matched the pattern of results displayed in Fig. 2, so that Fig. 2 can be considered as representative of the results detailed below.

The P1 component was larger for the early expectancy compared to the late expectancy, $F(1,11) = 11.67$, $P < 0.01$ (see Fig. 2). As can be observed in Fig. 2, the CNV was more negative for the early expectancy at the short temporal window [435–475] ms, $F(1,11) = 9.69$, $P < 0.01$. Thus, the state of increased preparation matched the expected target onset.

The topographical distribution of the ERPs elicited by early and late cues is also depicted in Fig. 2 (see panel B at the left head and the right head, respectively). The mentioned P1 effect was evident at around 147 ms over occipital sites. The CNV started earlier (see panels of 371 ms) and was more negative for the subsequent intervals (443 ms, 471 ms) for the early expectancy over frontal–central sites. At the same time, there was a marginally significant higher positive anticipatory activity for the early-expectancy wave compared to the late-expectancy at the [427–527] ms temporal window, $F(1,11) = 3.86$, $P = 0.075$. Remarkably, this activity distributed over posterior electrodes, and roughly matched the time of the expected target appearance (see 443 ms, 471 ms).

2.2.2. ERPs evoked by targets

The visual components evoked by targets appearing at the short SOA, recorded at occipital sites, are shown in Fig. 3 for valid and invalid trials (i.e., early expectancy-short SOA and late expectancy-short SOA, respectively). Mean amplitude and

latency measures were submitted to a 2 (validity: valid/invalid) \times 3 (hemisphere: left/midline/right) repeated-measures ANOVA.

The most relevant result was that targets appearing at the cued time interval yielded a larger P1 amplitude than targets appearing earlier than expected, $F(1,11) = 5.64$, $P < 0.04$.

The characteristic N2 waveform was clearly observed only at three frontal electrodes, so that the ANOVA only included validity as a single factor. N2 was also modulated by temporal attention, such that its peak was attenuated, $F(1,11) = 8.62$, $P < 0.02$ and appeared earlier, $F(1,11) = 11.18$, $P < 0.01$ in valid trials (367 ms) compared to invalid trials (376 ms).

The P300 component evoked by the target recorded at central–parietal sites is also depicted in Fig. 3 for valid and invalid trials (see lower panel). Separate 2 (validity: valid/invalid) \times 3 (hemisphere: left/midline/right) repeated-measures ANOVAs were conducted for the amplitude and latency of the P300 component. The P300 amplitude was larger in invalid trials, $F(1,11) = 7.4$, $P < 0.02$ and its peak appeared earlier in valid trials (510 ms) than in invalid trials (520 ms), $F(1,11) = 8.85$, $P < 0.02$ for the selected time window.

3. Discussion

Behavioral data revealed faster RTs for expected vs. unexpected targets at both the short and the long SOA, which suggests that attentional resources can be flexibly deployed to different points in time. However, most temporal orienting studies have observed validity effects exclusively at the short SOA (e.g., Coull and Nobre, 1998). It is assumed that a reorienting process from short to long intervals is engaged when an invalid target appears later than expected, so that the predicted cost in RT for invalid targets is not observed at the long SOA. We have shown that the reorienting process can be controlled by manipulating the participant's certainty about the target occurrence (Correa et al., 2004). Specifically, validity effects at the long SOA were only observed in the groups that included catch trials (i.e., a proportion of 0.25). We interpreted that catch trials increased the uncertainty of target occurrence, such that the reorienting process was impaired. The present data replicated previous findings, revealing significant attentional effects at the long SOA with a catch trial proportion of 0.125. However, validity effects at the long SOA seemed to be smaller compared to the short SOA, which might suggest that the reorienting process was not completely prevented by the presence of catch trials. Thus, invalid trials may not be equivalent for the short and the long SOA conditions (see Coull et al., 2000, for neuroimaging evidence), so that the early expectancy-long SOA was not a pure condition of non-attention in our experiment, albeit catch trials were included. Consequently, the ERP analyses focused on the short SOA.

