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Frontal and parietal ERPs associated with duration discriminations with or without task interference

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ABSTRACT

The main objective of this study was to examine fronto-parietal networks underlying visual duration discriminations. Two types of interference tasks were used to augment cognitive load: line orientation associated with the right hemisphere and multiplication with the left. Both subtasks deteriorated duration discriminations, more severely for line orientation. Relative to the condition without interference, the dual task paradigm decreased amplitudes of the contingent negative variation (CNV) wave, predominant at frontal sites, and the P300 wave, predominant at parietal sites. Inversely, amplitudes of a later appearing positive component (LPC) and its parietal counterpart of opposite polarity (LNC) increased with spatial or numeric task interference. These results are concordant with the view that fronto-parietal networks underlying duration discriminations act in a concerted fashion, with the LPC/LNC waves acting as a warning signal to mitigate errors during high cognitive load.

Keywords:

Duration discrimination
Interference task
Prefrontal cortex
Posterior parietal cortex

1. Introduction

Several models have been developed regarding neural mechanisms of time estimation (Droit-Volet and Wearden, 2003). The scalar timing model of Gibbon et al. (1984) is the most cited, having been applied successfully in animal (Gibbon, 1977) and human (Droit-Volet and Wearden, 2002; Wearden and McShane, 1988) studies. According to this model, time estimation consists of three phases: internal clock, memory, and decision making. The internal clock marks out time through the activity of a pacemaker. Brain structures underlying time estimation include neocortex, basal ganglia, and cerebellum (Harrington and Haaland, 1999; Lalonde and Hannequin, 1999; Rubia and Smith, 2004). It has been proposed that subcortical regions are mainly involved

in the pacemaking stage, particularly the cerebellum and basal ganglia (Artieda et al., 1992; Densen, 1977; Harrington et al., 1998a; Ivry, 1996; Ivry and Spencer, 2004; Malapani et al., 1998; Matell and Meck, 2000, Matell et al., 2004; Pastor et al., 1992; Rammsayer, 1997, Rammsayer and Vogel, 1992; Smith et al., 2002; Wahl and Sieg, 1980). On the basis of sequential motor learning, rhythmic timing, and duration discriminations, Ivry and Spencer (2004) propose a model by which information is treated in cerebellum before basal ganglia. Matell and Meck (2000), Matell et al. (2004) propose the beat striatal frequency (BSF), by which the encoding of durations is assured by striatal-neocortical loops.

Based on studies with functional magnetic resonance imaging (fMRI) and with lesioned subjects, the prefrontal cortex (PFC)

appears to be involved at several levels, including selective attention (Casini and Ivry, 1999; Harrington et al., 1998b; Olton et al., 1988), memory (Basso et al., 2003; Chiba et al., 1997; Gruber et al., 2000; Mangels et al., 1998; Meck et al., 1987; Nichelli et al., 1995), and decision making (Harrington et al., 2004; Rao et al., 2001). With event-related potentials (ERPs), a negative wave of low onset, the contingent negative variation (CNV), is predominant in frontal regions during timing (Macar and Vidal, 2004). The CNV seems to be involved at several stages: pacemaking (Ladanyi and Dubrovsky, 1985; Macar and Bonnet, 1997; Macar et al., 1999), memory (Monfort and Pouthas, 2003; Pfeuty et al., 2003; Pouthas, 2003), and decision making (Macar and Vidal, 2003). More recently, a positive wave of slow onset, the late positive component of timing (LPC_t), predominant at PFC sites, has been described during visual duration discriminations (Paul et al., 2003). Because positive potentials reflect disassembly of neural networks (Timsit-Berthier and Gérono, 1998), the LPC_t may be involved in filtering out irrelevant information during decision making (Paul et al., 2003).

Although less extensively investigated than PFC, the posterior parietal cortex (PPC) also plays a role in time estimation, as demonstrated in lesion (Harrington et al., 1998b) and other types of analysis during sensorimotor synchronization (Rubia et al., 2000), tapping (Larsson et al., 1996), reproduction of rhythms (Penhune et al., 1998), and time estimation (Basso et al., 2003; Lewis and Miall, 2002) tasks. Such results are not surprising in view of enriched bidirectional connexions existing between PFC and PPC, as well as their subcortical targets (Cavada and Goldman-Rakic, 1991; Houdé et al., 2003; Schmahmann and Pandya, 1990). PFC–PPC interactions have been described in various tasks (Petrides and Pandya, 1984; Schwartz and Goldman-Rakic, 1984), in particular regarding working memory (Cabeza and Nyberg, 2000; Friedman and Goldman-Rakic, 1994), cognitive switching (Dove et al., 2000; Sohn et al., 2000), and memory retrieval (Wagner et al., 2001). In addition to normal human subjects (Basso et al., 2003) and monkeys (Onoe et al., 2001), unusual fronto-parietal patterns have been described in schizophrenic patients during time estimation (Ojeda et al., 2002). These data are interesting in view of the link between ERPs at prefrontal (contingent negative variation, CNV) and parietal (P300) sites recorded during duration discriminations in normal subjects (Le Dantec et al., 2007).

