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Working memory influences on auditory novelty processing in the human brain

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Para ti, papá,
que me enseñaste a creer sólo en la ciencia

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Summary

Novel events in the environment generate an involuntary orienting response which may have a different impact on the performance of ongoing tasks depending on the specific situation in which humans are immersed. The five studies that form this thesis studied several factors that can modulate responses towards novel sounds and the specific impact that these sounds have on behaviour. This issue was approached measuring the performance of healthy, young individuals on simple visual tasks while they attempted to ignore irrelevant sounds. The auditory stimulation consisted in all cases of a stream of repetitive, equal tones. Occasionally, and in an unpredictable manner, one of these repetitive tones was replaced by an environmental novel sound. In five studies, three different techniques were used to measure brain responses related to novel sounds: event-related potentials (ERP), magnetoencephalography (MEG) and functional magnetic resonance imaging (fMRI).

In different studies, involuntary orienting towards novel sounds resulted in a disruption or a facilitation of visual task performance. The results of the present studies indicate that novel sounds generate a combined alerting and orienting response. The impact that novel sounds have on behaviour may thus depend on the relative contribution of the alerting and orienting components, which can be determined by the demand of the visual task. However, the same sequence of brain responses was elicited by novel sounds in the present studies, irrespective of their behavioural outcomes.

We investigated the modulation of brain responses elicited by novel sounds when participants had to perform visual tasks that involved the maintenance of information in working memory (WM). Generally, the results show that in conditions of WM load, the orienting of attention towards novel sounds is diminished. The neurophysiological mechanism underlying diminished orienting was the inhibition of brain responses in auditory cortex and also in inferior frontal cortex, both areas that were involved in the processing of novel sounds. Moreover, the processing of novel stimuli in these areas was not completely abolished, but rather it was attenuated at a late phase, circa 300 ms after the occurrence of the novel sound. At this stage, preattentive change detection processes had been completed in these same areas.

Finally, we showed that interference by novel sounds can also be modulated by cognitive control mechanisms. We investigated brain responses to auditory stimuli presented immediately after participants had been distracted by a novel sound. The results showed that, following distraction, sensory responses related to task-relevant visual information were enhanced in visual cortex, while auditory processing areas were inhibited. The results of these studies have provided further insight into the cerebral mechanisms of attention control, demonstrating specific interactions and mutual modulations between endogenous and exogenous attention.

Original publications

I. SanMiguel, I., Corral, MJ., Escera, C. (2008). When loading working memory reduces distraction: behavioural and electrophysiological evidence from an auditory-visual distraction paradigm. *Journal of Cognitive Neuroscience, 20*(7): 1131-1145.

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Glossary of abbreviations

ACC	Anterior Cingulate Cortex
ADHD	Attention deficit hyperactivity disorder
AFN	After novel sound
ANOVA	Analysis of variance
BA	Brodmann area
BOLD	Blood-oxygenation level dependent
DEV	Deviant tone
DMS	Delayed match to sample
DP	Distraction potential
ECD	Equivalent current dipole
EEG	Electroencephalogram
EOG	Electro-oculogram
ER	Error rate
ERF	Event-related field
ERP	Event-related potential
FFA	Fusiform face area
FEF	Frontal eye fields
fMRI	Functional magnetic resonance imaging
HR	Hit rate
HRF	Hemodynamic response function
IFG	Inferior frontal gyrus
IOR	Inhibition of return
IPL	Inferior parietal lobule
IPS	Intra parietal sulcus
ISI	Inter-stimulus interval
IT	Inferior temporal cortex
MEG	Magnetoencephalogram
MFG	Middle frontal gyrus
MMN	Mismatch negativity
MR	Miss rate
NOV	Novel sound
NP3	Novelty-P3
OR	Orienting response
PFC	Prefrontal cortex
RON	Reorienting negativity
RT	Response time

SCD	Scalp current density
SD	Standard deviation
SEM	Standard error of the mean
SFG	Superior frontal gyrus
SOA	Stimulus onset asynchrony
SPL	Superior parietal lobule
STD	Standard tone
STG	Superior temporal gyrus
STM	Short term memory
TPJ	Temporo-parietal junction
WCST	Wisconsin card sorting test
WM	Working memory

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“Working memory and attention are inextricably inter-related. When an animal attends to an object, information associated with that object enters working memory. Conversely, information in working memory is information that is associated with objects to which an animal has attended. Thus, working memory represents the objects of attention”

Eric I. Knudsen (2007). Annu. Rev. Neurosci, 30, p.60.

1. Introduction

1.1. Novelty and involuntary guidance of attention

Our sensory systems are specifically designed to detect changes. For example, the first step towards visual object identification is accomplished by ganglionar cells in the retina that respond uniquely to discontinuities in the image defining the contour of each object (Kuffler, 1953). In general, invariable stimulation carries little if any information, therefore, neurons respond preferentially to onsets and offsets while continued stimulation results in habituation of responses. That is, we perceive the world through its discontinuities.

Hence, salient or novel events that significantly deviate from the context in which they occur hold a special status and are preferentially processed in the brain. These salient events typically generate an orienting response (OR, Sokolov, 1963) that comprises at least two components: a physiological burst of arousal resulting from a sudden transient increase in reticular or thalamic non-specific activation and a reflexive orienting of attention towards the salient event (Näätänen, 1990; Näätänen, 1992). The arousal related effects are known to facilitate sensory and motor functions as well as their central integrations. Altogether, the OR serves the purpose of preparing the individual to promptly respond towards the novel event, therefore guiding behaviour.

1.2. Voluntary and involuntary selection must be in balance

Involuntary orienting towards a novel event is an adaptive response that may however come in detriment of ongoing cognitive processes, a phenomenon which we will refer to as distraction. In this sense, being distracted by an event means bringing this event into your focus of attention, and therefore disengaging from what was previously being attended. Although involuntary attention is necessary in order to guide actions in relation to the world around us, an appropriate balance between reflexively orienting towards salient events and maintaining the voluntary focus of attention must be attained.

The selection of relevant information is accomplished by the attentional mechanisms, which are typically divided in voluntary and involuntary (Corbetta & Shulman, 2002; Näätänen, 1992; Posner, Snyder, & Davidson, 1980; Yantis & Jonides, 1990). Through voluntary or endogenous control, attention is directed to the relevant aspects of the task at hand, using previous knowledge and expectancies. This is a cognitively driven process and therefore the attentional effects that result from it are often termed also “top-down” effects. Conversely the involuntary or exogenous control of attention is stimulus-driven (“bottom-up”) and directs the individual to potentially relevant aspects that would otherwise go unnoticed outside of the main attentional focus. Involuntary attention is often assumed to operate in an automatic fashion. A weighted balance between voluntary and involuntary attention control is necessary for appropriate behaviour. In a simple example, as important as it is to be able to maintain concentration on our work despite all the distractors going on inside the office as we try to focus, we should never be so focused as to fail reacting to the fire alarm, or to other much less surprising events. The key to the control of attention lies thus in the mechanisms by which automatic and controlled processes are maintained in the proper balance.

1.3. But what is attention?

We live our daily lives surrounded by a rich stimulating context. From all the stimuli that are available to us at a certain moment, relevant information must be selected for further processing. What we pay attention to and how in the world around us determines every one of our acts. The control of attention is thus, in a way, the control of human behaviour and it is a key concept for understanding the functioning of the mind.

1.3.1. Limited resources

The concept of attention becomes important due to a fundamental limitation of the nervous system: not everything can be processed at the same time. Thus, it has been proposed that we have a limited pool of processing resources (Kahneman, 1973). Attending to something means selecting this item at a particular moment among all other possible representations (either external such as different stimuli, or internal such as a stream of thought) to be processed. Attention is limited because we cannot simultaneously select all available pieces of information to be processed.

Evidence from dual-task (Pashler, 1993; Pashler, 1994) and task-switching (Barceló, Escera, Corral, & Perianez, 2006; Meiran, 1996; Rogers & Monsell, 1995) paradigms illustrates the limitations of attention. Indeed, performing two tasks at the same time results in a decrement in performance. This is even more pronounced when the two tasks belong to the same modality, indicating that the attentional resources are at least in part modality specific (Alais, Morrone, & Burr, 2006; Duncan, Martens, & Ward, 1997).

1.3.2. Selective attention tasks

The study of attention has been traditionally approached using selective attention tasks in which participants have to selectively attend to a specific stream of stimuli and detect targets in this stream while ignoring irrelevant distractors. Participants may be asked, for example, to attend to stimuli in a particular sensory modality, appearing at a specific spatial location or stimuli pertaining to a particular category and perform a task on only these stimuli, while ignoring all other stimuli. Covert orienting tasks (e.g., Hillyard, Hink, Schwent, & Picton, 1973; Posner et al., 1980; Posner & Petersen, 1990) are a particular kind of attention tasks that have proven very useful in clarifying the nature of attentional effects and in elucidating their neurophysiological basis. In a typical visual covert orienting task, subjects have to attend at a location indicated by a cue without physically orienting towards this location (i.e., maintaining gaze at fixation) and subsequently respond to a target that may or may not appear at the attended location. Visual cues serve as warning signals for the upcoming appearance of the target, generating an alerting effect that shortens response time and improves accuracy. Moreover, if the cue is informative of the location of the upcoming target, performance benefits from an additional orienting of attention towards the target location. Conversely, if the target appears at a different location, its detection is impaired. Although spatial attention seems to be of fundamental importance, attention can also be directed to features or objects (Beauchamp, Cox, & DeYoe, 1997; Corbetta, Miezin, Dobmeyer, Shulman, & Petersen, 1990; Corbetta, Miezin, Dobmeyer, Shulman, & Petersen, 1991; McAdams & Maunsell, 2000; O'Craven, Rosen, Kwong, Treisman, & Savoy, 1997; O'Craven, Downing, & Kanwisher, 1999; Saenz, Buracas, & Boynton, 2002; Treue & Martinez Trujillo, 1999; Valdes-Sosa, Bobes, Rodriguez, & Pinilla, 1998). Moreover, effects of involuntary attentional capture are also demonstrated in covert orienting tasks. In a typical test, shortly flashing a light at one location will facilitate a subsequent response to a target stimulus at that same location and disrupt responses to target stimuli at different locations (Hopfinger & Mangun, 1998). These effects also operate in a crossmodal fashion, e.g., presenting an auditory, non-predictive cue also results in faster response times to subsequent visual targets presented at the same location as the auditory cue (Spence & Driver, 1997).