Concerning electrophysiological data, the typical major findings of temporal orienting research (e.g., Griffin et al., 2002; Miniussi et al., 1999) have been replicated using a different system for ERP recording and analysis (see Fig. 2). In particular, the negative deflection related to the CNV component developed earlier for early than for late expectancies. Moreover, the CNV was larger at the short SOA for the

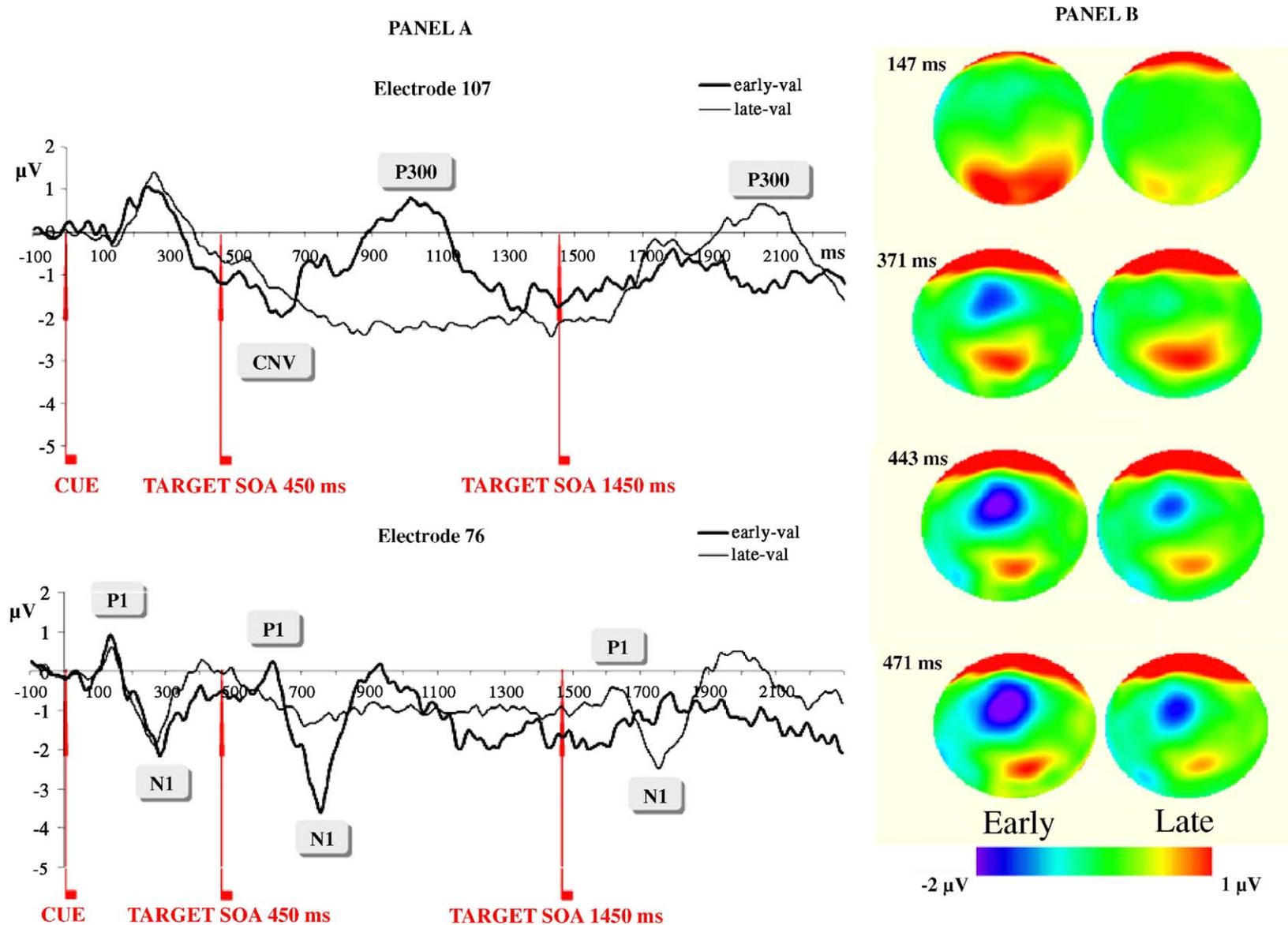


Fig. 2 - (A) On the left, shows the ERP waveforms (positive is plotted upward) evoked by valid-early (thick line) and valid-late cues (thin line), recorded at central electrodes (the electrode 107, adjacent to Cz, is shown in the left upper panel) and occipital electrodes (the electrode 76, between O1 and O2 is shown on the left lower panel). The onset of relevant