

When Loading Working Memory Reduces Distraction: Behavioral and Electrophysiological Evidence from an Auditory–Visual Distraction Paradigm

Iria SanMiguel, María-José Corral, and Carles Escera

Abstract

■ The sensitivity of involuntary attention to top–down modulation was tested using an auditory–visual distraction task and a working memory (WM) load manipulation in subjects performing a simple visual classification task while ignoring contingent auditory stimulation. The sounds were repetitive standard tones (80%) and environmental novel sounds (20%). Distraction caused by the novel sounds was compared across a 1-back WM condition and a no-memory control condition, both involving the comparison of two digits. Event-related brain potentials (ERPs) to the sounds were recorded, and the N1/MMN (mismatch negativity), novelty-P3, and RON components were identified in the novel minus standard difference waveforms. Distraction was reduced in the WM condition, both behaviorally

and as indexed by an attenuation of the late phase of the novelty-P3. The transient/change detection mechanism indexed by MMN was not affected by the WM manipulation. Sustained, slow frontal and parietal waveforms related to WM processes were found on the standard ERPs. The present results indicate that distraction caused by irrelevant novel sounds is reduced when a WM component is involved in the task, and that this modulation by WM load takes place at a late stage of the orienting response, all in all confirming that involuntary attention is under the control of top–down mechanisms. Moreover, as these results contradict predictions of the load theory of selective attention and cognitive control, it is suggested that the WM load effects on distraction depend on the nature of the distractor–target relationships. ■

INTRODUCTION

Selection of relevant information from the world around us is accomplished by the mechanisms of attentional control, which modulate neural responses to sensory stimuli (Luck & Hillyard, 2000; Hillyard & Anllo-Vento, 1998). These are conceptualized as two opposed sets of mechanisms, which interact for the control of attention: the voluntary or endogenous mechanisms of control, and the involuntary or exogenous mechanisms of control. A balance between the endogenous and exogenous mechanisms is necessary for adaptive behavior. On the other hand, evidence from dual-task (Pashler, 1993, 1994) and task-switching (Barceló, Escera, Corral, & Periáñez, 2006; Meiran, 1996; Rogers & Monsell, 1995) paradigms has shown that attention is also a limited resource. Indeed, performing two tasks at the same time results in a decrement in performance. Thus, the mechanisms of control of attention have to be maintained in balance within this limitation and fairly distribute the attentional resources over the relevant task and inputs at hand, while at the same time being flexible enough to shift to potential threats or simply to other new potentially relevant events (Berti, Roeber, & Schröger, 2004).

The endogenous and exogenous mechanisms of attentional control, however, have been mainly studied in

isolation, their interactions being largely ignored. In this way, voluntarily focusing attention at a cued location has been shown to increase correct responses and decrease reaction times at that location, as well as to modulate brain responses related to the target stimuli (Hopfinger & West, 2006; Arnott, Pratt, Shore, & Alain, 2001), providing evidence for the modulation of responses by endogenous mechanisms of control. Exogenous mechanisms of attentional control are also put at play in visual selective attention tasks. Indeed, salient stimuli are known to capture attention exogenously (Yantis & Jonides, 1990). Flashing a light briefly at one spatial location facilitates the response to a subsequent target stimulus at that same location and disrupts responses to target stimuli at different locations (Posner & Cohen, 1984). As the interactions between these two mechanisms of attentional control have been poorly understood, exogenous attentional capture has been thought to result from an automatic process, which does not depend on top–down influences or demands. However, recent evidence challenges the notion of “automatic processes” as it has been shown that these “automatic processes” can be modulated in a top–down fashion (Pashler, Johnston, & Ruthruff, 2001). If this is so, how involuntary is involuntary attention? It appears that although the two mechanisms of attentional control have so far been studied mainly in isolation, they interact and influence each other for the control of attention.

University of Barcelona, Catalonia, Spain

The concept of automaticity is generally based on two premises: whether the process can be controlled voluntarily based on behavioral goals, and whether it is independent from the available processing resources. Evidence has shown that these two premises do not always apply to the exogenous mechanisms of attentional control, and therefore, the involuntary capture of attention cannot be claimed to be “automatic.” Attentional capture by distractors is dependent upon the relationship between the distractor and the task stimuli (the “contingent orienting theory,” Folk & Remington, 1998, 1999; Folk, Remington, & Johnston, 1992). Thus, attentional capture by exogenous cues is never purely stimulus-driven. That is, involuntary orienting of attention can be modulated in a top-down fashion as a function of the current behavioral goals, and therefore, endogenous mechanisms are also playing a role in the so-called involuntary control of attention. Also, the amount of distraction can be modulated by cognitive load on selective attention tasks (Lavie, Hirst, De Fockert, & Viding, 2004). In these experiments, the independence of involuntary responses from the available cognitive resources (i.e., its automaticity) was tested under different conditions of working memory (WM) load, resulting in increased distraction in conditions of larger WM load. Converging evidence is provided by a number of studies (Lavie, 2005; Lavie & De Fockert, 2005; Yi, Woodman, Widders, Marois, & Chun, 2004; De Fockert, Rees, Frith, & Lavie, 2001; for a review, see Lavie et al., 2004). From these results, it is evident that automatic attentional mechanisms are not independent from the available processing resources.

The general conclusion that stems from all these arguments is that endogenous and exogenous attention mechanisms indeed interact when controlling the focus of attention, but it remains unclear how this interaction takes place. A clear link between attentional control and WM seems to emerge, with the evidence pointing toward a role of WM in controlling the balance between the exogenous and endogenous mechanisms of attention. Indeed, there is considerable evidence for a role of WM, and the corresponding cerebral regions, in the control of attention (Gazzaley, Cooney, McEvoy, Knight, & D’Esposito, 2005; Hester & Garavan, 2005; Vogel, Woodman, & Luck, 2005; Postle, Awh, Jonides, Smith, & D’Esposito, 2004; Corbetta & Shulman, 2002; Kane & Engle, 2002; Awh & Jonides, 2001; Awh, Anillo-Vento, & Hillyard, 2000; Downing, 2000; Rainer, Asaad, & Miller, 1998; for a review, see Awh, Vogel, & Oh, 2006). Thus, a proposal is starting to emerge suggesting that the ability to control attention and maintain the balance between the endogenous and exogenous mechanisms is influenced by, and related to, WM (Barceló et al., 2006; Hester & Garavan, 2005). Executive “top-down” control is assigned to the WM functions that are based in prefrontal cortex (PFC), putting forward a model where cognitive control stems from the active maintenance of patterns of activity in PFC that represent goals and the means to

achieve them, while providing top-down bias signals to other brain structures, in order to guide behavior (Duncan, 2001; Fuster, 2001; Miller & Cohen, 2001; Miller, 2000). This view is consistent with results of selective attention studies where it has been shown that the top-down effects over the involuntary system modulate neural responses at primary sensory areas of the cortex (e.g., reducing early responses to the distractor) (Hopfinger & West, 2006; Pinsk, Doniger, & Kastner, 2004; Spinks, Zhang, Fox, Gao, & Tan, 2004). Altogether, WM seems to be involved in the control of attention, and more specifically in the modulation of the processing of irrelevant information by attentional mechanisms.

However, the evidence that has been collected regarding the specific role of WM in attention control is contradictory. In some studies imposing WM load has resulted in increased distraction (Lavie et al., 2004), whereas other studies showed the opposite effect of loading WM, leading to the proposal that WM protects from distraction by exerting top-down control (Berti & Schröger, 2003). Indeed, a decrease in behavioral distraction as well as in blood oxygenation level-dependent activity in visual areas related to novel distractors has been found under conditions of high cognitive load (Spinks et al., 2004), and there is a great deal of evidence supporting the role of WM areas in PFC in the mediation of interference and distraction (Postle, 2005; Jensen, Gelfand, Kounios, & Lisman, 2002; Sakai, Rowe, & Passingham, 2002; Worden, Foxe, Wang, & Simpson, 2000; Klimesch, Doppelmayr, Schwaiger, Auinger, & Winkler, 1999). This function would be achieved by controlling the gain of activity in sensory areas of the posterior cortex, thus minimizing the disruption of WM storage processes by suppressing the sensory processing of potentially distracting information in the environment (Postle, 2006). Yet other evidence suggests that the effects of load depend on the type of objects used to load WM, and whether they share features with the target or the distractor (Kim, Kim, & Chun, 2005), a conclusion that is congruent with the provisions of the contingent orienting theory (Folk et al., 1992).

The goal of the present study was to investigate the interaction between endogenous and exogenous mechanisms in the control of attention and the role of WM in controlling this interaction. For this purpose, a possible modulation over exogenous mechanisms by top-down, endogenous factors was assessed by varying the WM load in the task. In order to achieve this, distraction (involuntary orienting) was induced by means of a well-established auditory-visual distraction paradigm (Escera, Yago, Corral, Corbera, & Nuñez, 2003; Escera, Corral, & Yago, 2002; Escera, Yago, & Alho, 2001; Gumenyuk et al., 2001; Escera, Alho, Schröger, & Winkler, 2000; Escera, Alho, Winkler, & Näätänen, 1998). The task resembles a natural situation in which subjects must concentrate on a demanding visual task while attempting to ignore irrelevant environmental sounds, as when trying to focus

on reading a book while ignoring environmental noise in a crowded cafeteria. This paradigm is particularly well suited to test the independence of the involuntary attentional mechanisms from endogenous factors because distraction here is thought to be purely exogenous and involuntary as the sounds are completely irrelevant to the task, and they are presented on a different sensory modality that is explicitly asked to be ignored (Escera et al., 1998, 2001, 2002, 2003; Yago, Escera, Alho, Giard, & Serra-Grabulosa, 2003; Yago, Corral, & Escera, 2001; Yago, Escera, Alho, & Giard, 2001; Alho, Escera, Díaz, Yago, & Serra, 1997; see review in Escera et al., 2000). Also, this paradigm allows the investigation of different phases of the orienting response by means of event-related brain potentials (ERPs). Typically, ERPs recorded during distraction in this behavioral setting reveal an early negativity and a subsequent positivity, followed by a second negativity. These waves provide an index of the main stages of exogenous attention control (Escera & Corral, 2003; Escera et al., 2000). First, a combined response (N1/MMN) including an enhancement of the auditory N1 component and the *mismatch negativity* (MMN) indexes, respectively, a transient detector mechanism and a mechanism for stimulus change detection, altogether leading to attention capture (Alho et al., 1998; Escera et al., 1998). Subsequently, the *novelty-P3* indexes the effective orienting of attention (Friedman, Cycowicz, & Gaeta, 2001; Escera et al., 1998, 2000). Two distinct phases—early and late—of this component have been identified (Polo et al., 2003; Yago et al., 2003; Escera et al., 1998, 2001), the later phase being sensitive to attentional manipulations (Escera et al., 1998, 2003). Finally, the *reorienting negativity* (RON) indexes the reorienting of attention back to the task after temporary distraction (Berti et al., 2004; Berti & Schröger, 2001; Schröger, Giard, & Wolff, 2000; Schröger & Wolff, 1998a, 1998b). A parallel line of evidence supports this theoretical proposal, in which an auditory–auditory version of the distraction paradigm is used (Berti & Schröger, 2001; Schröger & Berti, 2000; Schröger et al., 2000; Schröger & Wolff, 1998a, 1998b).