1.3.4. Importance of the attentional or task set

Involuntary attention capture has been traditionally thought to operate in an automatic fashion. Particularly, salient or sudden events were thought to result in an obligatory orienting of attention towards them, a response that would not depend on endogenous factors (Näätänen, 1992; Yantis & Jonides, 1990). However, in a series of behavioural experiments, Folk and colleagues (Folk, Remington, & Johnston, 1992; Folk & Remington, 1998; Folk & Remington, 1999) demonstrated that attentional capture by distractors is dependent upon the relation that the distractor maintains with the task stimuli. They proposed thus, in what they called the *contingent orienting theory* that exogenous attentional capture is never purely stimulus-driven, and instead it is dependent on whether the distractor event shares a feature property that is critical to the performance of the task at hand (Folk et al., 1992). That is, involuntary orienting of attention may also be modulated in a top-down fashion following the current behavioural goals. This "contingent orienting" view of involuntary attention postulates, therefore, that the current "cognitive or task set" determines the attentional configuration in a top-down fashion, and that the occurrence of a distracter in the sensory environment will capture attention exogenously, in a bottom-up manner, as much as it fits with the attentional configuration (Pashler, Johnston, &

Ruthruff, 2001). In a simple example, this view points out that when searching for a red circle, irrelevant red squares will capture attention more readily than other irrelevant stimuli that do not share properties with the target. Moreover, some stimuli are of intrinsic relevance, such as one's own name, and therefore will always be more potent attention-capturing signals (Moray, 1959).

1.3.5. A neurophysiological approach to attention

The neurophsysiological mechanism behind attentional selection appears to be the enhancement of neural responses related to the relevant representations (e.g. specific features, locations or sensory modalities), and a parallel inhibition of neural responses related to the irrelevant representations (Desimone & Duncan, 1995). This is reflected in the attentional modulation of neural responses recorded intracranially in primates (McAdams & Maunsell, 2000; Reynolds, Pasternak, & Desimone, 2000; Reynolds & Chelazzi, 2004; Treue & Martinez Trujillo, 1999), and in the modulation of electrophysiological (Hillyard et al., 1973; Woldorff et al., 1993) and hemodynamic (Chawla, Rees, & Friston, 1999; Corbetta et al., 1990) indices of brain activity in humans. For example, event-related potential (ERP) recordings have revealed that visual orienting cues affect early perceptual processes in visual extrastriate areas, increasing neural responses to the target stimulus appearing at the cued location (Eimer, 1994a; Eimer, 1994b; Luck et al., 1994; Mangun & Hillyard, 1991; Martinez et al., 1999; reviews in Hillyard & Anllo-Vento, 1998; Luck, Woodman, & Vogel, 2000).

Attentional modulation seems to affect earlier processes in audition than in vision (Woldorff & Hillyard, 1991; Woldorff et al., 1993). Moreover directing attention to one sensory modality enhances blood-oygenation level dependent (BOLD) signal in modality specific cortex for the attended modality, while it inhibits activity in the modality specific cortex of the unattended modality (Shulman et al., 1997) in both bimodal and unimodal presentation (Johnson & Zatorre, 2005). Furthermore, the mere presence of stimuli in one modality inhibits the other modality-specific cortex (Laurienti et al., 2002).

1.3.6. Brain networks and models for attention

The previous sections have briefly summarized the effects of attention on behaviour and brain responses to specific stimuli, however, the mechanisms by which the control of attention is achieved are less clear. Posner & Petersen (1990) proposed that the control of attention is carried out by an independent network of brain areas, and that this attention system can be divided in several sub-systems or networks of areas. They proposed that each of the sub-systems perform different but interrelated functions. Recent revisions of this model have differentiated three fundamental components of attention respectively involved in orienting, executive control and alerting and carried out by independent networks of brain areas (Fan, McCandliss, Sommer, Raz, & Posner, 2002; Fan, McCandliss, Fossella, Flombaum, & Posner, 2005). The orienting network directs attention to specific locations and is associated with superior parietal areas, the temporo-parietal junction (TPJ) and the frontal eye fields (FEF). This network is mainly modulated by the neurotransmitter acetylcholine. The executive network is associated with frontal areas, particularly the anterior cingulate cortex (ACC) and the lateral ventral prefrontal cortex (PFC) and is mainly modulated by dopamine. This network is mainly involved in resolving conflicting stimulus information. Finally, the alerting network is associated with frontal and parietal areas lateralized to the right hemisphere, and is modulated by norepinephrine.

A different proposal has outlined two major networks following the voluntary and involuntary attention control distinction; a dorsal fronto-parietal network involved in goal-directed, “top-down” control and a right ventral fronto-parietal network responsible for “bottom-up” orienting (Corbetta & Shulman, 2002; Corbetta, Patel, & Shulman, 2008). The dorsal network enables the attentional selection of stimuli based on internal goals and expectancies and would then enclose the orienting and executive control networks of the model proposed by Posner and colleagues. On the other hand, the ventral network detects salient and behaviourally relevant stimuli, especially when they are unattended, sending and interrupt signal in order to shift the focus of attention, only when the unattended events are relevant. The areas forming the dorsal network are found in the dorsal parietal cortex, particularly along the intraparietal sulcus (IPS) and superior parietal lobule (SPL) and the dorsal frontal cortex along the precentral sulcus, including FEF. The ventral network is composed of the TPJ, and the ventral frontal cortex, including parts of middle frontal gyrus (MFG), inferior frontal gyrus (IFG), frontal operculum and anterior insula.

1.4. Working memory, prefrontal cortex and executive control

A line of research that has proved to be very productive in terms of elucidating the nature of interactions between voluntary and involuntary control are the studies that manipulate working memory (WM). These studies have provided evidence for top-down modulations of involuntary orienting and have pointed towards WM as a particularly important factor in the control of attention.

1.4.1. Baddeley's multicomponent model of working memory

Short term memory (STM) refers to the ability to hold a certain amount of information active for a short period of time. Short term memory is necessary due to the abovementioned limitations in processing capacity. Since not all representations can be activated and processed in parallel, the subset of information that is to be processed needs to be activated and held in some sort of temporary representation. Working memory (WM) refers to the fact that this information not only needs to be held but it must also be manipulated while it is active. Thus, while STM refers to a simple temporary storage of information, processing and executive functions are on the other hand assigned to WM (Baddeley, 2003; Repovs & Baddeley, 2006).

In the 1970s Baddeley and his colleagues proposed their influential multicomponent model of WM. This model postulates separate STM stores for visual and verbal information which are controlled by a central executive that has limited attentional capacity and is responsible for the manipulation of information (Baddeley & Hitch, 1974; see Repovs & Baddeley, 2006 for a recent revision of the model). More recently, the neuroanatomical substrates of this system have been outlined, corroborating existence of separate stores for different kinds of information (Courtney, 2004).

1.4.2. Working memory capacity

A number of studies have tried to establish the specific capacity limits of the short-term and working memory information stores. The capacity of verbal short term memory had initially been estimated at “seven plus or minus two” objects (Miller, 1956). However, this is a loose measure that, among other things, depends on the phonological length of the words being retained (Baddeley, Thomson, & Buchanan, 1975; Schweickert & Boruff, 1986). More recently, a general capacity limit of about four items or “chunks of information” has been established (Cowan, 2001). Accordingly, the capacity for visual objects has been established at three to four items. Moreover, objects defined by a conjunction of four features can be retained just as well as single-feature objects (Luck & Vogel, 1997; Vogel, Woodman, & Luck, 2001). However, the amount of visual information carried by each object can also affect visual STM capacity, being reduced for complex objects (Alvarez & Cavanagh, 2004). When the information that is being held needs to be manipulated, the capacity limits are reduced. For example, if a string of digits has to be repeated backwards rather than forward, a reduction of capacity of at least one digit normally occurs (Conklin, Curtis, Katsanis, & Iacono, 2000). Therefore, the capacity of *working* memory depends on the nature of the manipulation that has to be applied to the information that is held in memory.

1.4.3. A neurophysiological approach to working memory

In the 70's and 80's, studies carried out in monkeys performing on delay tasks showed activity on prefrontal neurons during the delay period of these tasks. In such tasks, the animal is briefly presented with a set of information (typically a cue or a command) that then has to be maintained over a delay that can be up to several seconds. After the delay, the animal has to give a response. The sustained activity of neurons during the delay was linked to working memory function (Funahashi, Bruce, & Goldman-Rakic, 1989; Fuster & Alexander, 1971). Following these influential studies, a large body of research has tried to define more precisely the role of prefrontal cortex in working memory performing both intracranial recordings in animals (see

Curtis & D'Esposito, 2004; Funahashi, 2006) and human neuroimaging studies (see Courtney, 2004).