Although recent data have contributed to our understanding of the neurobiology of timing, many questions remain on fronto-parietal links and hemispheric lateralization. While most results are concordant with the view that fronto-parietal networks are functionally associated and reflect memory demands (Ojeda et al., 2002; Quintana and Fuster, 1992, 1993, 1999; Quintana et al., 2003), functional dissociations have also been suggested (Bunge et al., 2002; Sohn et al., 2003). Although studies in schizophrenic patients indicate a complementary role of prefrontal and parietal association cortex (Quintana et al., 2003; Ojeda et al., 2002), other authors suggest that these structures intervene in distinct processes. For example, memory load modulated activity in PFC but not in PPC during retrieval (Sohn et al., 2003). PFC is particularly implicated in response selection and PPC in maintaining possible choices in memory (Bunge et al., 2002).

Le Dantec et al. (2007) began to establish relations between fronto-parietal structures in early processing, but few data are available at later phases. As Gibbons and Rammsayer (2005)

postulated, duration comparisons imply a parietal P300 component and a P500 frontal component. Thus, we sought to investigate whether the findings of Le Dantec et al., (2007) could be extended to later stages. The impact of hemispheric lateralization is varied and sometimes contradictory. In some tasks, right PFC seems predominant (Gruber et al., 2000; Harrington et al., 1998b; Maquet et al., 1996; Pouthas et al., 2000; Rao et al., 2001), in others the left (Binkofski and Block, 1996; Kawashima et al., 2000; Rubia et al., 1998), or both (Basso et al., 2003). Likewise, right PPC seems predominant in some tasks (Harrington et al., 1998b; Maquet et al., 1996; Mohl and Pfurtscheller, 1991; Rao et al., 2001) and in others both (Le Dantec et al., 2007).

To provide improved understanding of fronto-parietal interactions in early and late stages of processing and hemispheric lateralization, we altered cognitive load in normal subjects through two types of interference: judgment of line orientation and calculations. Spatial tasks (Corballis et al., 2000, 2002), including discrimination between angles (Mascetti et al., 2001; Tressoldi, 1989), mostly involve the right hemisphere, and calculations, in particular multiplications (Cohen et al., 2000; Dehaene et al., 2004; Delazer et al., 2003), involve the left. Our spatial subtask concerned line orientation and our numeric subtask two-digit multiplications. We determined which subtask is more likely to interfere with successive duration discriminations (S1 and S2) and whether ERPs predominant at frontal and parietal sites work in concert or else become dissociated with or without task interference.

2. Results

2.1. Behavior

Planned comparisons were conducted on success rates in the ERP study and reaction time (RT) in the behavioral study by three-way analyses of variance (ANOVA) with task, duration, and order as main factors. The percentage of correct responses was similar in the two studies (data not shown). As illustrated in Fig. 1, subjects performing duration discriminations without interference performed better than those with spatial ($F[1,18] = 9.3$; $P < 0.007$) or numeric ($F[1,18] = 4.7$; $P < 0.044$) interference. Moreover, subject responses were faster without interference than spatial ($F[1,18] = 173, 2$; $P < 0.001$) or numeric ($F[1,18] = 170, 9$; $P < 0.001$) task interference.

When directly compared, line orientation tasks deteriorated timing accuracy more severely than multiplications ($F[1,9] = 13.05$; $P < 0.006$). This was not the case for RTs. ANOVAs indicated a stimulus duration effect without interference ($F[1,9] = 10.93$; $P < 0.009$), and for multiplication ($F[1,9] = 10.73$; $P < 0.009$) or angle ($F[1,9] = 13.7$; $P < 0.004$) subtasks, as shorter stimuli were better discriminated than longer ones. Likewise, RTs were faster during short durations with spatial ($F[1,9] = 183.6$; $P < 0.001$) and numeric ($F[1,9] = 165.3$; $P < 0.001$) interference or without any interference at all ($F[1,9] = 5.5$; $P < 0.005$). Moreover, there was an interaction between stimulus duration and presentation order without interference ($F[1,9] = 45.95$; $P < 0.001$) and for multiplication ($F[1,9] = 56.81$; $P < 0.001$) or angle ($F[1,9] = 27.68$; $P < 0.001$) subtasks. The short duration was better discriminated in the long–short order, while the reverse was true for the longer