In the present study, following the views assigning a “top–down” executive control to WM (Duncan, 2001; Fuster, 2001; Miller & Cohen, 2001; Miller, 2000), and suggesting that WM protects from distraction (Berti & Schröger, 2003) by controlling the gain of activity in sensory processing areas (Postle, 2006), we expect to find a modulation over distraction by WM load, in the direction of reduced distraction under higher WM load. Consequently, an attenuation of behavioral and electrophysiological traces of distraction by increasing WM load is predicted. This should be reflected in the components of the orienting response. Although the N1/MMN mechanism is believed to be highly automatic and not under the influence of endogenous top–down factors (Restuccia, Della Marca, Marra, Rubino, & Valeriani, 2005; Harmony et al., 2000; Näätänen & Winkler, 1999; Näätänen, 1992),

the novelty-P3 response has been shown to be sensitive to modulation in a top–down fashion, particularly on its late phase (Restuccia et al., 2005; Escera et al., 1998, 2003; Harmony et al., 2000). Thus, in line with this, we expect to find a modulation of the novelty-P3 component, indexing a reduction of the effective orienting of attention, whereas the attention capture or transient/change detection mechanism, associated with N1/MMN, should remain unaffected. That is, the modulation would take place at a later stage of the orienting response. Further, the mechanisms that possibly lie behind the modulation effect will be isolated by examining the main effects of WM. These effects on primary sensory responses to task stimuli will be examined, expecting to find a modulation of primary sensory components in line with recent proposals (Postle, 2006).

METHODS

Subjects

Fifteen healthy university students (23–28 years; mean age = 25.7 years; 5 men) participated in the study. All but one were right-handed, all had normal or corrected-to-normal vision, and none of them reported any auditory deficit. This was confirmed by an audiometric test to measure the hearing capabilities before starting the experimental session resulting in auditory thresholds all below 40 dB. Four subjects were discarded due to technical problems or excessive blinking during the recording session. Subjects gave informed consent after the nature of the study was explained to them. The study protocol was approved by the ethical committee of the University of Barcelona.

Procedure

Subjects were presented with an adapted version of a very well-established auditory–visual distraction task (Escera et al., 1998, 2001, 2002, 2003). The task consisted of four blocks of 250 stimulus pairs (trials) delivered at a constant rate of one trial every 1250 msec. Each trial consisted of an irrelevant auditory stimulus followed after 350 msec (onset-to-onset) by a visual imperative stimulus (Figure 1). The auditory sequence consisted of repetitive standard tones (600 Hz, 200 msec; $p = .8$), occasionally replaced by an environmental novel sound selected from a sample of 100 different exemplars ($p = .2$), such as those produced by a drill, hammer, rain, door, telephone ringing, and so forth. The novel sounds were digitally recorded, low-pass filtered at 10,000 Hz, and edited to have a duration of 200 msec, including rise and fall times of 10 msec, and an intensity of 85 dB SPL. The novel sounds were selected from a larger database as those rated most identifiable by an independent sample of subjects (Escera et al., 2003); they occurred only once within a stimulus block and were presented two times during the whole experiment. All sounds were delivered binaurally

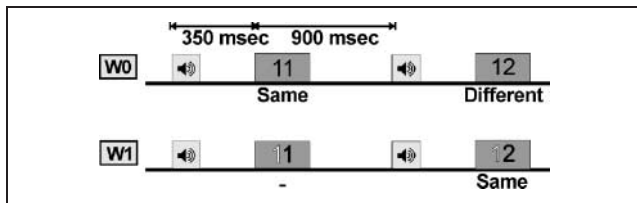


Figure 1. Stimulation sequence (above the line) and correct responses to the task (below the line) for the two conditions. In the W0 condition, subjects had to decide whether the two digits appearing on the screen were the same or different. In the W1 condition, subjects had to decide whether the first digit was the same or different to the first digit of the previous trial. Sounds were randomly standard (80%) or novel (20%).

through headphones (Sennheiser HD 555), in random order, with the only restriction that at least the first four stimuli of each block were standard tones, and that two novel sounds never appeared consecutively. Visual stimuli were pairs of combinations of the digits 1 and 2 (e.g., 11, 12, 21, or 22), presented on a computer screen for 200 msec. The probability of appearance was equal for all combinations. Visual stimuli subtended a vertical angle of 1.53° and a horizontal angle of 2.10° ($4 \text{ mm} \times 5.5 \text{ mm}$ at 150 cm from the subject's eyes). Auditory and visual stimuli were constructed and presented with the software Stim (NeuroScan).

Participants sat in a comfortable chair in a dimly lit and electrically and acoustically shielded room. The task consisted of making a decision on the two digits appearing on the screen, while ignoring the auditory stimulation. The specific instruction was to ignore the irrelevant auditory stimulation and to press, as fast and as accurately as possible, one response button for the equal stimuli and another response button for the different stimuli, with the index and middle fingers of the dominant hand. The response buttons were counterbalanced across subjects. The probability of both responses was equal. In order to reduce eye blinks and movements during the electroencephalogram (EEG) recording, subjects focused on a central fixation point between the two digits.

Two visual task conditions were used in the present experiment, one in which there was a load on WM (W1) and another without WM load (W0). In the W0 condition, subjects had to decide whether the two digits appearing at the same time on the screen were the same (11 or 22) or different (12 or 21). In the W1 condition, subjects had to compare the left digit appearing on the screen with the left digit seen in the two-digit number of the previous trial. In this manner, they should keep one digit into WM until the next trial, and then give their response, responding to every trial except the first one (Figure 1). There were two blocks per condition and the order of the blocks was counterbalanced across subjects using a Latin square design. Before the experimental session, subjects received practice blocks in the two con-

ditions without any auditory stimuli, until they reached a hit rate level of at least 75% in each condition. To prevent tiredness, a short rest period after each block was allowed.

EEG Recording

The EEG was continuously digitized at a rate of 500 Hz (bandpass 0.01–100 Hz) by a SynAmps amplifier (Compumedics NeuroScan) from 28 scalp Ag–AgCl electrodes positioned according to the extended 10–20 system (Fp1, Fp2, FC1, FC2, F3, F4, F7, F8, FT3, FT4, Fz, C3, C4, Cz, T3, T4, T5, T6, TP3, TP4, CP1, CP2, P3, P4, Pz, Oz, IN1, IN2). Two additional positions were placed on left and right mastoid (M1 and M2, respectively). The horizontal and vertical electrooculogram (HEOG/VEOG) were recorded with electrodes attached to the right canthus and below the right eye. The electrodes were mounted in an elastic cap (Electro-Cap International), and the common reference electrode for all electrodes was placed on the tip of the nose.

Data Analysis

Mean response time (RT) for correct responses, hit rate (HR), and error rate (ER) were calculated separately for the standard and novel sound trials and WM conditions. Distraction effects caused by novel sounds and WM effects were analyzed by means of analysis of variance (ANOVA) for repeated measures with the type of auditory stimulus (standard and novel) and WM load (W0 and W1) as factors, performed on HR, RT, and ER.

Continuous EEG data were bandpass filtered off-line between 0.1 and 30 Hz. Two different ERP averages were computed to analyze the distraction and the WM effects. ERPs were averaged for each auditory-stimulus trial type, with an epoch of 1450 msec including a preauditory stimulus baseline of 200 msec to analyze the distraction effect. A longer interval, partly including two consecutive trials, was used to analyze WM effects, with an epoch of 1800 msec starting at auditory stimulus presentation time, including a 200-msec baseline as well. Only standard trials were considered for this analysis. ERPs were averaged for each WM load condition separately in both analyses. All epochs with EOG or EEG exceeding $\pm 100 \mu\text{V}$ at any channel, as well as the first five epochs of each block and epochs of standard trials immediately following a novel trial, were automatically excluded from averaging. Signal processing was carried out by means of the Eeprobe (EEP) 2.3 program (ANT Software, Enschede, NL).

Distraction Effects

Difference waves were calculated by subtracting the ERPs elicited to standard trials from those elicited to novel trials, which allowed the identification of the

following components in the grand-average difference wave at Cz: N1/MMN as the largest negative peak in the 110–160 msec time window, novelty-P3 as the largest positive peak in the 180–380 msec time window, and RON as the largest negative peak in the 400–600 msec time window. Novelty-P3 was further divided in early (180–280 msec) and late (280–380 msec) subcomponents. Statistical analysis for N1/MMN and RON was carried out on the mean amplitude in the time windows defined above by means of repeated measures ANOVA including WM load (high vs. low) and electrode (N1/MMN: F3, Fz, F4, C3, Cz, and C4; RON: F3, Fz, F4, C3, Cz, C4, P3, Pz, and P4) as factors. Statistical analysis for novelty-P3 was carried out on the mean amplitude in the time windows defined above by means of repeated measures ANOVA including WM load (high vs. low), novelty-P3 phase (early vs. late), frontality (3 levels), and laterality (3 levels) as factors at F3, Fz, F4, C3, Cz, C4, P3, Pz, and P4.