The results have converged towards a functional specialization within prefrontal cortex, differentiating two core structural regions -the ventrolateral and dorsolateral PFC- that accomplish different functions within working memory. Two main interpretations have arisen regarding the functional organization of PFC. The “domain-specificity model” (Levy & Goldman-Rakic, 2000; Wilson, Scalaidhe, & Goldman-Rakic, 1993) views the dorsal/ventral distinction as a continuation of the dorsal/ventral “where/what” functional specialization of visual pathways. On the other hand, the “process-specificity” model (Petrides, 1995) postulates that the dorsal and ventral areas of lateral PFC are functionally specialized according to the type of processes that they carry out, rather that the content of these processes. Thus, while the ventrolateral PFC would be specialized, generally, in rehearsing or maintaining the contents of WM, the dorsolateral PFC would be implicated in executive control, or in manipulating the contents of WM (Ungerleider, Courtney, & Haxby, 1998).

More recent research, however, questions the exclusivity of any of these views and rather supports mixed models (D'Esposito, Postle, & Rypma, 2000). Certainly, some sort of functional specialization is present in the PFC regarding WM, however, this specialization might not strictly divide the different areas. In fact, it appears that the response properties of the single neurons of PFC are highly adaptive, suggesting that the PFC specialization adapts to the present task (Duncan, 2001).

Although PFC has emerged as a fundamental WM processing area, other areas also appear to be persistently activated during delayed matching tasks. Particularly, the inferior temporal cortex (IT) has been described in several studies involving visual working memory (Ranganath, Cohen, Dam, & D'Esposito, 2004; Ranganath, DeGutis, & D'Esposito, 2004; Ranganath & D'Esposito, 2005). Miller et al. (1996), described stimulus selective activity in IT during the delay period, as well as in PFC, but whereas the activity in IT was disrupted by intervening stimuli in the delay, the activity in PFC was not. Based on this evidence, they proposed that the PFC gives “top-down” inputs to sensory areas to maintain the current relevant stimuli representations active.

1.4.4. Relations between working memory and attention

Evidence from many studies points to a direct link between the control of attention and the concept of working memory. Working memory serves to maintain the distinction between relevant and irrelevant stimuli in selective attention tasks (Rainer, Asaad, & Miller, 1998). Also, the content of working memory guides attention (Downing, 2000), and rehearsal in spatial working memory is in part accomplished via covert shifts of spatial selective attention to the memorized location ("attention-based rehearsal", Awh, Anllo-Vento, &

Hillyard, 2000; Awh & Jonides, 2001; Postle, Awh, Jonides, Smith, & D'Esposito, 2004). Moreover, individual differences in working memory capacity correlate with the ability to select relevant information and suppress irrelevant information (Gazzaley, Cooney, Rissman, & D'Esposito, 2005; M. J. Kane & Engle, 2002; Vogel, McCollough, & Machizawa, 2005), and related to this, increased distractibility and working memory deficits are symptoms that very often occur together in pathology, especially when frontal cortex is affected. As discussed earlier, the frontal cortex is proposed to be the seat, at least partly, of both the control of working memory and the control of attention. Indeed the signals that modulate responses to attended vs. unattended stimuli on the sensory and association areas are thought to be generated in the frontal cortex (Courtney, Ungerleider, Keil, & Haxby, 1997; Egner & Hirsch, 2005; Kane & Engle, 2002; Miller et al., 1996; Smith & Jonides, 1998).

Thus, following this evidence, an executive, “top-down” control has been assigned to the working memory functions that are based on PFC. This further supports the notion of a link between WM and attention control, putting forward models in which cognitive control stems from the active maintenance of patterns of activity in the PFC that represent goals and the means to achieve them, while providing with top-down bias signals to other brain structures, in order to guide behaviour (Duncan, 2001; Fuster, 2001; Miller, 2000; Miller & Cohen, 2001).

1.5. The impact of novel sounds on behaviour

1.5.1. Facilitation by sudden sounds: Accessory stimulus effect

Sounds have been reported to facilitate or speed up responses in various ways. The most straightforward example of auditory stimulus facilitation comes from typical covert orienting tasks as described above (see section 1.3.2). Selective attention effects also take place across modalities (Driver & Spence, 1998a; Spence & Driver, 1997; Spence, Pavani, & Driver, 2000; Teder-Sälejärvi, Munte, Sperlich, & Hillyard, 1999) and therefore in such tasks the auditory stimulus could be presented as a precue that conveys some information about the forthcoming visual stimulus (e.g., its location or time of appearance), causing responses to the subsequent target to be faster and more accurate (Driver & Spence, 1998a; Eimer & Schröger, 1998). This kind of facilitation effect may be accomplished altering activity in sensory processing areas (Macaluso, Frith, & Driver, 2000) as suggested by increased amplitudes of visual ERPs to stimuli presented in the attended sound location (Eimer & Schröger, 1998).

However, cues that provide no information about the upcoming target, or even auditory stimuli presented at roughly the same time as the visual stimulus (often termed *accessory stimuli*) can also facilitate visual task performance. Such uninformative stimuli have been shown to shorten RT (Hackley & Valle-Inclan, 1998; Hackley & Valle-Inclan, 1999; Valls-Sole et al., 1995), increase response force (Stahl & Rammsayer, 2005), enhance the detectability (d') of a visual stimulus (McDonald, Teder-Sälejärvi, & Hillyard, 2000; Stein, London, Wilkinson, & Price, 1996), produce temporal order judgement effects (McDonald, Teder-Sälejärvi, Di Russo, & Hillyard, 2005), and shorten the latency of reflexive reactions such as the eye blink reflex to a reflexogenic stimulus (Carlsen, Chua, Inglis, Sanderson, & Franks, 2004; Low, Larson, Burke, & Hackley, 1996).

The neurophysiological mechanism behind the facilitation of monosynaptic reflexes by accessory stimuli is a noradrenergic modulation of motor neuron excitability. However, different mechanisms such as expectancy (Del-Fava & Ribeiro-do-Valle, 2004), immediate arousal (Niemi & Näätänen, 1981), response bias (Odgaard, Arieh, & Marks, 2003) or multisensory integration (Stein et al., 1996) may account for other facilitation effects of the described above. Among these, expectancy may only account for effects caused by cues that are presented shortly before the target, but never for accessory stimulus effects. Conversely, facilitation due to multisensory integration can only take place at short inter-stimulus intervals. Indeed, the facilitation effect depends on the interval between its onset and the onset of the target stimulus, and also on the intensity of the auditory cue (Stahl & Rammsayer, 2005).

McDonald, Teder-Sälejärvi and Hillyard (2000) found that a spatial non-predictive auditory cue enhances detectability (d') of a subsequent visual stimulus presented at the same location. This facilitation is presumably due to involuntary orienting in space to the sound location, regardless of the unpredictability of the spatial cue. By means of ERP recordings it was established that, unlike the case of facilitation by predictive cues, the initial sensory-evoked visual responses are unaffected by the validity of the unpredictive auditory cue (McDonald & Ward, 2000). McDonald, Teder-Sälejärvi, Di Russo and Hillyard (2003) suggested that feedback from multimodal to unimodal brain areas underlies this cross-modal spatial attention effect on visual perception (see also Driver & Spence, 1998b; Macaluso et al., 2000).

RT shortening by non-spatial warning sounds (Hackley & Valle-Inclan, 1998; Hackley & Valle-Inclan, 1999; Valls-Sole et al., 1995) on the other hand is more likely due to a burst of arousal mediated by the noradrenergic system (Fernandez-Duque & Posner, 1997). In this case, the unexpected sound does not appear to facilitate the sensory processing of the target; rather, it speeds up response selection processes that take place after the initial sensory-perceptual analysis has taken place but before the onset of the response-specific motor processes (Hackley & Valle-Inclan, 2003).

1.5.2. Distraction by unexpected sounds

As opposed to the examples above, sounds are often also a source of distraction. There is good evidence indicating that humans process sound pre-attentively, that is, sound is perceived and processed to some degree whether we wish so or not (Moray, 1959). For example, numerous studies have shown that our ability to memorise visual information presented in sequence is severely disrupted by the presentation of irrelevant sound, an effect referred to as the irrelevant sound effect (Jones, Macken, & Murray, 1993; Jones & Macken, 1995; Macken & Jones, 1995). Single unexpected or deviating sounds however can also result in significant distraction effects. Distraction caused by such novel sounds can be studied making use of the “oddball” paradigm (Escera, Alho, Winkler, & Näätänen, 1998). In this paradigm, subjects are instructed to classify visual stimuli, according to a particular category (i.e., odd/even numbers), while ignoring task-irrelevant short sounds that precede the visual targets typically by 300 ms. The task-irrelevant sounds are a ‘standard’, repeating tone, or ‘distracters’, i.e., stimuli that deviate in a single feature such as frequency, intensity or duration (deviant) or environmental (novel) sounds (i.e., a telephone ring). The distracting sounds increase response time and error rate in visual task performance, revealing behavioral distraction (Alho, Escera, Diaz, Yago, & Serra, 1997; Escera et al., 1998; Escera, Alho, Schröger, & Winkler, 2000; Escera et al., 2001; Escera, Yago, & Alho, 2001; Escera, Corral, & Yago, 2002; Escera, Yago, Corral, Corbera, & Nuñez, 2003; Escera & Corral, 2007; Yago, Corral, & Escera, 2001; Yago, Escera, Alho, Giard, & Serra-Grabulosa, 2003). This distraction effect can also be obtained when stimuli are presented only in the auditory modality (Berti & Schröger, 2003; Schröger & Wolff, 1998a; Schröger & Wolff, 1998b; Schröger, Giard, & Wolff, 2000). In the auditory only version, subjects are typically instructed to classify auditory stimuli in short/long categories, while ignoring a task-irrelevant change in the stimulus standard frequency. Again, the task-irrelevant auditory frequency change causes behavioral distraction.