stimuli, cue and targets is indicated. (B) On the right, shows the topographical distribution of the ERPs for early and late cues (see heads on the left and right hand-side in panel B, respectively) at 147, 371, 443 and 471 ms after cue onset, as viewed from above.

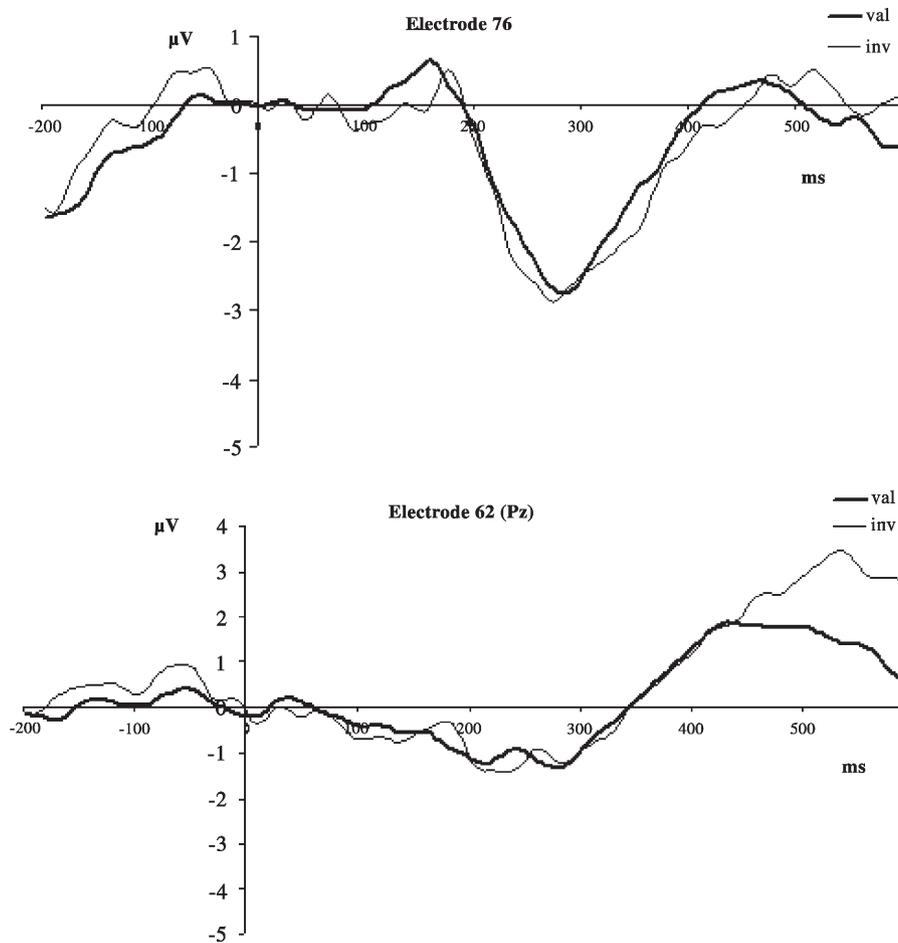


Fig. 3 – The upper panel shows the visual components evoked by targets appearing at the short SOA recorded at occipital sites for valid trials (thick line) and invalid trials (thin line), i.e., for early expectancy-short SOA and late expectancy-short SOA conditions, respectively. The lower panel shows the P300 component evoked by the target recorded at central–parietal sites for valid and invalid trials (the Cz electrode is shown). The target onset at the short SOA is indicated by the 0 ms point in the x-axis.