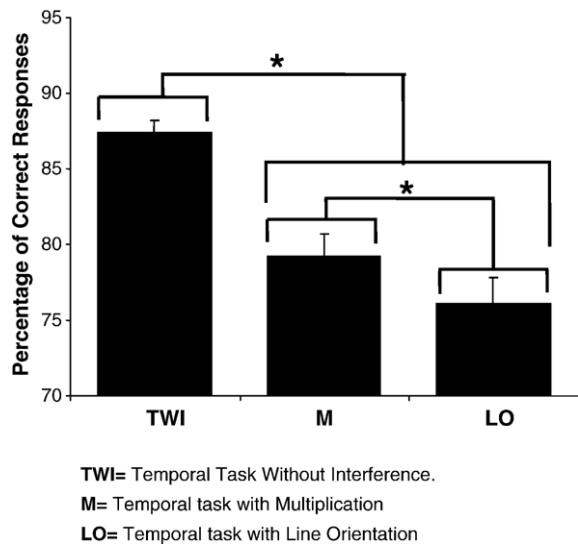


Fig. 1 – Percentage of correct responses obtained with (M=multiplication, LO=line orientation) or without interference (TWI).

discrimination. In the long–short order, performances were superior for brief durations. With respect to performance between interference tasks measured during the inter-duration interval, no difference was observed ($F[1,9] = 3.11$; $P = 0.099$), indicating equivalent levels of cognitive difficulty. Thus, poor time-related performances during distracting circumstances are due to the nature of the task, as opposed to a generalized action of cognitive loading.

2.2. ERPs

Under conditions without interference, CNVs were observed during each stimulus duration, separable as CNV_1 and CNV_2 components, maximal at frontal electrodes (Fp1, Fp2, F3, F4, F7, F8). Under conditions with interference, CNV_2 reversed its polarity (Figs. 2–4). A similar pattern emerged with the positive wave, maximal at parietal regions (P3/P4), but with a P300₂ nearer baseline under conditions with interference (Figs. 2–4).

As expected because of the interference tasks between first and second stimulus durations, no task-related differences in ERP amplitudes occurred after S1 ($P > 0.05$). During S2 (Fig. 4), CNV_2 amplitudes at F3/F4 electrodes were smaller with multiplication ($F[1,18] = 5.5$; $P < 0.03$) or line orientation ($F[1,18] = 7.26$; $P < 0.01$) interference than without it, as well as FP1/FP2 electrodes for line orientation ($F[1,18] = 4.51$; $P < 0.04$). A similar pattern emerged for P300₂ at P3/P4 electrodes with multiplication ($F[1,18] = 5.74$; $P < 0.027$) or line orientation ($F[1,18] = 4.93$; $P < 0.039$) interference.

The LPC was observed at longer delays than either previous component (Figs. 3 and 4). The positive portion of the wave was maximal at frontal sites and its negative counterpart (LNC) at parietal sites. The LPC was observable with or without interference. In contrast, the LNC was mostly prominent with interference. In contrast to previous waves, LPC amplitudes were larger with spatial interference than without it, the effect being significant at Fp1/Fp2 ($F[1,18] = 6.49$; $P < 0.02$), F3/F4 ($F[1,18] = 5.35$; $P < 0.03$), and F7/F8 electrodes ($F[1,18] = 11.37$; $P < 0.003$). The same

effect was observed with numeric interference, but significant only at F7/F8 electrodes ($F[1,18] = 8.70$; $P < 0.008$). Likewise, LNC amplitudes were larger at P3/P4 electrodes with spatial ($F[1,18] = 15$; $P < 0.001$) or numeric ($F[1,18] = 8.70$; $P < 0.008$) interference than without interference.

3. Discussion

3.1. Behavior

The short stimulus pair was more accurately discriminated and induced faster responses than the longer pair. This is probably due to unequal ratios between pairs, being larger for shorter than longer stimuli. As in previous studies (Le Dantec et al., 2007; Paul et al., 2003), stimulus order also influenced the results, with superior performances attained with short durations in the long/short order and longer durations in the reverse order. These data may be explained by different memory demands. For the short duration, a longer S2 may make S1 appear longer and inversely for the longer duration. These results are similar to those of Oshio et al. (2006), where monkey performances were superior in the short/long than the inverse order. Behavioral and PFC neuronal discharge rates indicated that monkeys responded on the basis of S1. It is possible that in our study subjects classified stimuli below approximately 900 ms as short and above 900 ms as long, perhaps only by considering S2, thus discriminating 800/400 and 1000/1400 ms more easily than 1400/1000 ms and 400/800 ms. Indeed, when presented as S2, 800 and 1000 ms is closely akin and thereby less easily identifiable.

As expected from dual task paradigms (Brown, 1997; Casini and Macar, 1999; Hicks et al., 1976; Macar, 1996), spatial and numeric interference deteriorated duration discriminations and augmented RTs. Taking into account selective attention models of time estimation (Zakay, 1989; Zakay and Block, 1995), the temporal processor shares attentional resources with non-temporal processors (Navon and Gopher, 1979; Wickens, 1984). The mobilization of attention from temporal to non-temporal processing is the likely cause of diminishing performances. Temporal and non-temporal tasks require working memory and thereby share the same neural circuitry (Meck and N'diaye, 2005). The augmented cognitive load required to perform the second task may either interfere with S1 through retroactive interference or with S2 through proactive interference.