Working Memory Effects

The effects of WM load on brain responses were analyzed by means of two different strategies, both comparing ERP measures obtained in standard trials. First, to test for specific effects on sensory (auditory and visual) and cognitive processing, the following components were identified on the standard trial ERPs as the largest peak in the specified latency windows and electrodes: auditory N1 (audN1, 85–135 msec at Cz), auditory P2 (audP2, 155–205 msec at Cz), visual P1 (visP1, 420–470 msec at Oz, 70–120 msec from visual stimulus onset), and visual N1 (visN1, 470–530 msec at Oz, 120–180 msec from visual stimulus onset). Two additional components related to target processing were identified: the N2b in the 515–640 msec time window (165–290 msec from visual stimulus presentation), and P300 in the 660–830 msec time window (310–480 msec from visual stimulus presentation). Statistical analysis for all components was carried out on the mean amplitude in the time windows defined above by means of repeated measures ANOVA including WM load (high vs. low) and electrode as factors. Amplitude analysis for the N2b component was carried out on different windows for each condition (W1: 545–600 msec; W0: 580–630 msec) due to a significant latency effect (see Table 1). The electrodes included in these analyses were different depending on the component as follows, audN1, audP2, and N2b: F3, Fz, F4, C3, Cz and C4; visP1 and visN1: IN1, IN2, Oz, T5, and T6; P300: P3, Pz, and P4. Post hoc tests were conducted wherever there were significant interactions between the main factors.

The second analytical strategy aimed to study overall changes in the scalp distribution of the brain response due to WM load. In general, as can be seen in Figure 5, the ERP obtained in the W1 condition was negatively displaced over almost the whole epoch, and this analysis aimed to characterize the scalp distribution of this

Table 1. ANOVAs for the Defined ERP Components

	ANOVA	
<i>AUD</i>		
N1	$F(1, 10) = 5.536$	$p = .040$
P2	$F(1, 10) = 18.137$	$p = .002$
<i>VIS</i>		
P1	$F(1, 10) = 0.218$	$p = .650$
N1	$F(4, 40) = 4.697$	$p = .009$
<i>TARGET</i>		
N2b (<i>latency</i>)	$F(1, 10) = 7.781$	$p = .019$
N2b (<i>amplitude</i>)	$F(1, 10) = 6.554$	$p = .028$
P300 (<i>latency</i>)	$F(1, 10) = 1.000$	$p = .341$
P300 (<i>amplitude</i>)	$F(2, 20) = 10.683$	$p = .003$

Results represent differences between the two WM conditions.

sustained negative potential. For this analysis, four longer, “cognitive” windows were defined as encompassing different stages of WM task performance. A first latency window started at the presentation of the sound and comprised the presentation of the visual stimulus (100–350 msec). The second window encompassed the presentation of the visual stimulus until the emergence of the visual P300 component (400–600 msec). The third latency window covered the P300 (650–850) and the subjects’ mean RT. The fourth latency window encompassed the time elapsed from 200 msec after the mean RT (760 msec) until the onset of the subsequent trial with the presentation of the next auditory stimulus (950–1150 msec). In order to study scalp distribution changes, analyses were carried out on the normalized mean amplitude (McCarthy & Wood, 1985) in these latency windows by means of repeated measures ANOVA including WM (high vs. low), frontality (3 levels), and laterality (5 levels) as factors at F7, F3, Fz, F4, F8, T3, C3, Cz, C4, T4, T5, P3, Pz, P4, and T6 electrode locations.

Where appropriate for all statistical analyses, degrees of freedom were corrected with the Greenhouse–Geisser method and the reported p values were based on these corrected degrees of freedom.

RESULTS

Performance

Figure 2 shows performance in the visual task. As can be seen, subjects had a high HR of about 95% in the W0 condition and a bit smaller (85%) in the W1 condition. This difference in HR between conditions was significant [$F(1, 10) = 5.39, p = .043$], indicating that loading WM

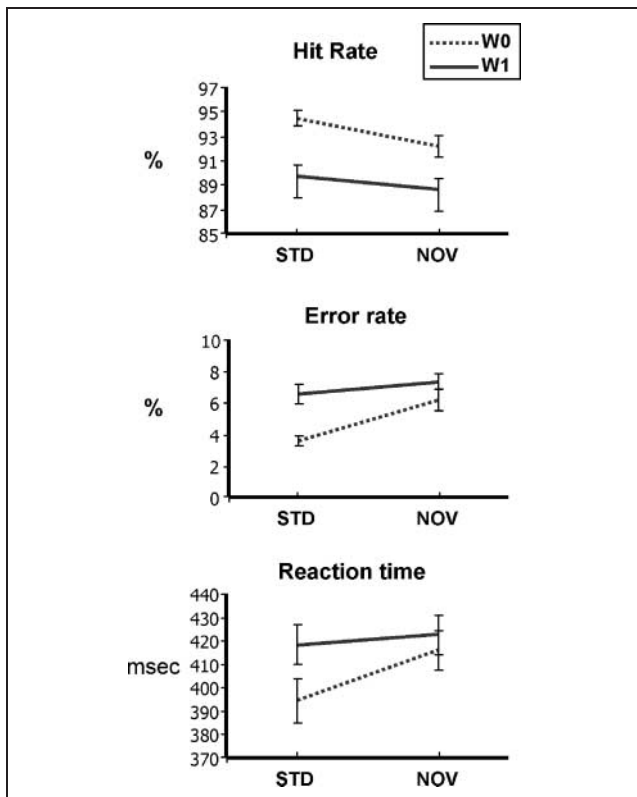


Figure 2. Performance on the visual task for the two experimental conditions. ER was larger and RT was longer in the W1 condition. Performance in novel trials was slower and less accurate compared to standard trials. The increase in RT after novel sounds was significantly smaller in the W1 condition. Bars indicate the standard error of the mean.

made the task more difficult to perform. The decrease in HR was caused by an increase in the ER [$F(1, 10) = 13.51, p = .004$] rather than by an increase in the number of missed stimuli. The WM effect was also evident in RT, as subjects were, on average, 15 msec slower in W1 than in W0 [$F(1, 10) = 8.77, p = .014$].

Subjects responded slower in novel trials than in standard trials [$F(1, 10) = 28.16, p < .001$], indicating that they were effectively distracted from main task performance by the unexpected occurrence of a novel sound in the two WM conditions. Distraction was also seen as a decrease in HR in novel trials as compared to standard trials [$F(1, 10) = 13.37, p = .004$]. The decrease in HR was due to an increase in the ER [$F(1, 10) = 12.97, p = .005$] rather than to an increase in the nonresponded stimuli.

Most interesting, the interaction of WM load condition (high vs. low) with trial type (standard vs. novel) also yielded significant effects in RT [$F(1, 10) = 9.78, p = .011$], indicating that the load manipulation reduced the increase in RT caused by the novel sounds. Subsequent post hoc tests revealed that although the distraction effect was highly significant in the W0 condition [$F(1, 10) = 25.97, p < .001$], it disappeared when loading WM [$F(1, 10) = 2.00, p = .188$].

Brain Responses

Distraction Effects

Novel minus standard difference waveforms are shown in Figure 3 for the two WM conditions. In the difference wave, the N1/MMN deflection was identified in the 110–160 msec window with a mean amplitude of $-0.1 \mu\text{V}$ in the W0 condition and of $-0.3 \mu\text{V}$ in the W1 condition. The mean amplitude difference between the two WM conditions was nonsignificant [$F(1, 10) = 0.24, p = .634$].

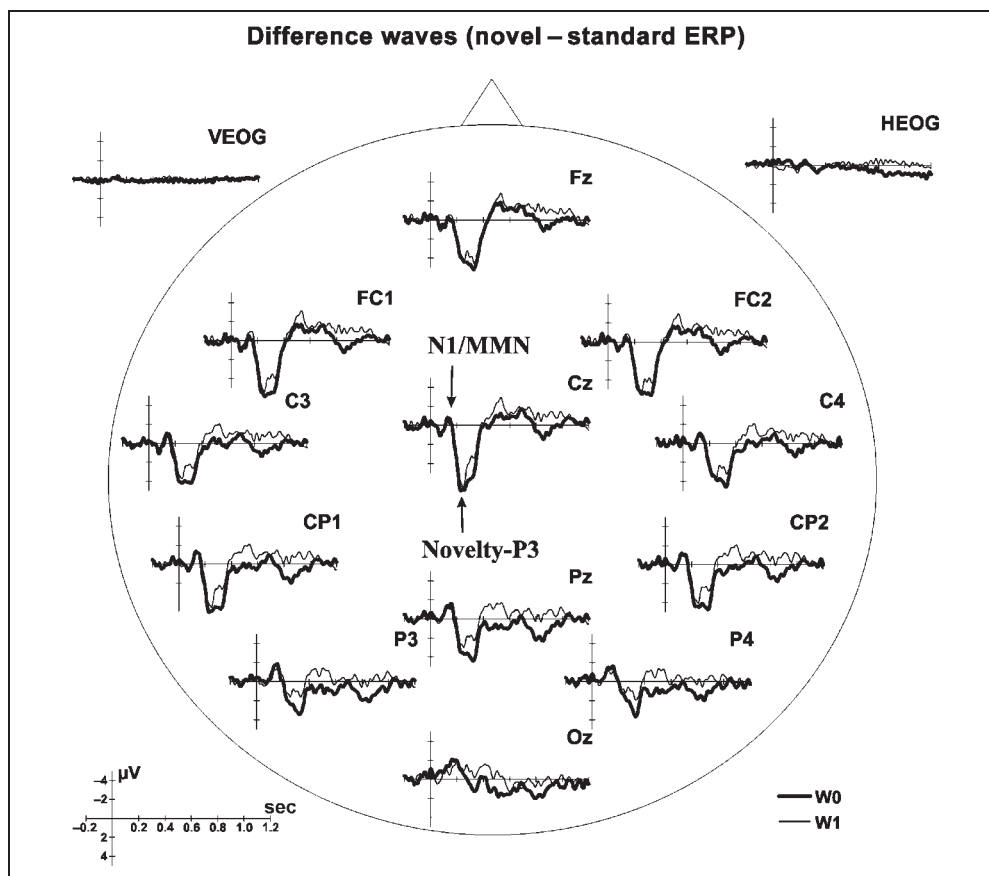
As for the novelty-P3, its early phase had a mean amplitude of $5.6 \mu\text{V}$ in W0 and of $4.9 \mu\text{V}$ in W1, and its late phase had a mean amplitude of $4.0 \mu\text{V}$ in W0 and of $2.9 \mu\text{V}$ in W1. ANOVA revealed that there was a significant amplitude difference of this component between the two WM conditions as indicated by the significant WM \times Frontality interaction [$F(2, 20) = 5.43, p = .031$], and the WM \times Phase \times Frontality interaction [$F(2, 20) = 4.65, p = .041$], with the novelty-P3 being reduced in the W1 condition. Subsequent analysis revealed that this effect was due to a reduction of the late phase of the novelty-P3 on parietal electrodes [WM \times laterality ANOVA on parietal electrodes, late phase; WM factor's $F(1, 11) = 6.51, p = .027$]. Post hoc tests for WM effects performed for all frontality levels on the early phase and for central and frontal sites on the late phase were all nonsignificant ($p > .05$ in all cases). These effects are illustrated in Figure 4, where the scalp distribution maps for the early and late phases of the novelty-P3 component in the two WM conditions are shown.