early expectancy, and appeared to be larger at the long SOA for the late expectancy condition, which suggests that temporal cues tuned the preparation process to the expected relevant moment. This preparation seemed already evident at processing stages prior to the CNV, since early cues showed a larger P1 component compared to late cues. To our knowledge, this result has not been previously reported in other attentional studies. The effect cannot be attributed to differential trial proportions, since both early and late blocks were balanced in that respect. It might be explained considering that our procedure gained sensitivity as expectancy was manipulated between blocks. Thus, the mental set developed during a homogeneous block of trials in which the expectancy does not change could be influencing processing, more strongly and at earlier stages, than when temporal expectancies have to be generated on line in trial-by-trial manipulations. Hence, the modulation of preparation induced by early cues could be observed as early as in P1. This result fits into behavioral experiments in the sense that the size of temporal-orienting effects in discrimination tasks is enhanced by a between blocks manipulation (Correa et al., 2004). In any case, further research would be necessary to elucidate this intriguing effect.

However, the most important result was found in the ERPs evoked by targets. Valid targets increased the P1 component compared to invalid targets over occipital sites. Effects of temporal attention on P1 had not been observed so far. The sensitivity of our procedure to find the effect on P1 could have been optimized by the use of a shape discrimination task in which temporal expectancy was manipulated between blocks. As said above, temporal orienting effects in choice-RT discrimination tasks are larger when expectancy is manipulated between blocks rather than within-blocks (Correa et al., 2004). Therefore, expectancy was manipulated between blocks in this task, in order to obtain robust behavioral and physiological effects. In contrast with the results of ERPs evoked by cues, the effect of targets on P1 can indeed be attributed to differential trial proportions (i.e., 75% valid vs. 25% invalid). Analogously to spatial attention studies, predictive cues generate expectancy and encourage participants to endogenously attend to the most likely (and therefore, relevant) time interval. Thus, this result suggests that visual attention was strategically focused on the relevant moment according to temporal expectancy, which enhanced the visual processing of targets appearing at expected times compared to other relatively less attended times.

Moreover, temporal attention modulated the N2 component. The increase of N2 by invalid targets replicated several studies (Correa and Nobre, *in preparation*; Griffin et al., 2002, Experiment 2, Miniussi et al., 1999). According to van Veen and Carter (2002), N2 may be considered as an index of general conflict detection. In our specific case, N2 could be reflecting processes involved in temporal expectancy disconfirmation. For example, N2 reflects a process of conflict detection between the expected and the actual temporal occurrence of the target, followed by a reconfiguration of the system to adapt behavior to the unexpected situation. Thus, N2 increased when temporal expectancy had been disconfirmed by a sudden target onset on invalid trials. On the other hand, attention could prevent conflict detection and reconfiguration processes, so that an expected target would produce a smaller N2. Likewise, this saving of processing time by attention may be the source of the smaller N2 latency observed on valid trials. The effect on N2 latency had been only observed in a previous experiment (Correa and Nobre, *in preparation*).

Furthermore, the P300 was influenced by the temporal orienting of attention. First, the P300 amplitude was increased in response to invalid targets. This result is discrepant with studies that found no differences between valid and invalid targets (Doherty et al., 2005; Griffin et al., 2002, Experiment 2, Miniussi et al., 1999), and other studies that found a larger P300 for valid targets (Correa and Nobre, *in preparation*; Griffin et al., 2002, Experiment 1, Lange et al., 2003). Considering that infrequent invalid targets produce an effect of surprise, P300 could reflect a process of novelty detection (Duncan-Johnson and Donchin, 1977). This inconsistency concerning effects on P300 amplitude is also found in spatial attention studies (Martin-Loeches et al., 1997). Further research would be required to isolate the experimental situations that determine the P300 component, and to better understand its psychological significance.