The line orientation task deteriorated performances more severely than the multiplication task. Because angle estimation engages particularly the right hemisphere (Mascetti et al., 2001) and multiplications the left (Dehaene et al., 2004) with hemisphere-specific actions for each subtask (Sockeel, 1998), these findings are concordant with the view of a more important contribution of the right hemisphere in duration discriminations. This hypothesis is all the more plausible in that the subtasks did not differ between each other in terms of accuracy and RT. Thus, poorer duration discriminations with line orientation interference is probably due to hemisphere-related factors. On the basis of shared anatomic substrates of working memory (Meck and N'diaye, 2005), our results point towards a specific contribution of right PFC in timing accuracy, in accordance with past data (Gruber et al., 2000; Harrington et al., 1998b; Maquet et al., 1996; Pouthas et al., 2000; Rao et al., 2001).

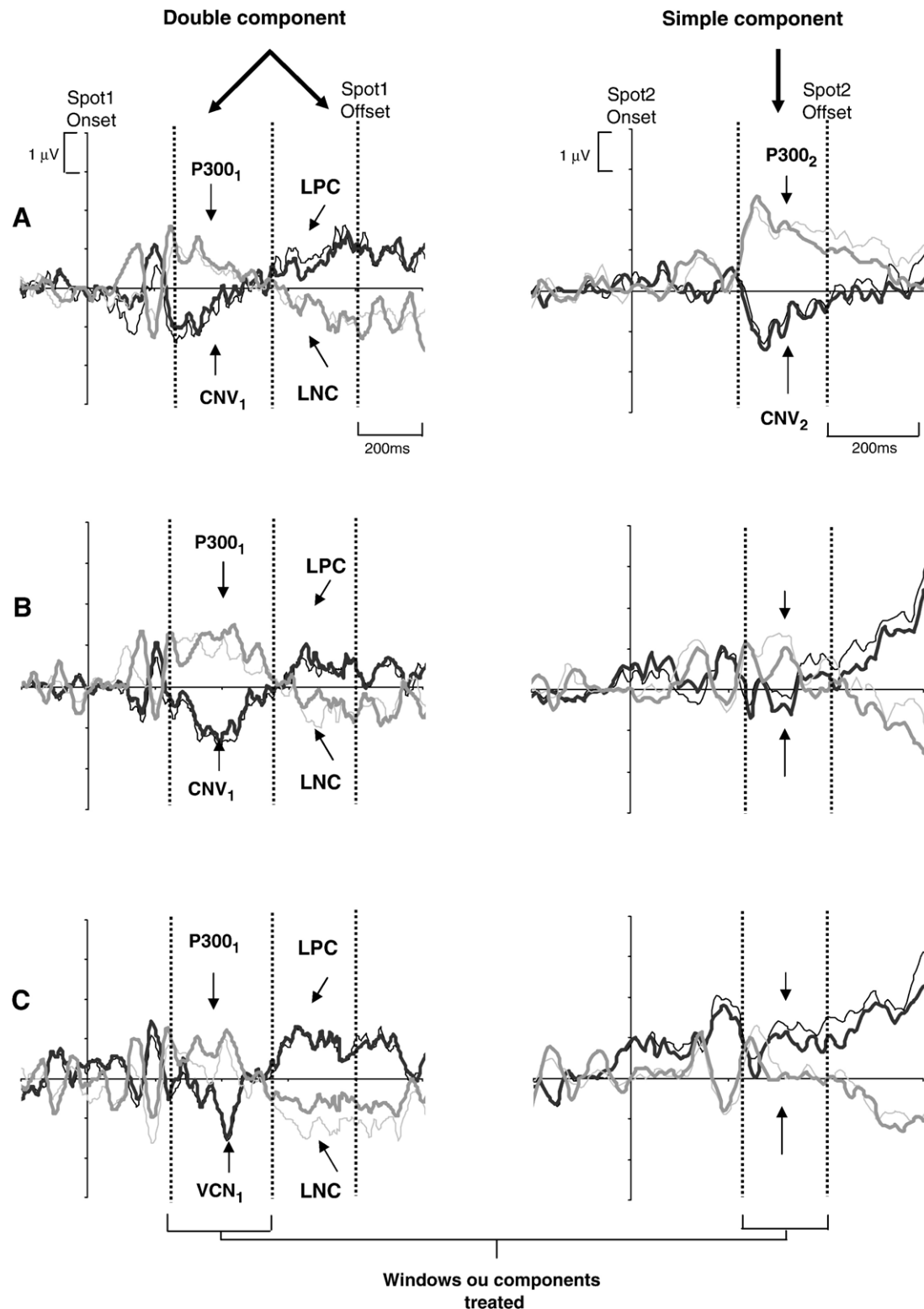


Fig. 2 - Electrophysiological activities recorded at Fp1 —, Fp2 —, P3 — and P4 — electrodes without interference (A) and for interference with line orientation (B) and multiplication (C) for the 800/400-ms duration.