Finally, a significant difference between the two WM conditions was also found for the RON component [WM factor's $F(1, 10) = 4.68, p = .056$; WM \times electrode interaction: $F(8, 80) = 7.52, p = .005$]. The amplitude of the RON component was larger in the W1 condition.

Working Memory Effects

Figure 5 shows the ERP waveforms elicited by standard trials in the two WM conditions. The specific latency windows that were submitted to statistical analysis and the ERP components that were identified are also shown. Table 1 summarizes the results of the ANOVAS performed on specific ERP components, revealing that all of them differed in amplitude between the W0 and W1 conditions. In the W1 condition, a sustained negativity was observed affecting the early part of the waveform until the emergence of the P300 component. This negativity was pronounced at frontal electrodes and partially disappeared at posterior electrodes, except for a phasic effect on the visual N1 component, on the left hemisphere [$F(4, 40) = 4.70, p = .009$]. This may suggest an effect of WM load over the extrastriate processing of the visual target stimulus. A pronounced effect on the P300 component was also found, its amplitude being reduced under WM load [$F(2, 20) = 10.68, p = .003$]. Following the P300 component, the sustained

Figure 3. Distraction potential (novel – standard waveforms) on a selected set of electrodes. The N1/MMN and novelty-P3 deflections can be identified. Amplitude of novelty-P3 was reduced in the W1 condition, particularly on its late phase.



negativity turned into a superimposed positivity in the W1 condition, lasting until the presentation of the subsequent sound and the beginning of the next trial.

In order to analyze sustained effects and scalp distribution changes of neuroelectric responses due to WM load, the normalized amplitude was compared across WM conditions in four “cognitive” latency windows. Figure 6 shows the scalp distribution for each of these four “cognitive” windows on each WM condition and the resulting map obtained by subtracting the ERPs from the two conditions. Table 2 shows a summary of the

ANOVA results for the four time windows under analysis. For the first latency window (100–350 msec), a sustained negativity was observed, being of larger amplitude in W1 compared to W0 [$F(1, 10) = 5.73, p = .038$]. This negativity appeared to have a fronto-right scalp distribution, however, the subtraction map on Figure 6 uncovered an additional parietal focus of activity in condition W1. This sustained negativity in W1 continued during the second latency window (400–600 msec), yielding significant results for the WM factor [$F(1, 10) = 7.75, p = .019$]. There was a left lateralized focus of activity on

Figure 4. Novelty-P3 scalp distribution for its early and late phases and for the two WM conditions. The two phases are identified on the novel minus standard waveform at Cz. The novelty-P3 shows a typical fronto-central distribution. Notice the clear attenuation of the novelty-P3 later phase in the W1 condition at parietal electrodes as compared to the W0 condition.

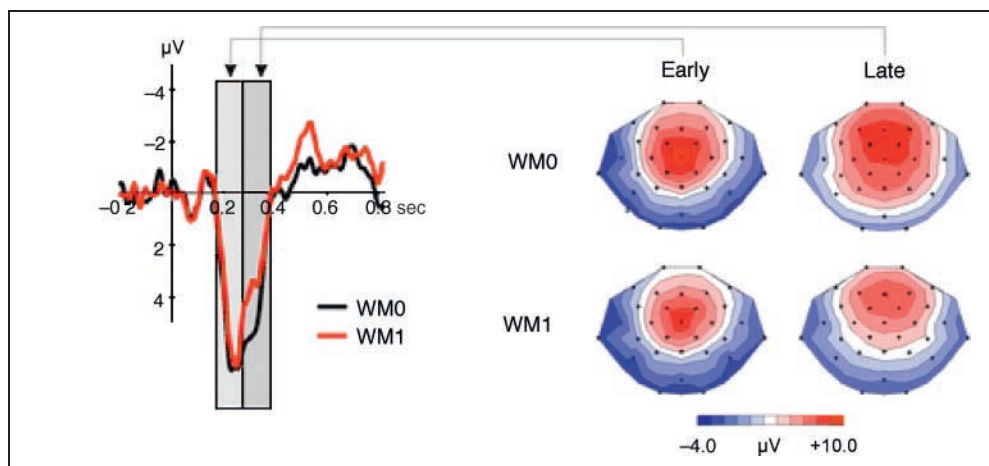
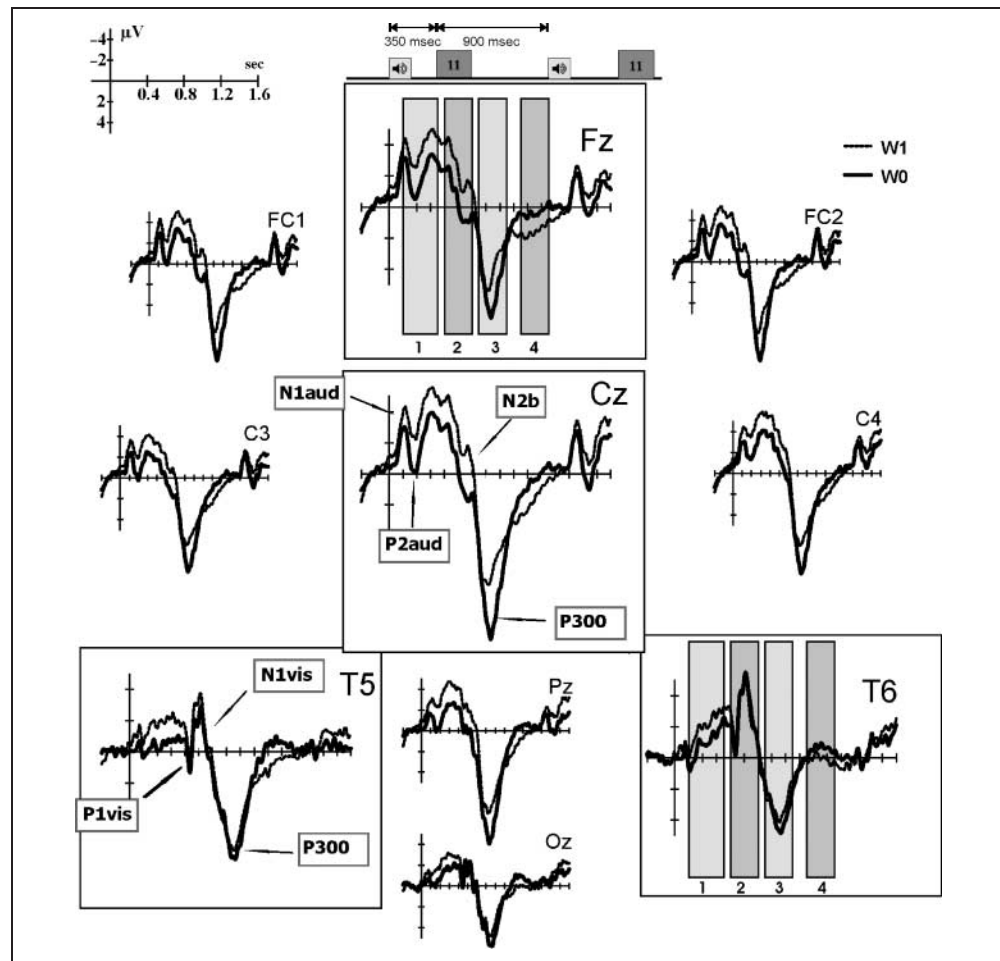


Figure 5. Standard ERP waveforms in the W0 and W1 conditions. The ERP components are analyzed and their latency windows are shown. The stimulation sequence is presented above, on the same time scale. Gray-shaded areas correspond to each of the four cognitive windows identified. Auditory and target components are labeled at Cz, visual components are labeled at T5. A sustained negativity was present in W1 during the first two windows over the frontal electrodes. This negativity was absent over posterior electrodes on the second window. Notice a phasic effect over visN1 on the left hemisphere. P300 was of larger amplitude in the W0 condition. A sustained positivity was present on the last window in condition W1.



both conditions [laterality factor's $F(4, 40) = 4.58, p = .034$]. Also, its distribution differed between conditions, as supported by a significant three-way $WM \times Frontality \times Laterality$ interaction [$F(8, 80) = 5.58, p = .004$]. The third latency window (650–850) covered the time window of the P300 component. The P300 activity was parietally distributed [frontality main effect, $F(2, 20) = 23.50, p < .001$], and left-lateralized [laterality main effect, $F(4, 40) = 24.59, p < .001$], in agreement with the well-characterized scalp distribution for the target P300 (Polich & Criado, 2006). There were no significant changes in P300 scalp distribution between the two conditions, suggesting a pure attenuation of P300 under WM load. During the final latency window (950–1150 msec), a prefrontal positivity was observed in both WM conditions. There was a significant difference between the two conditions [$F(1, 10) = 17.94, p = .002$], with W1 showing an enlarged prefrontal positivity and a second, more posterior, focus of activity [$WM \times Frontality$ interaction: $F(2, 20) = 5.97, p = .021$]. Subsequent post hoc tests confirmed a WM effect at prefrontal sites [$F(1, 10) = 6.30, p = .031$, *unnormalized data*] and a second focus at parietal sites [$F(1, 10) = 20.32, p = .001$], which extended also to central sites [$F(1, 10) = 8.00, p = .018$],