Deviating sounds are assumed to generate an orienting response because they do not match with a model of the ongoing stimulation (Sokolov, 1963; Sokolov, 1990). That is, as standard sounds are repeated, a pre-attentive representation of the stimulus' characteristics is created against which new incoming stimuli are compared. When a mismatch occurs between the incoming novel sound and the established neural model it results in an orienting response, that is, a shift of attention to the new stimulus. Recent work (Parmentier, Elford, Escera, Andrés, & SanMiguel, 2008) indicates that distraction in the auditory-visual version of the distraction task is likely due to the time consumed by orienting of attention towards the novel sound and re-orienting towards the primary task rather than to an impairment in the processing of the visual information. However, some evidence for the impairment of visual processing by deviating sounds has also been found (Alho et al., 1997), which is nevertheless compatible with the view that resources are depleted from the visual modality by involuntarily orienting to novel sounds.

1.5.3. Brain indices of novel sound processing: The “distraction potential”

The brain correlates of novel sound processing in the oddball paradigm have been extensively investigated by means of ERPs. In order to isolate activity related to novelty processing, standard tones are used as a baseline that is subtracted from the responses elicited by deviant tones or novel sounds. Using this simple calculation, a difference waveform is obtained that reveals a typical neuroelectric pattern which has been termed the *distraction potential* (Escera & Corral, 2003; see also Escera & Corral, 2007). The distraction potential is characterized by a tri-phasic waveform: an early negativity, a subsequent positivity, and a final negativity. These waves have been proposed to provide an index of three main stages of exogenous attention control (Escera et al., 2000; Escera & Corral, 2007): a) the *mismatch negativity* (MMN) and the mechanism of attention capture, b) the novelty-P3/P3a and the orienting of attention, and c) the *reorienting negativity* (RON) indexing the returning of attention towards main task performance after a momentary distraction.

N1 and mismatch negativity

The initial deflection of the distraction potential is a negative polarity event-related potential that appears in the 100-200 ms latency range from the onset of the deviating sound that has been termed *mismatch negativity* (MMN). The MMN has a fronto-central scalp distribution and inverts in polarity at electrode locations below the Silvian fissure, suggesting bilateral generators in the superior temporal cortex. Indeed, the MMN generators have been located in bilateral auditory cortex by means of human intracranial recordings (Halgren, Baudena, Clarke, Heit, Liegeois et al., 1995; Halgren, Baudena, Clarke, Heit, Marinkovic et al., 1995; Kropotov et al., 1995; Rosburg et al., 2005), magnetoencephalography (MEG) (Alho, Huotilainen, & Näätänen, 1995; Alho et al., 1998; Huotilainen et al., 1998) and fMRI measures (Liebenthal et al., 2003; Opitz, Mecklinger, Friederici, & von Cramon, 1999; Opitz, Rinne, Mecklinger, von Cramon, & Schröger, 2002; Rinne, Degerman, & Alho, 2005; Schonwiesner et al., 2007).

MMN is elicited by a discriminable change in any regular aspect of auditory stimulation (Näätänen, Gaillard, & Mantysalo, 1978; Näätänen & Alho, 1997) such as a change in frequency (Sams, Paavilainen, Alho, & Näätänen, 1985; Tiitinen, May, Reinikainen, & Näätänen, 1994), intensity (Näätänen, Paavilainen, Alho, Reinikainen, & Sams, 1989) duration (Näätänen, Paavilainen, & Reinikainen, 1989) or spatial origin of the sound (Schröger & Wolff, 1996). It is important to separate the different phenomena that might contribute to this response.

MMN is attributed to a genuine change detection mechanism, that is based on dynamic modelling of regularity in the acoustic environment and it is thus independent of specific physical, sensory-based aspects of stimulation (Näätänen, 1992). That is, MMN is elicited, for example, to abstract rule violations in a tone sequence (Carral et al., 2005; Carral, Corral, & Escera, 2005; Paavilainen, Simola, Jaramillo, Näätänen, & Winkler, 2001; Saarinen, Paavilainen, Schröger, Tervaniemi, & Näätänen, 1992) and omissions of stimuli in repeating sequences (Yabe, Tervaniemi, Reinikainen, & Näätänen, 1997). However, the genuine MMN change detection response might partially overlap and be confounded with other effects that are sensory-based and might also contribute to the change detection process in particular situations. For example, when compared to standard tones, complex novel sounds that cover a wider range of frequencies might also activate non-refractory populations of neurons, resulting in an enhanced auditory N1 response recorded at scalp (Alho et al., 1998). Moreover, sensory-based deviance detection also appears to be accomplished in the tonotopically organized primary auditory cortex, through stimulus-specific adaptation of single neuron responses (Schonwiesner et al., 2007; Ulanovsky, Las, & Nelken, 2003). Nevertheless, a genuine MMN response can be isolated using the appropriate controls.

P3a or novelty-P3

Subsequently to MMN, a large positive deflection showing a broad central scalp distribution might appear in response to deviating sounds in the 300 ms latency range which has been termed the P3a or novelty-P3 (NP3). The P3a differs from a similar response -the P3b- that is mainly elicited by target stimuli when these are attended. The P3b is also referred to as P300, although sometimes this expression is meant to encompass both P3a and P3b. While the P3b shows a central parietal scalp distribution, the P3a has a more frontal distribution, peaks slightly earlier and is mainly elicited by novel events that were unattended. In the psycophysiological literature, P3a has been taken as a cerebral signature of the OR (Friedman, Cycowicz, & Gaeta, 2001; Knight, 1984; Knight & Scabini, 1998; Squires, Squires, & Hillyard, 1975). Indeed, P3a amplitude correlates with the phasic skin conductance response (see also Knight, 1996; Lyytinen, Blomberg, & Näätänen, 1992) that indexes the OR. According to the most accepted view the P3a reflects the orienting of attention towards unexpected deviant or novel sounds (Escera et al., 1998; Escera et al., 2000; Friedman et al., 2001; Herrmann & Knight, 2001; Knight, 1984). Therefore, P3a might indicate the actual orienting of attention to an MMN-eliciting sound change occurring outside the current focus of attention (Escera et al., 2000). It has also been suggested that the P3a is associated with the evaluation of the novel event for subsequent behavioural action (Friedman et al., 2001). Along these lines, Polich (2007) has proposed that the P3a is the manifestation of a frontal attention mechanism engaged to evaluate incoming stimuli, and that processing of such stimuli then produces P3b activity related to context-updating operations and subsequent memory-storage.

Escera et al. (1998) distinguished two phases of the P3a response, specifically associating the late phase to the OR, as its amplitude is attenuated with the repetition of the eliciting novel event, paralleling the well-known habituation of the OR. According to this view, the early P3a would not reflect attention reorientation but rather a violation of a polisensorial model of the external world maintained in the temporo-parietal association cortex (Yamaguchi & Knight, 1991).

The neural substrate for the P3a response is still unclear. fMRI studies have shown that novel stimuli that typically elicit a P3a response also activate a widely spread network of brain areas including supratemporal (Domínguez-Borràs et al., 2008; Downar, Crawley, Mikulis, & Davis, 2000; Downar, Crawley, Mikulis, & Davis, 2001; Kiehl, Laurens, Duty, Forster, & Liddle, 2001; Kiehl et al., 2005), prefrontal (Bledowski, Prvulovic, Goebel, Zanella, & Linden, 2004; Downar et al., 2001) and parietal (Clark, Fannon, Lai, Benson, & Bauer, 2000; Downar et al., 2001) cortices. Several studies have also attempted to localize the neural sources of the P3a (Alho et al., 1998; Bledowski et al., 2004; Opitz et al., 1999; Opitz et al., 2002), however, there has not been enough consensus between different studies in any specific area as the genuine P3a source (see reviews in Linden, 2005; Ranganath & Rainer, 2003).

P3a and research on distractibility

Following the proposal that P3a reflects attention switching towards the novel event (Escera et al., 2000), modulations in the amplitude of the P3a component have been interpreted as an index of involuntary orienting and distractibility in the evaluation of several clinical populations. In two studies, Kaipio et al. (1999, 2000) found that the amplitude of the P3a component elicited by deviant or novel sounds in an oddball paradigm was enhanced in closed-head injury patients. They interpreted this result as a sign of increased distractibility in these patients, albeit without a concomitant measure of behavioural distraction. Lepisto et al. (2004) used a passive 3-stimulus oddball paradigm to investigate distractibility in children with depression and found an enhancement in the late phase of the P3a. This result was again interpreted as a sign of increased distractibility, and the authors suggested that it might underlie the concentration difficulties that compromise school performance in these children. Enhanced P3a amplitude has been further interpreted as a sign of increased distractibility without concomitant behavioural measures of distraction in autism (Ferri et al., 2003) and dyslexia (Russeler, Kowalczuk, Johannes, Wieringa, & Munte, 2002).

Furthermore, enhanced amplitude of P3a has been interpreted as a sign of increased distractibility even when dissociations between the behavioural and ERP results occurred. For example, Polo et al. (2003) found enhanced amplitude of P3a to novel sounds presented in an oddball sequence during the performance of a simple visual classification task in chronic alcoholics. However, behavioural measures of distraction did not differ between the patient and control groups. Polo et al. (2003) interpreted that alcoholics may compensate their increased distractibility in the laboratory situation by making an extra effort and that therefore ERPs may provide a more direct index for assessing distractibility.