3.2. ERPs

ERP data indicate that the encoding of durations imply at least two processing stages, corresponding to CNV/P300 followed by

LPC/LNC components, in accord with ERPs obtained in a temporal bisection task for a 200-ms target duration (Gibbons and Rammsayer, 2005). During test durations, a centro-parietal P300 appeared, presumably related to time estima-

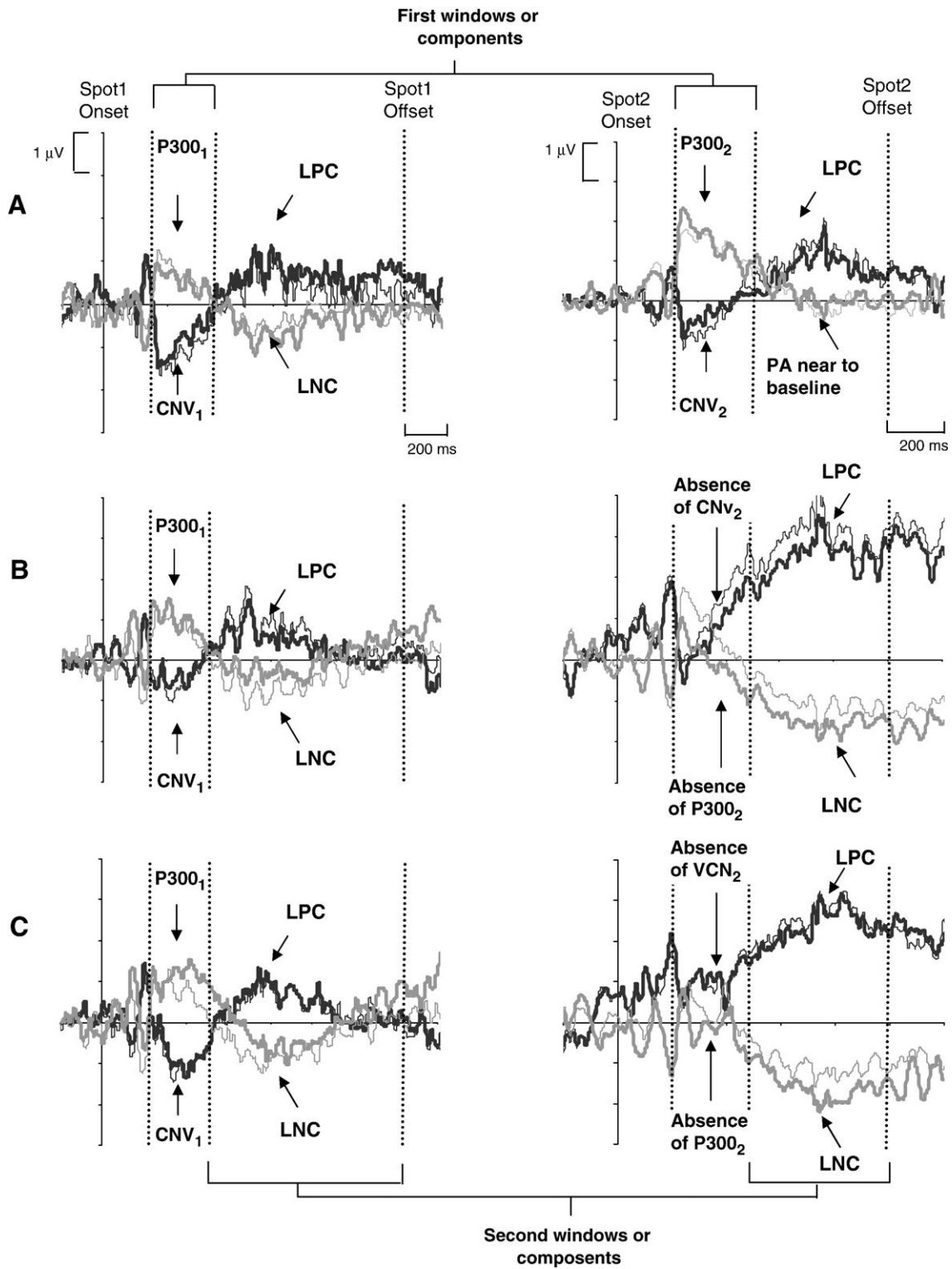


Fig. 3 - Electrophysiologic activities recorded at Fp1 —, Fp2 —, P3 — and P4 — electrodes without interference (A) and for interference with line orientation (B) and multiplication (C) for the 1400/1000-ms duration. PA = parietal activity.

tion, followed by a P500 fronto-central wave if this duration exceeded the target, probably related to expectancies. The appearance of these components is consistent with a two-process model of real-time comparisons between stimulus

durations and would be expected in our study, because S2 was never the same as S1.