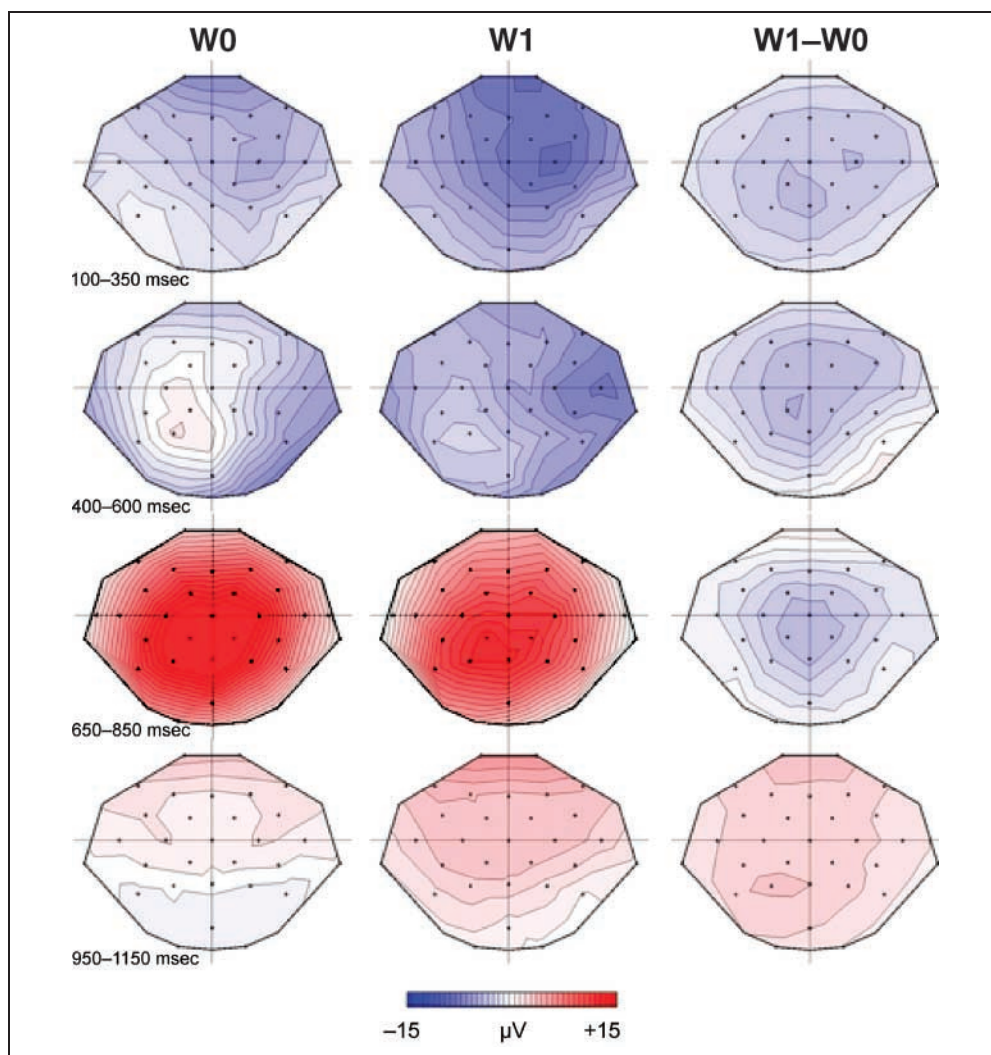
whereas no effect was found on frontal sites [$F(1, 10) = 1.90, p = .198$].

DISCUSSION

In the present study, the effects of WM load on distraction caused by task-irrelevant sounds were investigated to test whether involuntary attention was truly involuntary or was modulated by endogenous factors instead. The distraction task was, indeed, effective as the subjects were distracted by the unexpected occurrence of novel sounds. This was evident both as a reduction of HR and as an increase in RT on the trials preceded by a novel sound. The WM load manipulation was also effective, as the condition with WM load was harder to perform than the condition without WM load, resulting in slower RT and impoverished HR. Critically, there was a modulation of distraction by WM load, as loading WM decreased the distraction effect caused by the task-irrelevant novel sounds. These results confirm the departing hypothesis that the load on WM exerts a control over the mechanisms of involuntary attention, preventing distraction.

During behavioral distraction, a typical neuroelectric pattern, including N1-enhancement/MMN, novelty-P3,

Figure 6. Scalp distribution of the four cognitive latency windows and for the corresponding difference waveforms between WM conditions. The four windows were defined in relation to four a priori cognitive processes during visual task performance. First window: presentation of the auditory stimulus; second window: presentation of the visual stimulus; third window: P300 component and motor response; fourth window: intertrial interval after the behavioral response and preceding the next auditory stimulus. Significant distribution differences were found between WM conditions on the first, second, and fourth windows. Notice the activations elicited in the W1 condition in the subtraction maps. A negative left-parietal component was observed during the first two latency windows, and a simultaneous prefrontal and left-posterior activation was evident during the last window. As for the third latency window, encompassing the target P300, no changes in scalp distribution were observed, although its overall amplitude was attenuated in the W1 condition.



and RON components, was obtained in agreement with previous studies (Escera & Corral, 2003; Escera et al., 2000, 2001). The MMN response (Nätäänen & Winkler, 1999; Nätäänen, 1992) and the preceding N1-enhancement, which are both at play in novelty detection in the auditory cortex (Alho et al., 1998; Escera et al., 1998), were not affected by the WM load manipulation, indicating that the change-detection and transient-detection mechanisms, indexed respectively by these components, escape the influence of top-down modulation. Although recent studies have observed an attenuation of these components under different levels of task demands when a continuous perceptual-motor visual tracking task was used at two levels of difficulty (Yucel, Petty, McCarthy, & Belger, 2005a, 2005b), it is possible that what was found in these studies was N1 attenuation rather than MMN attenuation due to the large physical separation between standards and deviants. Muller-Gass, Stelmack, and Campbell (2006) have convincingly demonstrated that MMN is independent of visual task demands. Also, the automaticity of the N1/MMN responses

is supported by other evidence demonstrating their independence from the difficulty of the task being performed (Restuccia et al., 2005; Berti & Schröger, 2003; Harmony et al., 2000; Otten, Alain, & Picton, 2000; Alho, Woods, Algazi, & Nätäänen, 1992), or the predictability of the upcoming sound (Sussman, Winkler, & Schröger, 2003; Rinne, Antila, & Winkler, 2001).

The novelty-P3 component, which is an index of the effective orienting of attention toward the distracting event, showed two clearly distinct phases, in agreement with previous studies (Polo et al., 2003; Yago et al., 2003; Escera et al., 1998, 2001). The WM load manipulation resulted in a specific modulation of the second phase of this component. This result is in agreement with previous findings showing that the novelty-P3 can be modulated in a top-down fashion, its later phase being sensitive to attentional manipulations. Indeed, the later phase of the novelty-P3 was enhanced when the distracting novel sounds were identifiable to the listener (Escera et al., 2003) and also when they were contingent to the visual task stimuli as compared to when they appeared in

Table 2. ANOVAs for the Four Cognitive Windows Defined

	WINDOW ANOVAs			
	1st (100–350 msec)	2nd (400–600 msec)	3rd (650–850 msec)	4th (950–1150 msec)
WM	$F(1, 10) = 5.730, p = .038$	$F(1, 10) = 7.750, p = .019$	$F(1, 10) = 0.001, p = .979$	$F(1, 10) = 17.944, p = .002$
F	$F(2, 20) = 11.329, p = .003$	$F(2, 20) = 0.360, p = .631$	$F(2, 20) = 23.499, p < .001$	$F(2, 20) = 7.373, p = .013$
L	$F(4, 40) = 5.594, p = .012$	$F(4, 40) = 4.581, p = .034$	$F(4, 40) = 24.589, p < .001$	$F(4, 40) = 1.771, p = .197$
WMXF	$F(2, 20) = 2.720, p = .123$	$F(2, 20) = 2.369, p = .139$	$F(2, 20) = 0.437, p = .535$	$F(2, 20) = 5.967, p = .021$
WMXFXL	$F(8, 80) = 1.019, p = .379$	$F(8, 80) = 5.583, p = .004$	$F(8, 80) = 2.991, p = .065$	$F(8, 80) = 0.799, p = .473$

Factors: WM = WM condition; F = frontality with three levels; L = laterality with five levels.

isolation (Escera et al., 1998), both results demonstrating a bias of the orienting response toward behaviorally relevant stimuli. Moreover, several other studies using different paradigms have also shown that the novelty-P3 elicited by deviant stimuli is reduced when higher demands are imposed on the concurrent task (Restuccia et al., 2005; Berti & Schröger, 2003; Harmony et al., 2000, however, see also Munka & Berti, 2006). In the present study, the scalp distribution analysis of the novelty-P3 revealed that the WM load modulation was due to an amplitude attenuation of the late phase of the novelty-P3 over parietal areas in the W1 condition. This might have resulted from an attenuation of the posterior parietal novelty-P3 generator described by Yago et al. (2003). According to these authors, this novelty-P3 contribution might represent the readjustment of a multimodal template of the environment with fresh information provided by the recently encoded novelty, as noted in previous proposals (Knight, 1997; Yamaguchi & Knight, 1991). Consequently, although we cannot confirm the spatial origin from our present data, the present results lead us to speculate that the WM load had a specific effect over this component of the novelty-P3, and thus, the load imposed on the WM system could have prevented the new information from being properly integrated into the template of the environment.