Van Mourik et al. (2007) used an auditory oddball sequence during the performance of a concomitant visual task to evaluate distractibility in children suffering from attention deficit hyperactivity disorder (ADHD). They found enhanced amplitude of the late phase of the P3a component elicited by novel sounds in the ADHD group; however RT prolongation to visual targets following the novel sounds was not larger for ADHD children than for controls. Furthermore, novel sounds reduced omission errors in both groups and significantly more in the ADHD group. Therefore, novel sounds facilitated performance and did so slightly more in the ADHD group, in which an enhanced P3a was found. Van Mourik et al. (2007) interpreted the enhanced P3a as a sign of larger orienting towards the novel sound, an effect which could underlie the enhanced distractibility reported in these children. These authors proposed that the behavioural facilitation effect was due to the novel sounds generating an optimal level of arousal. An earlier study with ADHD children, however, found the opposite effect, with more omitted responses in the performance of the visual task in the ADHD children group after novel sounds (Gumenyuk et al., 2005). In this latter study, the late phase of the P3a component was also enhanced in the ADHD group, while the earlier phase was reduced. Gumenyuk et al. (2005) interpreted that these ERP results reveal deficient control of involuntary attention that may underlie their abnormal distractibility.

P3a has also been used to investigate the development of the involuntary attention mechanisms during childhood and adolescence (Gumenyuk, Korzyukov, Alho, Escera, & Näätänen, 2004; Wetzel, Widmann, Berti, & Schröger, 2006). In these studies, the amplitude of P3a decreased from younger to older children and behavioural measures of increased distraction were found in the younger groups compared to the older children. Wetzel et al. (2006) concluded that distractibility, as indicated by behavioural and ERP measures decreases from childhood to adulthood.

Reorienting negativity

Finally, following MMN and P3a, a third component might appear in the difference waveform that forms the distraction potential, the *reorienting negativity* (RON). RON is a broad negative deflection that typically appears in the 400-600 latency range from sound onset and presents a frontal scalp distribution. However the latency of RON appears to be time-locked to the task relevant stimulation rather than the irrelevant sounds (Escera et al., 2001). Moreover, RON only appears when a specific task is performed and the deviating sounds act as distractors, and not in passive listening conditions or when participants are asked to actively discriminate the deviating sounds (Schröger & Wolff, 1998a). Therefore, the most widely accepted interpretation is that RON indexes the reorienting of attention back to the task after temporary distraction (Berti & Schröger, 2001; Berti, Roeber, & Schröger, 2004; Schröger & Wolff, 1998a; Schröger & Wolff, 1998b;

Schröger et al., 2000). More specifically, the RON is proposed to reflect an attentional process at the level of the central executive system of WM, and it is linked to the characteristics of the relevant information that needs to be reactivated after distraction. Indeed, Munka & Berti (2006) showed that in a condition requiring WM the RON component was increased compared with a condition without (or only little) WM demand. Two different phases of the RON have been distinguished that might respectively indicate the refocusing on task-relevant information at the WM level, and a general reorientation of attention after distraction (Escera et al., 2001; Munka & Berti, 2006).

1.6. Avoiding distraction: task difficulty and executive control

1.6.1. Conflict and conflict adaptation

A particular situation in which distraction can apparently be overridden by endorsing executive control is in the case of conflict (Gratton, Coles, & Donchin, 1992). Conflict is one of the most intensively investigated sources of distraction. The interest in conflict was probably initially driven by the emergence of Stroop tasks (MacLeod, 1991; Stroop, 1935) as a relatively simple setting to test it. In the classical Stroop task, subjects are required to name the colour in which a word is printed while ignoring the meaning of the word which is written. The meaning of the word might be congruent (the word “red” written in red ink) or incongruent (the word “red” written in green ink) with the ink colour. When the meaning is incongruent with the ink, distraction occurs and response times are slowed. This type of conflict tasks have been extended and conflict can be generated in virtually any combination of relevant and irrelevant aspects of task stimuli, so long as the to-be-ignored aspect of the task primes the opposite response to the relevant or target aspects of the task.

Interestingly, in Stroop-like tasks the distraction effects are dramatically reduced or even absent in incongruent trials that immediately follow another incongruent trial. This effect is referred to as “conflict adaptation” (Gratton et al., 1992). Conflict adaptation reflects a dynamic adjustment in the executive control exerted over behaviour, which is based on preceding performance and aims at reducing the distraction effects. According to the conflict monitoring model, conflict adaptation results from a top-down bias of processes associated with the current task set that is triggered whenever a conflict is detected in the previous trial (Botvinick, Braver, Barch, Carter, & Cohen, 2001; Botvinick, Cohen, & Carter, 2004). That is, when the outcomes of our actions do not match with the expectations, as when an error is committed, a signal is triggered for the need to make readjustments in the specific way in which the task was being executed. Areas in the prefrontal cortex are then engaged in biasing the activation in primary sensory or motor areas in order to adjust behaviour.

The reduction of the deleterious effects of conflict on performance can in principle be achieved either through amplification of cortical responses to task-relevant information or through inhibition of responses to task-irrelevant information. To resolve this question, Egner & Hirsch (2005) used a variant of the Stroop task that presented celebrity faces with congruent or incongruent names printed on them. When participants were instructed to respond to the face stimuli rather than to the printed names, cortical responses in fusiform face area (FFA; a cortical area responsive to face stimuli) were amplified in incongruent trials following incongruent trials. The results thus support the hypothesis that conflict triggers an up-regulation of responses to task-relevant stimulation.

1.6.2. Lavie's load theory of selective attention and cognitive control

The impact of distractors on behaviour can also be regulated depending on the difficulty of the task being performed. On one hand, when the maintenance of information in WM is required during the performance of a selective attention task, distraction by conflicting stimuli is enhanced (Lavie, Hirst, De Fockert, & Viding, 2004). This result has been replicated in several different studies (e.g., De Fockert, Rees, Frith, & Lavie, 2001; Lavie & De Fockert, 2005; Lavie, 2005; Yi, Woodman, Widders, Marois, & Chun, 2004). On the other hand, increasing the difficulty of the task to be performed (e.g. by making target stimuli perceptually more difficult to discriminate) has been found to reduce the processing of irrelevant distractors in several other studies (e.g., Pinsk, Doniger, & Kastner, 2004; Rees, Frith, & Lavie, 1997; Yi et al., 2004).

Lavie et al. (2004) proposed an explanation for these findings based on the limited processing resources account in their "*load theory of selective attention and cognitive control*". They proposed that, in the first examples, loading working memory exhausts the resources necessary to inhibit responses to distractors, and therefore distraction increases as a function of load. However, when the task is loaded perceptually and not cognitively –as is the case of the second group of examples-, the main task may exhaust all perceptual processing resources. Therefore, fewer (or no) resources would "spill over" to process the distractor, resulting in a decrease of distraction with increasing perceptual load. This theory represents also a resolution for the long standing early vs. late selection debate, which questions whether attentional selection takes place at an early stage of processing based on simple perceptual features or whether a certain amount of semantic processing of all stimuli is needed before the relevant aspects can be selected and the irrelevant aspects are discarded. According to the perceptual vs. cognitive load distinction, early attentional selection will take place when perceptual processing resources are exhausted by the relevant aspects of stimuli. Conversely, late attentional selection will take place when perceptual processing resources are available to process the irrelevant or distracting stimuli.

1.6.3. Other evidence of distraction attenuation under load

The proposal of Lavie (2005) contrasts however with other studies that show that when performing a cognitively demanding task, the processing of disruptive or irrelevant stimuli is down-regulated rather than enhanced. For example, Spinks, Zhang, Fox, Gao & Tan (2004) found that during the performance of an arithmetic task, behavioural distraction elicited by irrelevant novel visual stimuli was reduced with increasing difficulty of the task, paralleled by a reduction in BOLD activation to the distractors in visual areas. Gazzaley et al. (2005) also found that during the performance of a delayed memory task, BOLD activity related to distracting pictures of scenes was specifically inhibited when they were presented amongst the faces that had to be remembered; relative to passive viewing conditions. Along these lines, a decrease in amplitude of ERP responses to distracting faces has been found when they were presented during the delay of a face memory task (Sreenivasan & Jha, 2007).

Moreover, it has been proposed that the WM system plays a crucial role in the executive control of attention, specifically preventing irrelevant information from entering the WM store in order to avoid interference with the information that is being held in order to perform the task (Postle, 2005). However, the reduced processing of irrelevant aspects of stimulation under conditions of WM load might also be due to an exhaustion of resources in overlapping attentional control and WM maintenance areas (Linden, 2007; Mayer et al., 2007).

1.6.4. Modulations on involuntary orienting are reflected in the distraction potential

Automaticity of MMN

The MMN mechanism is believed to be highly automatic and not under the influence of endogenous top-down factors (Näätänen, 1990; Näätänen, 1992). Strong arguments for the preattentive nature of the MMN come from studies showing that it can be elicited during sleep (Atienza, Cantero, & Escera, 2001), in comatose patients (Kane, Curry, Butler, & Cummins, 1993) and even in vegetative state (Wijnen, van Boxtel, Eilander, & de Gelder, 2007). The automaticity of the MMN responses is further supported by evidence demonstrating their independence from the difficulty of the task being performed (Alho, Woods, Algazi, & Näätänen, 1992; Berti & Schröger, 2003; Harmony et al., 2000; Otten, Alain, & Picton, 2000; Restuccia, Della Marca, Marra, Rubino, & Valeriani, 2005), or the predictability of the upcoming sound (Rinne, Antila, & Winkler, 2001; Sussman, Winkler, & Schröger, 2003).