Fronto-parietal regions seem to initiate these wave components conjointly, as reported with the same task at other

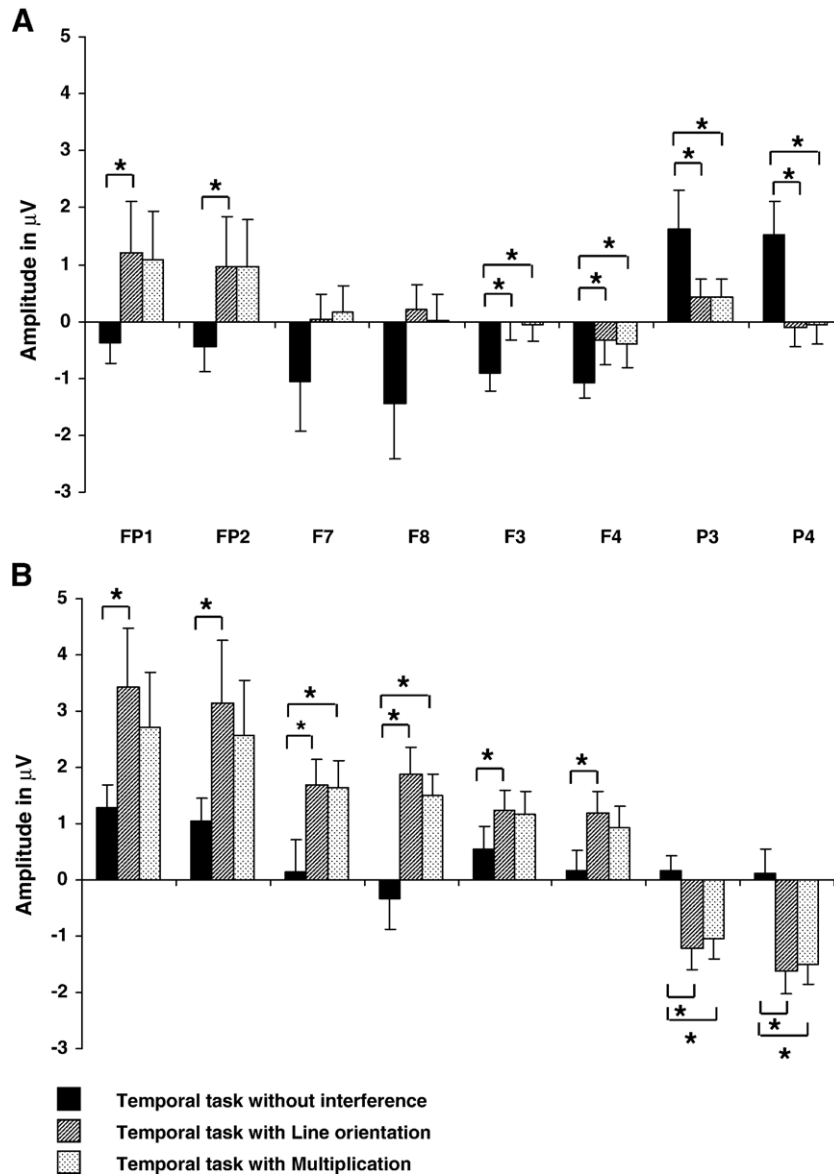


Fig. 4 – Histogram representing amplitudes recorded for CNV₂ and P300_z (A) and LPC/LNC (B) at frontal (FP1, FP2, F7, F8, F3, F4) and parietal (P3, P4) electrodes during the second stimulus duration.

durations (Le Dantec et al., 2007). During S2 processing, amplitudes of the frontal-dominant CNV and parietal-dominant P300 decreased under dual task relative to single task conditions. These results are concordant with the hypothesis of shared anatomic circuitries underlying working memory between a temporal task on one hand and spatial/calculation tasks on the other (Meck and N'diaye, 2005), as well as similarities of functions between frontal and parietal cortex reported for memory (Collette and Van der Linden, 2002; Mull and Seyal, 2001), selective attention (Behrmann et al., 2004; Sylvester et al., 2003), and duration discriminations (Basso et al., 2003; Macar and Vidal, 2004; Ojeda et al., 2002; Rubia et al., 2000). It is assumed that the dual task paradigm perturbs neural structures underlying selective attention and working memory of duration discriminations either through retroactive interference of S1 or proactive interference of S2. Because ERPs depend on excitatory thresholds

of neural assemblies (Birbaumer et al., 1990; Elbert, 1993), we assume that interference decrease this threshold during S2 processing and thereby deteriorates performances relative to a single task condition. As indicated by Birbaumer et al. (1990) and Rockstroh et al. (1982), negative and positive ERPs often work in concert to facilitate information processing, the former reflecting activation and the latter deactivation of neural circuits of cognitive operations. The added cognitive load associated with the dual task paradigm appears to disturb cell assemblies associated with time estimation, as revealed by the absent CNV and P300 waves. Thus, concurrent memory tasks interfere with each other when dependent on shared cerebral structures (Klingberg, 1998).