The RON, an index of the reorienting of attention back toward the task-relevant aspects of stimulation after the temporary distraction (Schröger & Wolff, 1998b), was enhanced in the W1 condition. More specifically, the RON is proposed to reflect an attentional process at the level of the central executive system of WM, and it is thus linked to the characteristics of the relevant information that needs to be reactivated after distraction. For example, Munka and Berti (2006) showed that in a condition requiring WM, the RON component was increased compared with a condition without (or only few) WM demand. In the present task, the amount of information carried by the relevant stimuli was greater in the memory condition than in the no-memory condition and this was thus reflected in an enhancement of the RON component in this condition. This apparently contradicts the

results of a similar study (Berti & Schröger, 2003) in which a decrease in RON amplitude was found when WM was loaded. However, in this latter study, the amount of information carried by the relevant stimuli did not vary across conditions, as in this study the specific instruction in the WM condition was to withhold the response until the next trial, rather than to compare the previous trial with the present one. Thus, the amount of information carried by the task stimuli that needs to be reactivated after distraction was the same in both conditions. Most probably, these two studies reflect modulations on two different phases of the RON that cannot be distinguished here due to temporal proximity between the task-relevant and -irrelevant aspects of the stimulation, and that respectively indicate the refocusing on task-relevant information at the WM level, and a general reorientation of attention after distraction (Munka & Berti, 2006; Escera et al., 2001).

Taken together, the data obtained in the present experiment support a model in which, in a first stage, the analysis of the auditory input to search for changes in the acoustic environment would take place mostly automatically, and in a second stage, the orienting of attention would be triggered, with an effectiveness depending on ongoing task demands. Both behavioral and electrophysiological data confirm our hypothesis of a modulation over involuntary orienting of attention by load on WM, supporting an interaction between the endogenous and exogenous mechanisms of attentional control, in agreement with previous evidence of top-down modulation of involuntary attention (Pashler et al., 2001).

It should be noted that although in the present study increasing the WM load reduced distraction, in agreement with some previous findings (Spinks et al., 2004; Berti & Schröger, 2003), other studies have described opposite effects, that is, increasing WM load increased distraction (Muller-Gass & Schröger, 2007; Lavie et al., 2004). The findings reviewed by Lavie (2005) have been conceptualized in the frame of the “load theory of selective attention and cognitive control,” which poses that loading a task cognitively will reduce the amount of resources available to actively suppress the interference by distractor stimuli.

In this proposal, distraction is defined as the interference that a response conflict generated by the distractor produces on task performance, being in this sense similar to a Stroop effect. Indeed, when interpreting the modulation of this “incongruence distraction” effect by WM, Lavie concludes that a load on WM will only increase distraction when a conflict between targets and a salient competing distractor needs to be resolved. However, the distractor stimuli in the present task were not “competing” in the sense that they did not have any possible response, and thus, there was also no response conflict generated by them. The distractor stimuli were, in the present study, completely task-irrelevant and resulted in involuntary attentional capture, the attention being then oriented outside of the task display. We therefore suggest that the kind of “distraction” measured in these two tasks is different, and thus, can be affected by WM load in opposite directions.

Also, the amount of physical separation between targets and distractors, regardless of whether there is a response conflict, may be an important factor influencing the effects of load on distraction. Using an auditory–auditory distraction paradigm, Muller-Gass and Schröger (2007) found that distraction caused by irrelevant frequency changes increased with load when subjects had to make a duration discrimination task on the same tones. Muller-Gass and Schröger proposed that greater attention to the task-relevant stimulus enhanced the processing of all stimulus characteristics, including the irrelevant distracting frequency change. Although in this latter study cognitive resources might have been needed in order to suppress the irrelevant information contained in the task-relevant stimuli, in the present study, however, more resources were allocated to the visual task, reducing, in turn, auditory processing and distraction. Furthermore, other factors can have an important role in determining the direction of these results. Kim et al. (2005) reported evidence showing that the effects that WM load have on distraction depend on the type of WM load used, and whether the type of information being maintained in WM overlaps with mechanisms involved in target or distractor processing. Also, whereas load in the present study was imposed in an *n*-back fashion, and its effects were assessed by comparing a no-load situation (0-back) with a low-load situation (1-back), the studies supporting Lavie’s model typically impose the load by a delayed memory recognition task and compare low-load situations (remember one digit) versus high-load situations (remember 6 digits).

It could be argued that the influence of WM could be shown in a more straightforward manner by comparing different levels of load on a task. However, here subjects must perform exactly the same task—assess if two digits are the same or different—in both conditions. The difference lies in whether this comparison is made in WM or not. Furthermore, there are also no differences in temporal contingency or preparation processes between

conditions, as the timing of events was perfectly predictable. Note (Figure 6, first window) the presence of an equally large contingent negative variation (Walter, Cooper, Aldridge, McCallum, & Winter, 1964) component in both conditions, indicating preparation processes building up before the appearance of each visual stimulus. There is, of course, a qualitative difference between conditions, which is the involvement of the WM system. Although a quantitative approach may seem to be a “cleaner” comparison, the no-load versus load and low load versus high load comparisons may provide different types of information. As described by Baddeley (2003), WM is a system composed of a control system (“central executive”) and several subsidiary storage systems. A quantitative comparison might only measure the effects of an increase in the contents of the WM system, whereas a qualitative comparison will give information about the effects of activating the whole system, and particularly the central executive. There does not necessarily have to be an increase in the activity of the central executive due to an increase in the amount of items to be held in WM, thus using this approach, we might be missing activations due to the implication of the WM system that do not necessarily increase as a function of load. In fact, it is argued that protecting from distraction is one of the functions carried out by the central executive (Postle, 2005). A quantitative approach would measure the effects of amount of load but not the processes implicated when recruiting WM. In the present study, we did not intend to clearly separate the contributions of different components of the WM system, but rather, the implications of its recruitment (as a unified system) during distraction, thus a qualitative comparison appeared to be the best choice to answer this question. Moreover, there might be a ceiling effect in the effects of WM on distraction, reached already with very few items to be held in memory. Notice that the distraction effect was dramatically reduced with the implication of only a one-digit load.

WM effects were assessed over sensory (visual and auditory) ERP components, resulting in significant differences between the WM load conditions. However, these differences were apparently due to an overlapping sustained negativity, affecting all these components, and therefore, these significant differences should not be taken as a phasic modulation over sensory responses caused by WM load. This led us to adopt a different strategy to examine the sustained WM load effects. Nevertheless, two specific ERP components were apparently modulated in a phasic manner by WM load. First, the N1 response to the visual stimulus, known to originate in visual extrastriate areas (Di Russo, Martinez, & Hillyard, 2003; Di Russo, Martinez, Sereno, Pitzalis, & Hillyard, 2001; Martinez et al., 1999; Mangun, Hopfinger, Kussmaul, Fletcher, & Heinze, 1997; Heinze et al., 1994), was enhanced by WM load. This N1-enhancement observed in W1 might result from a specific gating of the processing of task-relevant information in early sensory areas, probably

due to an increase of focused attention to the task-relevant stimulation under conditions which require subsequent recall from WM (Luck & Hillyard, 2000; Hillyard & Anllo-Vento, 1998). A higher amount of processing resources focused on the task could, in turn, underlie the reduction observed in the distraction effect, as highly focused attention can inhibit distraction (Yantis & Jonides, 1990). On the other hand, the P300 amplitude was reduced by WM load. The P300 component is thought to reflect the degree of task-relevant information processing, or demands placed upon perceptual or central resources, its amplitude being determined by factors such as task difficulty or amount of memory load (Kok, 2001). Thus, the amplitude reduction observed here of the P300 parallels other findings (Bosch, Mecklinger, & Friederici, 2001; Watter, Geffen, & Geffen, 2001; Klaver, Smid, & Heinze, 1999; McEvoy, Smith, & Gevins, 1998; see also review in Kok, 2001) and further supports the effectiveness of the load manipulation on the task.

In general, two sustained waveforms were found to be related to WM processing. First, a sustained negative wave with a parietal distribution was found, extending over the first and second analysis windows when WM was loaded. This is in agreement with other evidence supporting the presence of negative slow waves over parietal areas in memory tasks, their amplitude being dependent on the amount of load (Vogel & Machizawa, 2004; Rämä et al., 2000; McEvoy et al., 1998). Indeed, these negative slow waves have been related to continued processing in WM (Kok, 2001). Here, several cognitive processes were undertaken during the two analysis windows covered by the sustained negativity in the W1 condition, including retention, interference by the sound, retrieval, and memory comparison. Thus, due to the temporal continuity of these cognitive processes in the present task, it cannot be determined whether this negativity was specifically related to one or more of them. The second sustained wave extended over the fourth analysis window, with a positive polarity and a prefrontal scalp distribution, also presenting a second focus of activity over left parietal areas. In this case, this positive sustained wave can be more directly related to retention operations because retention was presumably the only cognitive operation performed during this time window in the W1 condition. Sustained frontal positivities during the retention interval of memory tasks have been reported previously (Rämä et al., 2000; McEvoy et al., 1998), and these sustained positive waves have been related to memory storage operations (Kok, 2001). This result could therefore be interpreted in terms of the models granting a general executive function to WM and PFC (Duncan, 2001; Fuster, 2001; Miller & Cohen, 2001; Miller, 2000), suggesting that under conditions of load, there is a prefrontal activation that might represent the active maintenance of the task goals and information. This activation, on the other hand, maintains activation in more posterior sensory representation areas, which would be represented here by the left-lateralized parietal activation

found during retention, which could be interpreted as verbal rehearsal of the digit (Smith & Jonides, 1998). Further evidence supports the interpretation of WM resulting in PFC activation and, in turn, a reduction of distraction. In a functional magnetic resonance imaging experiment, Postle (2005) found that activity during the delay of a WM task increased with distraction over PFC, whereas it decreased in the inferior occipito-temporal cortex, where activity related to the primary responses to the distractor should be observed. It was concluded that PFC activity, triggered by the distractor stimuli, suppresses the input of sensory information, thus preserving the contents of WM from being disrupted by distractor stimuli. Indeed, the study of individual differences in WM capacity reveals that one of the components of WM is being able to maintain information in memory in the face of potential interference (Jarrold & Towse, 2006).