Modulations of novelty-P3

The novelty-P3 amplitude can be modulated in a top-down fashion, its later phase being particularly sensitive to attentional manipulations. For example, the late phase of the novelty-P3 was enhanced when the distracting novel sounds were identifiable to the listener in an auditory visual oddball paradigm (Escera et al., 2003) and also when they were contingent on the visual task stimuli as compared to when they appeared in isolation (Escera et al., 1998). Moreover, when novel sounds are presented in a negative emotional context, distraction and novelty-P3 amplitude are larger compared to when they are presented in a neutral context (Domínguez-Borràs, Garcia-Garcia, & Escera, 2008b; Domínguez-Borràs, Garcia-Garcia, & Escera, 2008a; Garcia-Garcia, Domínguez-Borràs, SanMiguel, & Escera, 2008). These results demonstrate a bias of the orienting response towards behaviourally relevant stimuli. Conversely, other studies have shown that the novelty-P3 elicited by deviant stimuli is reduced when higher demands are imposed on the concurrent task (Harmony et al., 2000; Restuccia et al., 2005). Along these lines, the novelty-P3 response and the distraction effects elicited by deviating sounds were also attenuated by WM load in an auditory only oddball paradigm (Berti & Schröger, 2003).

1.7. Summary

Unattended sounds that significantly deviate from the auditory context in which they are presented capture attention involuntarily. This capture of attention may result in distraction. However, irrelevant sounds have also been shown to facilitate performance in certain circumstances. The factors determining whether attention-capturing sounds facilitate or disrupt task performance are unclear. Moreover, voluntary and involuntary mechanisms of attention control interact and the involuntary capture of attention is susceptible to modulation by endogenous, top-down factors. Distraction by irrelevant aspects of stimulation can be overridden by exerting executive control in the case of conflict, but it is unclear whether similar mechanisms may prevent distraction caused by novel sounds. Moreover, concomitant cognitive processing, and notably WM load may also modulate involuntary orienting. Indeed, WM seems to play an important role in the control of attention. However, contradictive results have been gathered as regards to the specific role of WM in attention control and whether placing demands on WM will enhance or reduce distraction. Specific brain indices are related to the processing of novel sounds that provide with useful tools for investigating the mechanisms that underlie attentional modulations of involuntary orienting and distraction.

2. Objectives and hypothesis

2.1. General aim

The aim of the present thesis was to study cognitive control in relation to attention. Although involuntary orienting has been long thought to reflect an automatic process, over the last two decades it has become apparent that it can in fact be modulated by top-down processes. We aimed at investigating how involuntary and voluntary mechanisms interact in the control of attention by exploring several factors that might determine the impact of novel sounds on ongoing cognitive processing, and the underlying brain mechanisms leading to the differential outcomes of novel sound detection on behaviour.

2.2. Specific aims and hypotheses

Study I

The aim of this study was to investigate the interaction between endogenous and exogenous mechanisms in the control of attention and further to establish the role of working memory in this interaction.

We hypothesized that involuntary orienting is not completely automatic but rather depends on the influence of endogenous, top-down factors and therefore can be modulated. Specifically, we hypothesized that the working memory system inhibits involuntary orienting under demanding situations. This top-down control exerted by the working memory system should be reflected in reduced behavioural and electrophysiological indexes of involuntary orienting towards novel sounds when a task involving a load on working memory is performed, in comparison to when no working memory is needed to perform the task.

Study II

This study investigated different mechanisms of interference control in the face of distraction by novel sounds. First, we further investigated the inhibition of distraction by working memory load and attempted to localize this inhibition to specific brain areas related to novelty processing. Second, we investigated dynamic adjustments in interference control after distraction. We hypothesized that after distraction caused by a novel sound, subsequent adjustments in executive control would take place in order to avoid distraction on the following trial. Therefore, we examined a possible inhibition of auditory processing areas or a possible enhancement of visual processing areas in trials immediately following distraction by a novel sound. Moreover, we examined whether these hypothetic sequential adjustments in interference control are also modulated by working memory load.

Study III

This study aimed at providing a precise spatio-temporal framework to the modulation of distraction by working memory load. While in Study I we investigated with electrophysiological recordings at which stage responses to novel sounds are modulated by working memory load and in Study II we investigated which specific brain areas are modulated by working memory load by means of hemodynamic responses, these two techniques measure different physiological responses occurring at rather different time scales. Therefore, here we used a technique (MEG) that provides both temporal and spatial resolution, in order to establish at which stage the activity of specific brain areas involved in novelty processing is modulated by working memory load. We hypothesized that novelty processing would be inhibited by working memory load in auditory cortex at a late stage processing. Therefore, initial deviance detection processes taking place at auditory cortex should remain unaffected by working memory load, while a subsequent response in this area, indexed by the P3am component, would be inhibited by load.

Study IV

Unexpected sounds result in distraction or facilitation of ongoing tasks in different circumstances. This study aimed at clarifying the critical factors that determine whether distraction or facilitation results. Moreover, a controversy exists between studies showing quantitative modulations of the distraction effect by working memory load. While some studies show reduced distraction under situations of load, other studies show the opposite, increased distraction. Therefore, this study intended to provide further insight into this controversy.

We hypothesized that the attentional or task set determines the direction of the unexpected sound effects on performance. Specifically, we manipulated the structure of the visual task and the contingencies between the irrelevant sounds and the task-relevant stimulation. Task demands were also manipulated by modifying target duration and event rate. We expected that at least one of these factors should determine the direction of the novel sound effects. Moreover, we expected that working memory load should result in quantitative modulations of the sound effects.

Study V

This study focused on the novel sound facilitation effect that was described in Study IV. We aimed at determining the nature and locus of this facilitation effect through the recording of electrophysiological responses. Moreover, we investigated whether the facilitation effect is modulated by working memory load through the same mechanisms that modulate the distraction effect.

The finding of facilitation by novel sounds presented in a regular oddball sequence posits an important question on the electrophysiological responses that are elicited by these sounds. If the same sequence of electrophysiological responses is elicited by novel sounds whenever they lead to distraction or facilitation, the extended use of these electrophysiological responses as indices of distraction or distractibility would be undermined. Therefore, we explored electrophysiological responses elicited by novel sounds in the case in which these sounds facilitate task performance.

3. General methods

The studies that compose this thesis have been conducted in the following laboratories and research centres:

Studies I and IV: Cognitive Neuroscience Research Group, Department of Psychiatry and Clinical Psychobiology, University of Barcelona, Spain.
Study II: Institute for Cognitive Neuroscience, Department of Neuropsychology and Behavioral Neurobiology and Center for Advanced Imaging, Bremen University, Germany.
Study III: Department of Neuropsychiatry, Hirosaki University School of Medicine, Japan.
Studies IV and V: Wolfson Centre of Clinical and Cognitive Neuroscience, School of Psychology, Bangor University and North Wales Clinical School, UK.

3.1. Participants

A total of 105 volunteers ranging in age from 17 to 45 years old (mean age 23; 35 male and 70 female) participated in the studies of this thesis. Participants were typically undergraduate university students that were reimbursed or received course credits for their participation. All participants were healthy individuals that reported no history of psychiatric or neurological disorders, had normal audition and normal or corrected-to-normal vision. Participants gave written consent to participate after the nature of the experiments was explained to them, which were all approved by the corresponding local ethical committees.

3.2. Tasks and stimuli

In all studies, participants performed computerized visual tasks while listening to irrelevant auditory stimulation through headphones. They were instructed to focus on the visual task while ignoring the irrelevant sounds and to respond to the visual-task stimuli as accurately and quickly as possible by pressing the corresponding response button.

3.2.1. Tasks

In studies I, II and III slight modifications of a standard auditory-visual distraction oddball paradigm as described in Escera et al. (1998) were used. In these tasks, participants had to respond to each visual stimulus, which were all shortly preceded with a fixed interval (300-350 ms in different studies) by an auditory stimulus that could either be a standard tone or a novel sound.

In studies IV and V the standard auditory-visual distraction paradigm was integrated into a visual short term memory task, presenting auditory stimuli with a fixed stimulus onset asynchrony (SOA) throughout the duration of the whole trial. As in studies I-III, the target stimulus was shortly preceded with a fixed interval by an auditory stimulus that could either be a standard tone or a novel sound.

The visual tasks to be performed were either simple visual classification tasks or WM tasks in different studies and conditions. Whenever simple classification tasks were employed, participants were to classify visual stimuli in either one of two categories such as face or non-face stimuli.

Two different types of memory tasks were employed, n-back tasks (studies I, II and III) and delayed visual recognition tasks (studies IV and V). The n-back tasks employed in studies I, II and III, were all 1-back. Participants had to compare each stimulus (a single digit) with the stimulus presented in the previous trial, therefore maintaining always one digit in memory and updating the contents of WM in each trial. In the delayed visual recognition tasks, in each trial participants had to encode from one to three face stimuli that had to be maintained in memory through a short delay. Upon target presentation they had to indicate whether the target face matched any of the face stimuli held in memory.

3.2.2. Auditory stimuli

In all studies, auditory stimuli were presented as a stream of two types of sounds: sinusoidal tones (standard) and complex environmental sounds (novel). The stream of sounds typically consisted of repeating standard tones with a fixed SOA that were occasionally replaced by novel sounds in a small percentage of trials.

Standard tones had a frequency of 600 Hz and a duration of 200 ms. Novel sounds were randomly selected from a sample of 100 unique exemplars such as those produced by a drill, hammer, rain, door or telephone ringing. The sounds were digitally recorded, low-pass filtered at 10,000 Hz, and edited to have a duration of 200 ms, including rise and fall times of 10 ms. Additionally, novel sounds were equalized for root-mean-square energy to keep the energy contour of all auditory stimuli constant over time (see Domínguez-Borràs et al., 2008 for details). The novel sounds were all similar in spectrotemporal features. The sample of sounds used was selected from a larger pool of sounds that was rated by a sample of 30 subjects on a 1-5 likert-scale of semantic familiarity (see Escera et al., 2003). The 100 exemplar sample used in the present studies was chosen between the most highly rated (2.54 mean rate; ±0.5) sounds.