On the other hand, results of P300 latency are convergent in temporal orienting studies (see Table 1). The P300 peak appeared earlier for valid targets compared to invalid targets. It is considered that temporal attention enhances and synchronizes processes of decision and preparation for responses (Miniussi et al., 1999). In sum, it seems that one idiosyncratic feature of temporal attention is the ability to modulate the latency of cognitive processes in order to synchronize them to the behaviorally relevant moment.

4. General conclusions

The present experiment confirmed that focusing attention on a point in time improves behavioral performance, decreasing RTs in detection tasks (see Nobre, 2001) as well as in discrimination tasks (e.g., Correa et al., 2004). Moreover, electrophysiological results suggest that, underlying this improvement, there is an increase of preparatory activity which is time-locked to the expected target occurrence. Thus, the temporal course of the preparation process can be flexibly modulated according to the participant's temporal expectancy induced by the cue. Previous studies have linked such a process to the CNV component (Loveless and Sandford, 1974; Miniussi et al., 1999; Walter et al., 1964).

In addition, the ERP methodology allowed us to explore the locus of such attentional effects. Electrophysiological studies that used detection of visual targets as task have mainly found that temporal attention influences late components (N2 and P300), which are mostly related to motor processing. Our results have replicated the modulation of N2 and P300, supporting thus the notion that temporal attention produces a motor preparation. However, the finding of behavioral benefits in the discrimination task raised the possibility of a perceptual preparation. Hence, attention could facilitate perceptual processes involved in discriminating object features. Alternatively, it could be argued that attention exclusively facilitated decision or motor response processes demanded in choice-RT discrimination tasks (Nobre, 2001).

Nevertheless, our physiological data provided further evidence to the perceptual hypothesis. First, we observed a marginal increment of anticipatory activity over the parietal-occipital area just before the predicted moment of the target arrival (see Fig. 2). Activity preceding stimuli presentation is generally balanced for cued and uncued conditions, in order to isolate effects of spatial attention on visual processing (see Näätänen, 1975). Although this logic makes sense in spatial attention research, it may not be similarly applicable to temporal attention. Thus, it could be assumed that the synchronization of this anticipatory activity to relevant moments is precisely the hallmark of temporal orienting, so that it should not be balanced for attended and unattended conditions. Presumably, the fact that this activity was observed over the occipital area could be indicative of perceptual enhancement.

Furthermore, the significant enhancement of a component traditionally linked to visual processing (P1) represents more compelling evidence of perceptual enhancement produced by temporal attention. Despite the strict correction of the pretarget activity for both conditions, attended targets still evoked a larger P1 component relative to unattended targets. This finding represents the first empirical evidence of P1 enhancement produced by the temporal orienting of attention, and is in line with previous physiological studies that have found attentional enhancements at early stages of processing (Doherty et al., 2005; Griffin et al., 2002, Experiment 1, Lange et al., 2003). As we have seen in the review, common to all these studies is the demand of perceptual processing optimization in order to accomplish the task, rather than the demand of just speeded responses.

This finding leads to question whether spatial and temporal attention modulates visual stimulus processing in an analogous fashion. Whereas spatial attention can easily influence early stages of processing, it seems that temporal attention yields less evident effects on early processes. This difference could be due to the fact that the brain lacks a retinotopic map in visual areas to code temporal features analogous to the map involved in visuospatial coding. Thus, neural representations of specific locations can be directly amplified by spatial attention (Mangun, 1995), whereas higher perceptual demands would be necessary to capture the effects of temporal attention.

Furthermore, the explanation we emphasize here is based on how relevant for the task is the optimization of information at a specific level of processing. Thus, the attentional

enhancement of perceptual processing would be clearly observed when such a processing is relevant, and so, demanded by the task.