Our data also disclose two components of later onset, the LPC and LNC. Unlike the previously reported LPCt (Gontier et al., in press; Paul et al., 2003), the LPC is observed during the memory

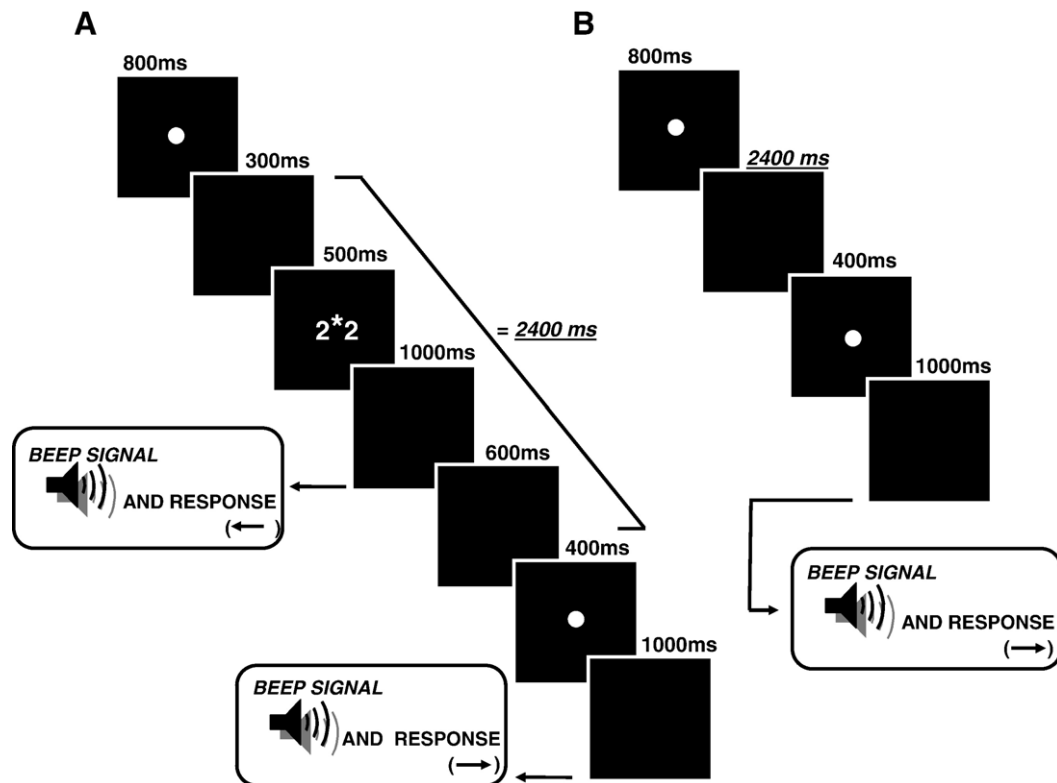


Fig. 5 – Schematic representation of duration discriminations for interference with the multiplication task (A) and without it (B) for the 800/400-ms duration.

phase and may correspond to the P500 component. In an opposite manner to CNV and P300 components, the amplitude of the frontal-predominant LPC and its parietal counterpart, the LNC, was elevated in dual task relative to single task conditions. This may be due to a compensatory action for the reduced amplitudes of earlier appearing waves. Indeed, different studies indicate that augmented cognitive load or cerebral dysfunction is manifested by recruitment of additional neural circuits (Crespo-Facorro et al., 2001; Klingberg et al., 1997; Ojeda et al., 2002; Quintana and Fuster, 1992, 1993, 1999; Quintana et al., 2003). Augmented cognitive load caused by task interference may deactivate one fronto-parietal system (CNV/P300) in favor of another (LPC/LNC), less effective in view of lower subject performances. Likewise, Ojeda et al. (2002) showed that the perturbed fronto-parietal system in schizophrenic subjects was compensated by increased activity in inferior PFC without attenuating behavioral deficits.

Although both interference tasks with equal levels of difficulty augmented LPC amplitudes, this effect was seen for a higher number of frontal electrodes during line orientation (Fp1/Fp2, F3/F4, F7/F8) than multiplication (F7/F8). Because judgment of line orientations deteriorated duration discriminations more severely than multiplications, LPC amplitudes were particularly enhanced when errors were frequent. Under dual task conditions, the LPC component may compensate for reduced activity of earlier appearing ERPs by mitigating deteriorating performances, thereby functioning as a warning signal. With task interference, LPC/LNC and CNV/P300 waves are shifted in concert but in opposite ways, in conformity with the complementary

action of fronto-parietal networks in other tasks (Crespo-Facorro et al., 2001; Ojeda et al., 2002; Quintana and Fuster, 1992, 1993, 1999; Quintana et al., 2003). Further studies must determine to what extent these data can be generalized to other temporal and non-temporal tasks.

Although no definite conclusion can be reached on hemispheric effects, CNV/P300 waves seemed more affected by line orientation than multiplication, the former known to activate more particularly the right side of the brain. For the CNV, differences in amplitude were obtained during dual relative to single task conditions for spatial interference at Fp1, Fp2, F3, and F4 electrodes, but only at F3, and F4 electrodes for numeric interference. Thus, line orientation appears to activate a wider assembly of neurons in neocortex. Likewise, the LPC was significantly enhanced at all frontal electrodes after spatial interference, but only at F7 and F8 electrodes after numeric interference. We suggest that right hemisphere interference predominantly affects earlier appearing waves, compensated by a wider activation of frontal regions.