In summary, distraction by irrelevant sounds was reduced—both behaviorally and also as indexed by a reduction of novelty-P3 amplitude—when imposing WM load on primary task performance. This indicates that, as predicted, exogenous attention mechanisms are modulated by top-down endogenous factors. This modulation took place at a late stage of the orienting response, and there was no effect on the automatic change-detection mechanism indexed by N1/MMN. A possible mechanism behind this modulation may be related to the sustained positive activity recorded over frontal scalp positions under conditions of load. According to this view, this activity could have a top-down executive function of enhancing and maintaining sensory activation related to the task (e.g., visN1 enhancement), while reducing activation caused by interfering irrelevant stimuli (e.g., novelty-P3 reduction).

Acknowledgments

This work was supported by the Spanish Ministry of Education and Science (BSO2003-02440 and SEJ2006-00496/PSIC) and the Generalitat de Catalunya (SGR2005-000953 and 2005FI 00467). We thank four anonymous reviewers for helpful comments during the preparation of this article.

Reprint requests should be sent to Carles Escera, Cognitive Neuroscience Research Group, Department of Psychiatry and Clinical Psychobiology, Faculty of Psychology, University of Barcelona, P. Vall Hebron 171, E-08035 Barcelona, Catalonia, Spain, or via e-mail: cescera@ub.edu.

REFERENCES

- Alho, K., Escera, C., Díaz, R., Yago, E., & Serra, J. M. (1997). Effects of involuntary auditory attention on visual task performance and brain activity. *NeuroReport*, *8*, 3233–3237.
- Alho, K., Winkler, I., Escera, C., Huotilainen, M., Virtanen, J., Jääskeläinen, I. P., et al. (1998). Processing of novel sounds and frequency changes in the human auditory cortex: Magnetoencephalographic recordings. *Psychophysiology*, *35*, 211–224.

- Alho, K., Woods, D. L., Algazi, A., & Näätänen, R. (1992). Intermodal selective attention: II. Effects of attentional load on processing auditory and visual stimuli in central space. *Electroencephalography and Clinical Neurophysiology*, *82*, 356–368.
- Arnott, S. R., Pratt, J., Shore, D. I., & Alain, C. (2001). Attentional set modulates visual areas: An event-related potential study of attention capture. *Cognitive Brain Research*, *12*, 383–395.
- Awh, E., Anllo-Vento, L., & Hillyard, S. A. (2000). The role of spatial selective attention in working memory for locations: Evidence from event-related potentials. *Journal of Cognitive Neuroscience*, *12*, 840–847.
- Awh, E., & Jonides, J. (2001). Overlapping mechanisms of attention and spatial working memory. *Trends in Cognitive Sciences*, *5*, 119–126.
- Awh, E., Vogel, E. K., & Oh, S.-H. (2006). Interactions between attention and working memory. *Neuroscience*, *139*, 201–208.
- Baddeley, A. (2003). Working memory: Looking back and looking forward. *Nature Reviews Neuroscience*, *4*, 829–839.
- Barceló, F., Escera, C., Corral, M. J., & Periáñez, J. A. (2006). Task switching and novelty processing activate a common neural network for cognitive control. *Journal of Cognitive Neuroscience*, *18*, 1734–1748.
- Berti, S., Roeber, U., & Schröger, E. (2004). Bottom-up influences on working memory: Behavioral and electrophysiological distraction varies with distractor strength. *Experimental Psychology*, *51*, 249–257.
- Berti, S., & Schröger, E. (2001). A comparison of auditory and visual distraction effects: Behavioral and event-related indices. *Cognitive Brain Research*, *10*, 265–273.
- Berti, S., & Schröger, E. (2003). Working memory control involuntary attention switching: Evidence from an auditory distraction paradigm. *European Journal of Neuroscience*, *17*, 1119–1122.
- Bosch, V., Mecklinger, A., & Friederici, A. D. (2001). Slow cortical potentials during retention of object, spatial, and verbal information. *Cognitive Brain Research*, *10*, 219–237.
- Corbetta, M., & Shulman, G. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nature Reviews Neuroscience*, *3*, 201–215.
- De Fockert, J. W., Rees, G., Frith, C. D., & Lavie, N. (2001). The role of working memory in visual selective attention. *Science*, *291*, 1803–1806.
- Di Russo, F., Martinez, A., & Hillyard, S. A. (2003). Source analysis of event-related cortical activity during visuo-spatial attention. *Cerebral Cortex*, *13*, 486–499.
- Di Russo, F., Martinez, A., Sereno, M., Pitzalis, S., & Hillyard, S. A. (2001). The cortical sources of the early components of the visual evoked potential. *Human Brain Mapping*, *15*, 95–111.
- Downing, P. E. (2000). Interactions between visual working memory and selective attention. *Psychological Science*, *11*, 467–473.
- Duncan, J. (2001). An adaptive coding model of neural function in prefrontal cortex. *Nature Reviews Neuroscience*, *2*, 820–829.
- Escera, C., Alho, K., Schröger, E., & Winkler, I. (2000). Involuntary attention and distractibility as evaluated with event-related brain potentials. *Audiology & Neuro-Otology*, *5*, 151–166.
- Escera, C., Alho, K., Winkler, I., & Näätänen, R. (1998). Neural mechanisms of involuntary attention to acoustic novelty and change. *Journal of Cognitive Neuroscience*, *10*, 590–604.
- Escera, C., & Corral, M. J. (2003). The distraction potential (DP), an electrophysiological tracer of involuntary attention control and its dysfunction. In I. Reinvang, M. W. Greenlee, & M. Herrmann (Eds.), *The cognitive neuroscience of individual differences* (pp. 63–76). Oldenburg: Bibliotheks- und Informationssystem der Universität Oldenburg.
- Escera, C., Corral, M. J., & Yago, E. (2002). An electrophysiological and behavioral investigation of involuntary attention towards auditory frequency, duration and intensity changes. *Cognitive Brain Research*, *14*, 325–333.
- Escera, C., Yago, E., & Alho, K. (2001). Electrical responses reveal the temporal dynamics of brain events during involuntary attention switching. *European Journal of Neuroscience*, *14*, 877–883.
- Escera, C., Yago, E., Corral, M. J., Corbera, S., & Nuñez, M. I. (2003). Attention capture by auditory significant stimuli: Semantic analysis follows attention switching. *European Journal of Neuroscience*, *18*, 2408–2412.
- Folk, C. L., & Remington, R. (1998). Selectivity in distraction by irrelevant feature singletons: Evidence for two forms of attentional capture. *Journal of Experimental Psychology: Human Perception and Performance*, *24*, 847–858.
- Folk, C. L., & Remington, R. (1999). Can new objects override attentional control settings? *Perception & Psychophysics*, *61*, 727–739.
- Folk, C. L., Remington, R. W., & Johnston, J. C. (1992). Involuntary covert orienting is contingent on attentional control settings. *Journal of Experimental Psychology: Human Perception and Performance*, *18*, 1030–1044.
- Friedman, D., Cycowicz, Y. M., & Gaeta, H. (2001). The novelty P3: An event-related brain potential (ERP) sign of the brain's evaluation of novelty. *Neuroscience and Biobehavioral Reviews*, *25*, 355–373.
- Fuster, J. M. (2001). The prefrontal cortex—An update: Time is of essence. *Neuron*, *30*, 319–333.
- Gazzaley, A., Cooney, J. W., McEvoy, K., Knight, R. T., & D'Esposito, M. (2005). Top-down suppression deficit underlies working memory impairment in normal aging. *Nature Neuroscience*, *8*, 1298–1300.
- Gumenyuk, V., Korzyukov, O., Alho, K., Escera, C., Schröger, E., Ilmoniemi, R. J., et al. (2001). Brain activity indices of distractibility in healthy children of school age. *Neuroscience Letters*, *314*, 147–150.
- Harmony, T., Bernal, J., Fernandez, T., Silvia-Pereyra, J., Fernandez-Bouzas, A., Marosi, E., et al. (2000). Primary task demands modulate P3a amplitude. *Cognitive Brain Research*, *9*, 53–60.
- Heinze, H. J., Mangun, G. R., Burchert, W., Hinrichs, H., Sholz, M., Munte, T. F., et al. (1994). Combined spatial and temporal imaging of brain activity during selective attention in humans. *Nature*, *372*, 543–546.
- Hester, R., & Garavan, H. (2005). Working memory and executive function: The influence of content and load on the control of attention. *Memory & Cognition*, *33*, 221–233.
- Hillyard, S. A., & Anllo-Vento, L. (1998). Event-related brain potentials in the study of visual selective attention. *Proceedings of the National Academy of Sciences*, *95*, 781–787.
- Hopfinger, J. B., & West, V. M. (2006). Interactions between endogenous and exogenous attention on cortical visual processing. *NeuroImage*, *31*, 774–789.
- Jarrold, C., & Towse, J. N. (2006). Individual differences in working memory. *Neuroscience*, *139*, 39–50.
- Jensen, O., Gelfand, J., Kounios, J., & Lisman, J. E. (2002). Oscillations in the alpha band (9–12 Hz) increase with memory load during retention in short-term memory task. *Cerebral Cortex*, *12*, 877–882.
- Kane, M. J., & Engle, R. W. (2002). The role of prefrontal cortex in working memory capacity, executive attention, and general fluid intelligence: An individual differences perspective. *Psychonomic Bulletin & Review*, *9*, 637–671.
- Kim, S.-Y., Kim, M.-S., & Chun, M. M. (2005). Concurrent working memory load can reduce distraction. *Proceedings of the National Academy of Sciences*, *102*, 16524–16529.