Then, in studies of spatial attention, the enhancement of information at the perceptual level is important even for a simple detection task, as this task involves perceptual uncertainty regarding the spatial location of the forthcoming target. Indeed, the effects of spatial attention using this task are usually observed at the perceptual level (Mangun, 1995). In contrast, in studies of temporal attention, the perceptual enhancement is unnecessary for the detection task, given that the foveal presentation of a simple object lacks of perceptual uncertainty, that is, it is not perceptually demanding. More relevant, however, is to enhance late processing to release the prepared motor response at the appropriate moment. In fact, the effects of temporal attention using ‘onset detection’ tasks are clearer at the motor level than at the perceptual level.

Interestingly, when perceptually demanding tasks are used, such as a ‘feature detection’ task involving spatial uncertainty (Griffin et al., 2001), or a discrimination task involving object uncertainty (as that used in the present experiment, see also Lange et al., 2003), the effects of temporal attention are also observed at the perceptual level.

Accordingly, we suggest that spatial attention and temporal attention could engage a similar mechanism of processing modulation, which has a partially different manifestation depending on the nature of the representations and the processing demands being involved. To conclude, the present research supported the hypothesis drawn from the review, that is, temporal attention not only modulates late motor processing, but also early visual processing when perceptually demanding tasks are used. Further research, however, should elucidate the experimental conditions in which the early ERP components are modulated in a specific manner.

5. Experimental procedures

5.1. Participants

Nineteen students from the University of Granada took part in the experiment as volunteers in exchange for course credits. All participants gave informed consent prior to their inclusion in the study. They reported normal or corrected to normal vision. Data from seven participants were rejected due to unsatisfactory recordings. Data from the same 12 participants were accepted for both behavioral and ERP analyses (age range: 18–26 years, mean age: 21; 10 women, 2 men). All participants were right-handed.

5.2. Apparatus and stimuli

E-prime software (Schneider et al., 2002) controlled the experiment. The experiment was run on a PC connected to a 17 inch monitor. This computer was connected to a Macintosh computer, which recorded continuous EEG (materials used for the EEG recording will be described below).

All stimuli appeared in the center of the screen. On each trial, a fixation point (“+” symbol; font: Arial 24), a temporal cue and a target were presented. The cue was the word ‘EARLY or ‘LATE’, colored in black (Tahoma 16, in italics. In Spanish: ‘PRONTO or ‘TARDE’, subtending 0.67° of visual angle in height,

and 3.91° and 3.25° in width, respectively). The target was either the letter ‘O’ or the letter ‘X’, 8 mm in height by 8 mm in width (Arial 24. 0.76°). The two target letters appeared with a probability of 0.50. Participants pressed with their left index the left key of a button box for one target, and pressed the right key (with their right index) for the other target. The assignment of targets to response keys was counterbalanced across participants.

5.3. Task

Participants were seated at approximately 60 cm in front of the monitor. Instructions concerning the task were displayed on the screen. Participants were explicitly informed that the temporal cue would help them to predict when the target would appear. Auditory feedback (a 2000 Hz tone of 50 ms) and visual feedback (the word “incorrect” colored in red for 500 ms) were provided on error trials. Participants were encouraged to respond as quickly and accurately as possible, and to avoid eye blinks and movements during stimulus presentation.

The sequence of events on a trial is displayed in Fig. 4.

The fixation point was displayed in black on a white background for a random interval ranging between 1500 and 2500 ms. The temporal cue then appeared for 100 ms. After that, the screen remained blank for a variable delay of 350, 850 or 1350 ms, depending on the SOA for that trial. The target was displayed for 100 ms and was then replaced by a blank screen in waiting for the discrimination response, for a maximum delay of 1900 ms. Following the response (or the 1900 ms delay), the screen either remained blank on correct trials or displayed the feedback message on incorrect trials (i.e., anticipations, incorrect discriminations or response on catch trials) for 500 ms. There was an intertrial interval of 1000 ms in which eye blinks were less disrupting.