In conclusion, our results reveal the importance of fronto-parietal networks during duration discriminations and indicate that CNV/P300 amplitudes are crucial components of effective information processing. PFC and PPC appear to work in concert during temporal processing, as an added cognitive load caused by task interference augmented the range of brain activation. Right hemisphere regions seem particularly implicated in durations, since task interference predominantly affecting the right side of the brain caused a severer behavioral deficit than one affecting the left.

4. Experimental procedures

4.1. Subjects

Twenty subjects equally participated in the study, with a mean age of 24.5 (SD: 3.25). For half of them, behavioral and ERP data were measured with task interference and the other half without interference, with each subgroup matched for age and sex. All subjects were right handed according to Oldfield (1971) criteria and had normal or corrected-to-normal visual acuity. The protocol adhered to guidelines of the European Council Directive (86/609/EEC) for the ethical treatment of human subjects.

4.2. Stimuli

For duration discriminations, tiny white spots of light were used, 1 pixel in size, presented on a dark screen with 100% luminance. In the interference tasks, line angles and numbers were presented and controlled to attain 100% luminance.

4.3. Experimental procedures

Two pairs of duration discriminanda were presented in a semi-random fashion: 400 vs. 800 ms and 1000 vs. 1400 ms in either order. The stimuli were presented 100 times in the ERP study and 20 times in the behavioral study, between which the line orientation or the calculation subtask was given. The line orientation task consisted of four line angles: 80°, 85°, 95°, and 100°. The multiplication task consisted of calculations from 2×2 to 6×6, i.e., 2×2, 2×3, 2×4, 3×2, 3×3, 3×4, etc., up to 6×6, excluding 4×4. In the ERP part, as shown in Fig. 5A, each trial in the interference condition contained S1, followed by a blank dark screen 300 ms in duration, an interfering stimulus lasting 500 ms, a second blank dark screen 1000 ms in duration preceding the beep sound used to warn the subjects that an answer is expected, a third blank dark screen lasting 600 ms, S2, followed by a beep sound 1 s in duration. The auditory stimulus is necessary to avoid motor-related ERPs (Rockstroh et al., 1982). In the behavioral study, no delay was imposed after S2, with subjects instructed to respond as quickly as possible. The difficulty related to interference was controlled by analyzing the impact of each subtask alone. The results showed no difference in performance levels between the two subtasks, indicating equivalent cognitive loads.

The condition without interference was conducted in an identical manner to either interference subtask, except for an interstimulus interval 2400 ms in duration (300 + 500 + 1000 + 600) (Fig. 5B). In duration discriminations, subjects pressed the left directional key when S2 was shorter than S1 and the right directional key when it was longer. In the line orientation subtask, subjects pressed the left-sided directional key if the angle was judged to be lower than 90° and the right-sided directional key if it was higher than 90°. Likewise, in the multiplication subtask, subjects pressed the left-sided directional key if the calculation was judged to be lower than 16 and the right-sided directional key if it was higher than 16.

4.4. EEG recordings

The EEG was recorded with a 32-electrode array displayed according to the 10–20 classification system with respect to a reference electrode placed in the frontocentral position. As used by Bertrand et al. (1985), ERPs for each electrode were then determined as a function of a mean reference calculated from the following 20 electrodes: F3, C3, P3, F7, T3, P7, F4, C4, P4, F8, T4, P8, Cz, Fz, Pz, CP3, TP7, CP4, TP8, CPz. The average reference for 20 electrodes took into account the unequal distribution of anterior and posterior sites, thereby assuring us of equivalent spatial sampling at these sites. The signals were amplified, digitized, sampled (1 point per 3.92 ms), filtered (0.1 Hz to 100 Hz), and stored on an IBM-compatible computer with Deltamed™ software. The baseline consisted of the average amplitude of the 250-ms period immediately preceding the onset of each stimulus. Electrode impedance was kept below 5 KΩ. The EEG was continuously recorded during the experiment and codes, synchronized to stimulus delivery, were used to average epochs off-line. All epochs corresponded to 2400 ms after stimulus onset (the longest duration was 1400 ms plus the 1000-ms interval between S2 offset and the auditory tone). As recommended by Picton et al. (2000), the subjects were told to limit eye movements and, during wave averaging, artifacts from ocular movements ($N \pm 100 \mu\text{V}$) recorded at FP1 and FP2 electrodes were eliminated. Activity $N \pm 100 \mu\text{V}$ was automatically rejected by the software. After grand averaging, the data were filtered at 48 Hz and visualized in the form of electrophysiologic signals or topographic maps.

Temporal windows were determined after grand averaging: 250 to 500 ms for the CNV and the P300 and 500 to the end of stimulus duration for the LPC and LNC (Figs. 2 and 3). For short durations, only the 800-ms stimulus permitted observation of LPC and LNC (Fig. 2). Thus, we restricted our analyses of these components to longer durations.

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