3.2.3. Visual stimuli

Visual stimuli were simple digits presented at the centre of the screen or face stimuli randomly selected from a set of six black and white neutral expression male faces as in Ekman & Friesen (1976) and eight scrambled images of equivalent size and shape, created by scrambling the face stimuli.

3.3. Behavioural and brain activity measures

3.3.1. Behavioural measures

Behavioural measures of accuracy and response speed were collected in all studies. Accuracy was measured as correct responses within a limited time window after target presentation (hit rate, HR), errors (error rate, ER) and missed trials without response in this time window (miss rate, MR). Differences in accuracy and response speed between the conditions of interest were explored by means of analysis of variance (ANOVA) for repeated measures. Greenhouse-Geisser correction was applied to all analyses whenever violations of sphericity occurred and corrected p values and uncorrected degrees of freedom are reported. The significance level was set at p=0.05.

3.3.2. Brain activity measures: ERPs, fMRI and MEG

Brain activity measures were acquired in all studies except study IV. In studies I and V ERP measures were collected, while in study II fMRI measures were collected and in study III we collected MEG measures. All of these techniques allow the non-invasive observation of brain activity in vivo; however, each of the techniques used is based on different physiological phenomena and provides data in different anatomical and temporal resolution scales. Due to these fundamental differences, a certain degree of discrepancy between techniques can be expected. Moreover, the combination of different techniques allows a more comprehensive view of the phenomena under study.

3.3.3. Electroencephalography and Event-related potentials

Event-related potentials reflect brain electrical activity elicited in response to a particular event or related to a particular brain process. The small voltage deflections that constitute the ERPs are extracted from the larger overall electrical brain activity recorded at the scalp (the electroencephalogram, EEG) in which they are confounded through the averaging of multiple epochs in which the same event or process has occurred, time-locked to a particular stimulus. The electrical activity recorded at the scalp is generated by groups of neurons firing synchronously and represents the summation of post-synaptic potentials (Allison, Wood, & McCarthy, 1986). In order to be able to record this signal at the scalp, the population of neurons that generates it must be arranged in an “open field” configuration, meaning that their individual electric fields must summate to yield a dipolar field. Pyramidal cells in the cortex are arranged in such a configuration, parallel to each other, and likely make a major contribution to the activity recorded at scalp (Nunez & Srinivasan, 2006; Scherg & Picton, 1991). Therefore, this technique allows measuring neuronal activity directly (albeit from a distance) and yields a temporal resolution in the range of the millisecond.

Electrical signals, however, are distorted as they travel through the various layers of brain, skull and scalp and therefore the spatial origin of the signal cannot unequivocally be discerned. Moreover, signals arising at subcortical structures will make a smaller contribution to the ERPs recorded at scalp. The EEG is measured as an electric potential difference between two electrodes placed on the head of the subject. In the present studies, the EEG was measured inside a Faraday cage, using an elastic cap with electrodes inserted on it, following the position guidelines of the American Electroencephalographic Society. A common reference was used for all electrodes and impedance was kept below 5 kΩ. After acquisition, the data was processed offline. First, it was filtered to remove electrical noise, epochs containing movement artefacts were rejected or corrected and epochs pertaining to the different events of interest were averaged separately. The amplitude and latency of the ERP components of interest was then contrasted statistically across conditions by means of ANOVA.

3.3.4. Magnetoencephalography and Event-related magnetic fields

Any electrical current produces an orthogonally oriented magnetic field. The MEG technique measures the magnetic fields associated to the electrical currents that the EEG measures. As in the case of ERPs, event-related magnetic fields (ERFs) related to particular events can be extracted from the MEG signals. However, MEG detects only tangential components of the current source. Therefore, the signal detected by MEG arises mainly in the sulci of the cortex, where the pyramidal cells are parallel to the surface of the head, rather than the gyri. Moreover, deep sources in the brain might contribute to the MEG signal even less than to the EEG signal, as the magnitude of magnetic fields generated by the neurons is smaller than the magnitude of electric fields. However, MEG signals are less distorted by the various layers of brain, skull and scalp and therefore the sources of the MEG signals can be assessed through various inverse source modelling approaches, granting MEG a better spatial resolution than EEG, with the same temporal resolution (Eulitz, Eulitz, & Elbert, 1997; Hari, Levanen, & Raij, 2000; Hämäläinen, Hari, Ilmoniemi, Knuutila, & Lounasmaa, 1993).

MEG measures must be collected in a magnetically shielded room generally from a helmet shaped magnetometer which incorporates a distributed set of sensor elements. In particular, in study III we used an ELEKTA Neuromag device (Helsinki, Finland) which incorporates two orthogonal planar gradiometers and one magnetometer coupled to a multi-SQUID for each sensor and thus provides three independent measurements of the magnetic fields.

In order for source modelling to be possible, the exact position of the head with respect to the sensors has to be determined. To this aim, head position indicator coils are placed at specific sites on the subject’s head and their locations are measured using a 3D digitizer with respect to a 3-axis head coordinate system. The head position is then aligned to the MEG sensor coordinate system before source modelling (Hämäläinen et al., 1993).

As in the ERP analysis, prior to source modelling, MEG data is also filtered and artefacts must be rejected or corrected. In the present thesis, source modelling of the ERFs of interest in study III was accomplished by fitting discrete equivalent current dipoles (ECDs) using least squares search in a spherical volume conductor model for the head (Breier, Simos, Zouridakis, & Papanicolaou, 2000; Papanicolaou et al., 2003; Sarvas, 1987; Simos et al., 2001). Differences in source location, source strengths and latencies of the ERFs across conditions were assessed by means of ANOVA.

3.3.5. Functional magnetic resonance imaging

Functional magnetic resonance imaging is based on a fundamentally different physiological response than EEG or MEG. While EEG and MEG measure signals that are directly generated by neurons, the fMRI technique measures what is termed the BOLD signal. The BOLD signal is a hemodynamic measure that reflects the rate of oxygen uptake and the blood flow delivered to the brain regions and, as such, it is an indirect measure of neural activity.

The BOLD signal is based on a certain property of oxy- and deoxygenated haemoglobin: oxygenated haemoglobin is diamagnetic, while deoxygenated haemoglobin is paramagnetic. Due to this property, highly oxygenated blood shows more magnetic resonance signal than deoxygenated blood, therefore, the MR signal reflects the oxygen uptake in different brain areas (Ogawa & Lee, 1990; Ogawa, Lee, Kay, & Tank, 1990; Ogawa, Lee, Nayak, & Glynn, 1990). Neural activity requires energy, and therefore, an increase in oxygen consumption takes place during neural activity. In order to supply the energy needed to the neurons, blood inflow to active areas can increase as much as 40%. The BOLD signal mostly reflects excitatory postsynaptic potentials (Logothetis, 2007), which are the major cause of increased oxygen needs (Attwell & Iadecola, 2002).

The hemodynamic response is a relatively slow process taking approximately five seconds to reach its peak, and therefore the temporal resolution of fMRI is severely limited. Conversely, the blood delivery is highly specific to the areas that require it, and therefore the spatial resolution of fMRI can be of even less than 1mm (Yacoub, Shmuel, Logothetis, & Ugurbil, 2007) under optimal conditions; significantly better than the spatial resolution of EEG and MEG. fMRI images as typically coregistered and superimposed on anatomical magnetic resonance images in order to observe the activation pattern on the individual anatomy.

4. Results

Study I.

SanMiguel, I., Corral, MJ., Escera, C. (2008). When loading working memory reduces distraction: behavioural and electrophysiological evidence from an auditory-visual distraction paradigm. *Journal of Cognitive Neuroscience, 20*(7): 1131-1145.

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.

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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, Anllo-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 previsions 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; Nätäänen & Winkler, 1999; Nätäänen, 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

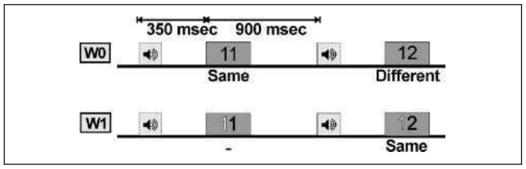


Figure 1. Stimulation sequence (above the line) and correct responses to the task (below the line) for the two conditions. In the W0 condition, subjects had to decide whether the two digits appearing on the screen were the same or different. In the W1 condition, subjects had to decide whether the first 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 mm × 5.5 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 conditions 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 ±100 μV 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 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.

Table 1. ANOVAs for the Defined ERP Components

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

Results represent differences between the two WM conditions.

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

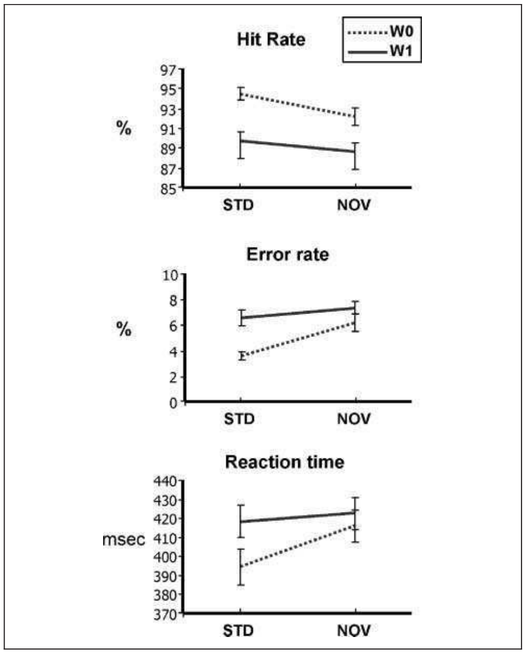


Figure 2. Performance on the visual task for the two experimental conditions. ER was larger and RT was longer in the W1 condition. Performance in novel trials was slower and less accurate compared to standard trials. The increase in RT after novel sounds was significantly smaller in the W1 condition. 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 μV in the W0 condition and of -0.3 μV in the W1 condition. The mean amplitude difference between the two WM conditions was nonsignificant [$F(1, 10) = 0.24, p = .634$].