The whole session lasted about 100 min. Each session included one block of 20 practice trials and six blocks of 128 experimental trials. On half of the experimental blocks, the cue indicated that the target was likely to appear “early”. On the remaining blocks, the cue indicated that the target was likely to appear “late”. Blocks of early expectancy and late expectancy were successively alternated, and the order of delivery was counterbalanced across participants.

There were short breaks in the middle and at the end of each block, and a longer break in the middle of the experiment. Each experimental block consisted of 112 trials with target and 16 trials without target, thus producing a catch trial proportion of 0.125. The 112 target trials consisted of 84 validly cued trials and 28 invalidly cued trials, yielding a validity proportion of 0.75. Valid trials included the two following conditions: Early cue-450 ms SOA and late cue-1450 ms SOA. Invalid trials were equally distributed between the two uncued SOAs for both early and late cues. All the trials at the medium SOA were invalid. Once the participants finished the task, they were shown their own EEG and were informed about the purposes of the study.

5.4. EEG recording

The EEG recording was performed in an electrically shielded room, using a 128-channel Geodesic Sensor Net of Ag/AgCl electrodes (Tucker et al., 1994). The distribution along the scalp is depicted in Fig. 5.

The head-coverage included sensors lateral to and below both eyes to monitor horizontal and vertical eye movements (electro-oculogram, EOG electrodes). Impedances for each channel were measured and kept below 50 k Ω before testing, as recommended for the Electrical Geodesics high-input impedance amplifiers. All electrodes were referenced to the Cz electrode during the recording and were algebraically re-referenced off-line to calculate

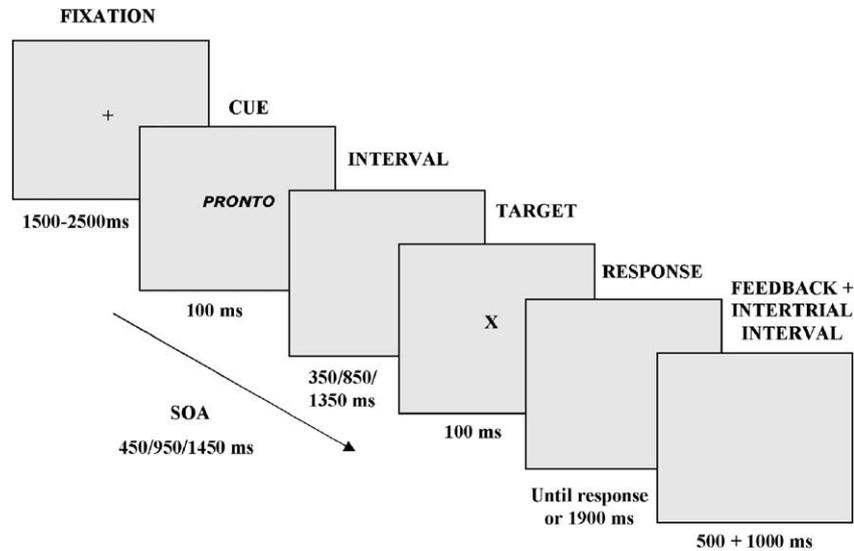


Fig. 4 – Sequence of events on a trial.

the average reference. The EEG was amplified with a band pass of 0.1–100 Hz (elliptic filter) and digitized at a sampling rate of 250 Hz.

5.5. ERP analysis

The continuous EEG was filtered offline by using a 30 Hz low-pass filter, and then segmented in epochs of [–200, 800] ms and [–200, 600] ms relative to the cue onset and the target onset, respectively. A 200 ms segment previous to the cue presentation was used to

calculate the baseline. A strict baseline correction was performed for the target, [–40, 40] ms, in order to minimize unspecific preparatory effects prior to target presentation (e.g., Griffin et al., 2002). Additionally, a long epoch of [–100, 2300] ms with a [–100, 0] ms baseline was created for visual inspection, to have a general impression of all the events occurring on a trial.