- Klaver, P., Smid, H. G. O. M., & Heinze, H.-J. (1999). Representations in human visual short-term memory: An event-related brain potential study. *Neuroscience Letters*, 268, 65–68.
- Klimesch, W., Doppelmayr, M., Schwaiger, J., Auinger, P., & Winkler, Th. (1999). “Paradoxical” alpha synchronization in a memory task. *Cognitive Brain Research*, 7, 493–501.
- Knight, R. T. (1997). Distributed cortical networks for visual hippocampal region to novelty detection. *Journal of Cognitive Neuroscience*, 9, 75–91.
- Kok, A. (2001). On the utility of P3 amplitude as a measure of processing capacity. *Psychophysiology*, 38, 557–577.
- Lavie, N. (2005). Distracted and confused?: Selective attention under load. *Trends in Cognitive Sciences*, 9, 75–82.
- Lavie, N., & De Fockert, J. (2005). The role of working memory in attentional capture. *Psychonomic Bulletin & Review*, 12, 669–674.
- Lavie, N., Hirst, A., De Fockert, J. W., & Viding, E. (2004). Load theory of selective attention and cognitive control. *Journal of Experimental Psychology*, 133, 339–354.
- Luck, S. J., & Hillyard, S. A. (2000). The operation of selective attention at multiple stages of processing: Evidence from human and monkey electrophysiology. In M. S. Gazzaniga (Ed.), *The new cognitive neurosciences* (pp. 687–700). Cambridge: MIT Press.
- Mangun, G. R., Hopfinger, J. B., Kussmaul, C., Fletcher, E., & Heinze, H. J. (1997). Covariations in PET and ERP measures of spatial selective attention in human extrastriate visual cortex. *Human Brain Mapping*, 5, 1–7.
- Martinez, A. L., Anllo-Vento, L., Sereno, M. I., Frank, L. R., Buxton, R. B., Dubowitz, D. J., et al. (1999). Involvement of striate and extrastriate visual cortical areas in spatial attention. *Nature Neuroscience*, 2, 364–369.
- McCarthy, G., & Wood, C. C. (1985). Scalp distribution of event-related potentials: An ambiguity associated with analysis of variance models. *Electroencephalography and Clinical Neurophysiology*, 62, 203–208.
- McEvoy, L. K., Smith, M. E., & Gevins, A. (1998). Dynamic cortical networks of verbal and spatial working memory: Effects of memory load and task practice. *Cerebral Cortex*, 8, 563–574.
- Meiran, N. (1996). Reconfiguration of processing mode prior to task performance. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 26, 1124–1140.
- Miller, E. K. (2000). The prefrontal cortex and cognitive control. *Nature Reviews Neuroscience*, 1, 59–65.
- Miller, E. K., & Cohen, J. D. (2001). An integrative theory of prefrontal cortex function. *Annual Review of Neuroscience*, 24, 167–202.
- Muller-Gass, A., & Schröger, E. (2007). Perceptual and cognitive task difficulty has differential effects on auditory distraction. *Brain Research*, 1136, 169–177.
- Muller-Gass, A., Stelmack, R. M., & Campbell, K. B. (2006). The effect of visual task difficulty and attentional direction on the detection of acoustic change as indexed by the mismatch negativity. *Brain Research*, 1078, 112–130.
- Munka, L., & Berti, S. (2006). Examining task-dependencies of different attentional processes as reflected in the P3a and reorienting negativity components of the human event-related brain potential. *Neuroscience Letters*, 396, 177–181.
- Nätäänen, R. (1992). *Attention and brain function*. Hillsdale, NJ: Erlbaum.
- Nätäänen, R., & Winkler, I. (1999). The concept of auditory stimulus representation in cognitive neuroscience. *Psychological Bulletin*, 125, 826–859.
- Otten, L. J., Alain, C., & Picton, T. W. (2000). Effects of visual attentional load on auditory processing. *NeuroReport*, 11, 875–880.
- Pashler, H. (1993). Doing two things at the same time. *American Scientist*, 81, 48–55.
- Pashler, H. (1994). Dual-task interference in simple tasks: Data and theory. *Psychological Bulletin*, 116, 220–244.
- Pashler, H., Johnston, J. C., & Ruthruff, E. (2001). Attention and performance. *Annual Review of Psychology*, 52, 629–651.
- Pinsk, M. A., Doniger, G. M., & Kastner, S. (2004). Push–pull mechanism of selective attention in human extrastriate cortex. *Journal of Neurophysiology*, 92, 622–629.
- Polich, J., & Criado, J. R. (2006). Neuropsychology and neuropharmacology of P3a and P3b. *International Journal of Psychophysiology*, 60, 172–185.
- Polo, M. D., Escera, C., Yago, E., Alho, K., Gual, A., & Grau, C. (2003). Electrophysiological evidence of abnormal activation of the cerebral network of involuntary attention in alcoholism. *Clinical Neurophysiology*, 114, 134–146.
- Posner, M. I., & Cohen, Y. (1984). Components of attention. In H. Bouman & D. Bouwhuis (Eds.), *Attention and performance* (pp. 531–556). Hillsdale, NJ: Erlbaum.
- Postle, B. R. (2005). Delay-period activity in prefrontal cortex: One function is sensory gating. *Journal of Cognitive Neuroscience*, 17, 1679–1690.
- Postle, B. R. (2006). Working memory as an emergent property of the mind and brain. *Neuroscience*, 139, 23–38.
- Postle, B. R., Awh, E., Jonides, J., Smith, E. E., & D’Esposito, M. (2004). The where and how of attention-based rehearsal in spatial working memory. *Cognitive Brain Research*, 20, 194–205.
- Rainer, G., Asaad, W. F., & Miller, E. K. (1998). Selective representation of relevant information by neurons in the primate prefrontal cortex. *Nature*, 393, 577–579.
- Rämä, P., Paavilainen, L., Anourov, I., Alho, K., Reinikainen, K., Sipilä, S., et al. (2000). Modulations of slow brain potentials by working memory load in spatial and nonspatial auditory tasks. *Neuropsychologia*, 38, 913–922.
- Restuccia, D., Della Marca, G., Marra, C., Rubino, M., & Valeriani, M. (2005). Attentional load of the primary task influences the frontal but not the temporal generators of mismatch negativity. *Cognitive Brain Research*, 25, 891–899.
- Rinne, T., Anttila, S., & Winkler, I. (2001). Mismatch negativity is unaffected by top-down predictive information. *NeuroReport*, 12, 2209–2213.
- Rogers, R. D., & Monsell, S. (1995). Costs of predictable switch between simple cognitive tasks. *Journal of Experimental Psychology: General*, 124, 207–231.
- Sakai, K., Rowe, J. B., & Passingham, R. E. (2002). Active maintenance in prefrontal area 46 creates distractor-resistant memory. *Nature Neuroscience*, 5, 479–484.
- Schröger, E., & Berti, S. (2000). Distracting working memory by automatic deviance-detection in audition and vision. In E. Schröger, A. Mecklinger, & A. Friederici (Eds.), *Working on working memory*. Leipzig: Universitätsverlag.
- Schröger, E., Giard, M.-H., & Wolff, C. (2000). Event-related potential and behavioural indices of auditory distraction. *Clinical Neurophysiology*, 111, 1450–1460.
- Schröger, E., & Wolff, C. (1998a). Behavioral and electrophysiological effects of task-irrelevant sound change: A new distraction paradigm. *Cognitive Brain Research*, 71, 71–87.
- Schröger, E., & Wolff, C. (1998b). Attentional orienting and re-orienting is indicated by human event-related brain potentials. *NeuroReport*, 9, 3355–3358.
- Smith, E. E., & Jonides, J. (1998). Neuroimaging analyses of human working memory. *Proceedings of the National Academy of Sciences*, 95, 12061–12068.
- Spinks, J. A., Zhang, J. X., Fox, P. T., Gao, J., & Tan, L. H. (2004). More workload on the central executive of working memory, less attention capture by novel visual distractors: Evidence from an fMRI study. *NeuroImage*, 23, 517–524.

- Sussman, E., Winkler, I., & Schröger, E. (2003). Top-down control over involuntary attention switching in the auditory modality. *Psychonomic Bulletin & Review*, *10*, 603–637.
- Vogel, E. K., & Machizawa, M. G. (2004). Neural activity predicts individual differences in visual working memory capacity. *Nature*, *428*, 748–751.
- Vogel, E. K., Woodman, G. F., & Luck, S. J. (2005). Pushing around the locus of selection: Evidence for the flexible-selection hypothesis. *Journal of Cognitive Neuroscience*, *17*, 1907–1922.
- Walter, W. G., Cooper, R., Aldridge, V. J., McCallum, W. C., & Winter, A. L. (1964). Contingent negative variation: An electric sign of sensorimotor association and expectancy in the human brain. *Nature*, *203*, 380–384.
- Watter, S., Geffen, G. M., & Geffen, L. B. (2001). The *n*-back task as a dual-task: P300 morphology under divided attention. *Psychophysiology*, *38*, 998–1003.
- Worden, M. S., Foxe, J. J., Wang, N., & Simpson, G. V. (2000). Anticipatory biasing of visuospatial attention indexed by retinotopically specific alpha-band electroencephalography increases over occipital cortex. *The Journal of Neuroscience*, *20*, 1–6.
- Yago, E., Corral, M. J., & Escera, C. (2001). Activation of the brain network of involuntary attention as a function of auditory frequency change. *NeuroReport*, *12*, 4093–4097.
- Yago, E., Escera, C., Alho, K., & Giard, M. H. (2001). Cerebral mechanisms underlying orienting of attention towards auditory frequency changes. *NeuroReport*, *12*, 2583–2587.
- Yago, E., Escera, E., Alho, K., Giard, M.-H., & Serra-Grabulosa, J. M. (2003). Spatiotemporal dynamics of the auditory novelty-P3 event-related brain potential. *Cognitive Brain Research*, *16*, 383–390.
- Yamaguchi, S., & Knight, R. T. (1991). Anterior and posterior association cortex contributions to the somatosensory P300. *Journal of Neuroscience*, *11*, 2039–2054.
- Yantis, S., & Jonides, J. (1990). Abrupt visual onsets and selective attention: Voluntary versus automatic allocation. *Journal of Experimental Psychology: Human Perception and Performance*, *16*, 121–134.
- Yi, D.-J., Woodman, G. F., Widders, D., Marois, R., & Chun, M. M. (2004). Neural fate of ignored stimuli: Dissociable effects of perceptual and working memory load. *Nature Neuroscience*, *7*, 992–996.
- Yucel, G., Petty, C., McCarthy, G., & Belger, A. (2005a). Visual task complexity modulated the brain's response to unattended auditory novelty. *NeuroReport*, *16*, 1031–1036.
- Yucel, G., Petty, C., McCarthy, G., & Belger, A. (2005b). Graded visual attention modulates brain responses evoked by task-irrelevant auditory pitch change. *Journal of Cognitive Neuroscience*, *17*, 1819–1828.