The epochs were submitted to software algorithms for identification of artifacts. Trials with eye blinks or saccades (i.e., deflections larger than ±50 μV in EOG electrodes), and trials that

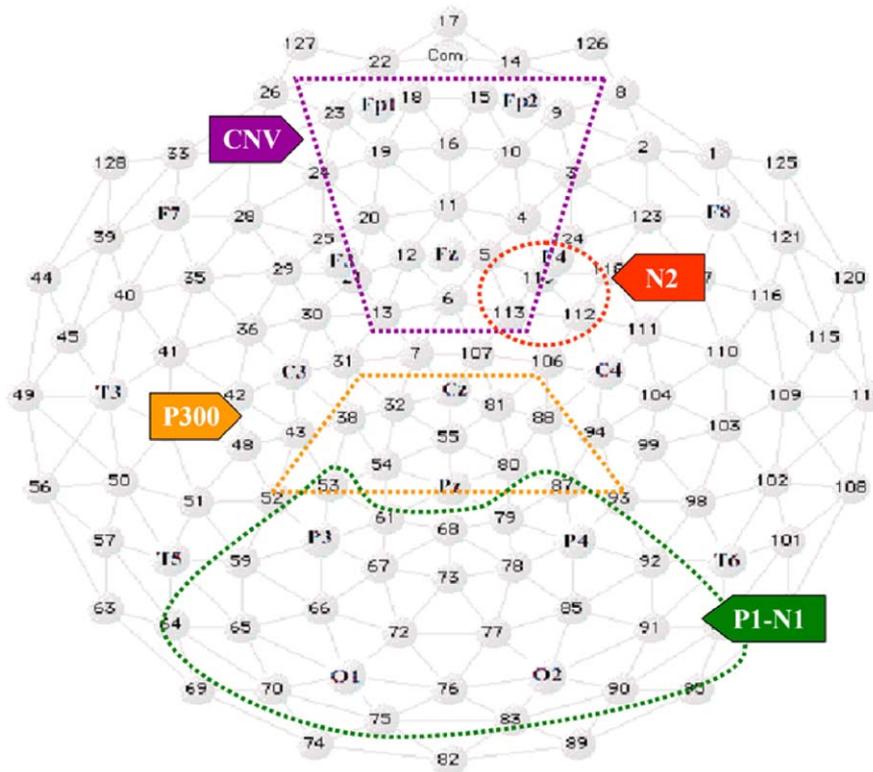


Fig. 5 – Sketch of the electrodes distribution around the scalp as viewed from above (the top of the figure represents the frontal area). The electrodes selected for analyses are specified for each component (P1/N1, N2, P300 and CNV). Additional sites according to the 10–20 International system are shown for further reference.

did not meet the behavioral performance criteria were rejected. Data from participants with less than 25 artifact-free trials per condition were discarded.

The epochs were then averaged separately for cues and targets according to the experimental conditions. ERP waves elicited by temporal cues were separated into early-expectancy and late-expectancy conditions. ERPs evoked by targets were separated into valid and invalid trials. Given that analyses focused on the short SOA (see Discussion), the valid condition included trials in which the cue was 'early' and the target appeared at the short SOA, whereas the invalid condition included trials in which the cue was 'late' and the target appeared at the short SOA.

Identifiable ERP components (P1, N1, N2, CNV and P300) were analyzed at electrode locations and temporal windows where they were most evident. The selected electrodes are shown in Fig. 5. The temporal windows were [139–179], [247–287] and [435–475] ms for P1, N1 and CNV components of the cue analysis. In the target analysis, the temporal windows were [127–167], [247–287], [359–399] and [499–539] ms for the respective P1, N1, N2 and P300 components. The mean amplitude and latency of the largest peak were analyzed by repeated-measures ANOVAs for each component. The experimental condition (i.e., early vs. late for the cue analysis, and valid vs. invalid for the target analysis) and hemisphere (left, midline and right) were included as factors. The value for each hemisphere was calculated by averaging all the electrodes included in that hemisphere.

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