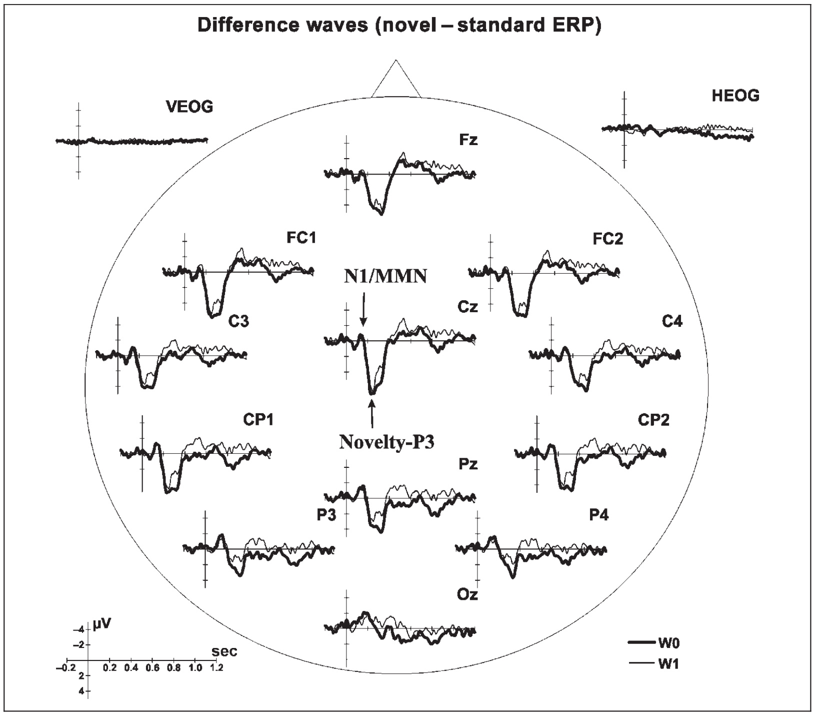
As for the novelty-P3, its early phase had a mean amplitude of 5.6 μV in W0 and of 4.9 μV in W1, and its late phase had a mean amplitude of 4.0 μV in W0 and of 2.9 μV in W1. ANOVA revealed that there was a significant amplitude difference of this component between the two WM conditions as indicated by the significant WM × Frontality interaction [$F(2, 20) = 5.43, p = .031$], and the WM × Phase × 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 × 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 × 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

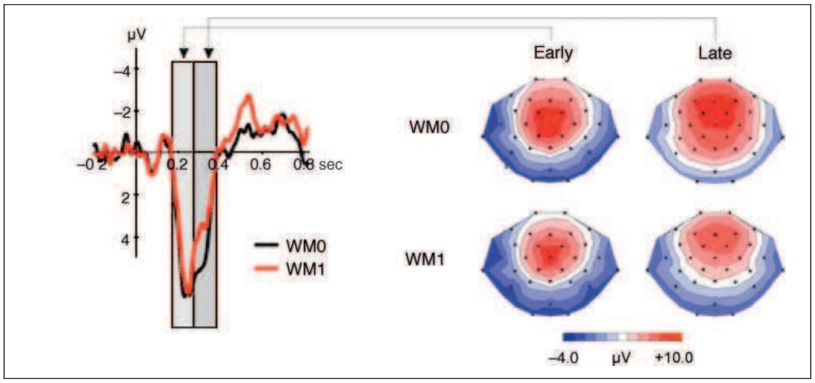
Figure 3. Distraction potential (novel − standard waveforms) on a selected set of electrodes. The N1/MMN and novelty-P3 deflections can be identified. Amplitude of novelty-P3 was reduced in the W1 condition, particularly on its late phase.



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 substraction 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.



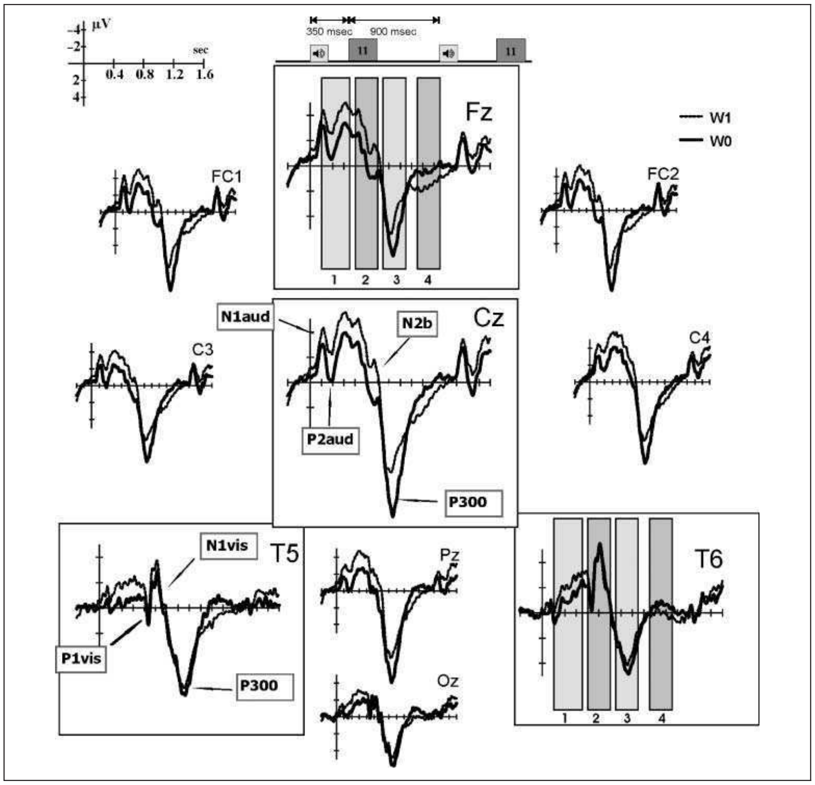


Figure 5. Standard ERP waveforms in the W0 and W1 conditions. The ERP components are analyzed and their latency windows are shown. The stimulation sequence is presented above, on the same time scale. Gray-shaded areas correspond to each of the four cognitive windows identified. Auditory and target components 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.

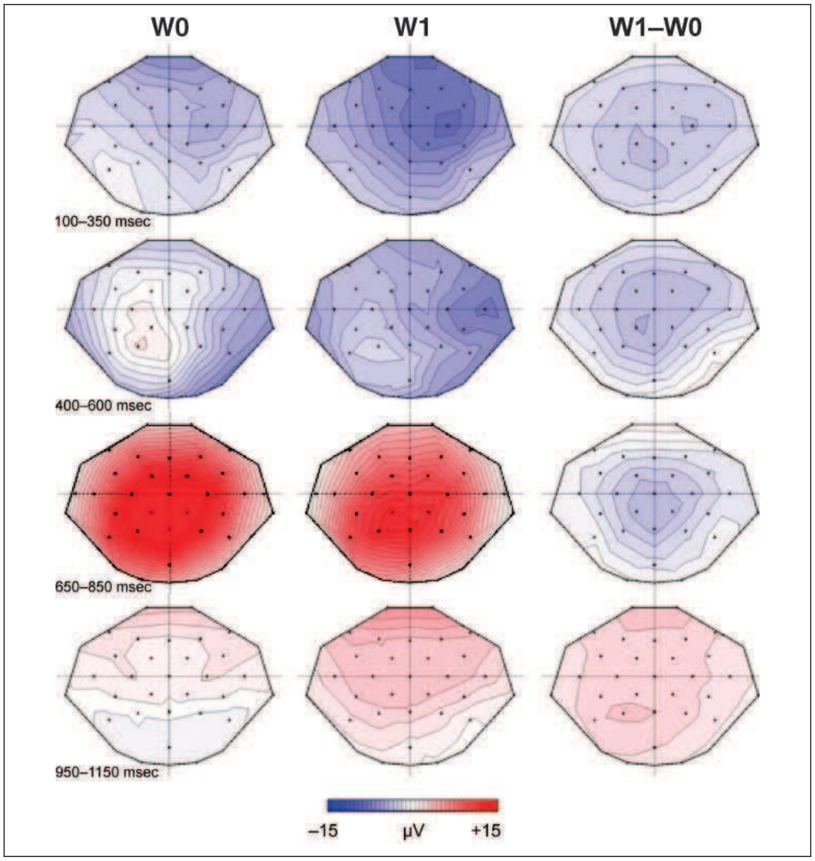
both conditions [laterality factor's $F(4, 40) = 4.58$, $p = .034$]. Also, its distribution differed between conditions, as supported by a significant three-way WM × Frontality × Laterality interaction [$F(8, 80) = 5.58$, $p = .004$]. The third latency window (650–850) covered the time window of the 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 × 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, & Näätänen, 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).

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Study II.

SanMiguel, I., Trautmann, S., Escera, C., Erhard, P., Fehr, T., Domínguez-Borràs, J., Herrman, M. Brain mechanisms underlying coping with distracting sounds: an fMRI investigation of WM modulation and interference control of novel sound processing.

Brain mechanisms underlying coping with distracting sounds: an fMRI investigation of working memory modulation and interference control of novel sound processing

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ABSTRACT

Novel sounds trigger an involuntary orienting response that results in temporary distraction from ongoing tasks. This involuntary orienting response, however, has been shown to be susceptible to top-down modulation. Here, we investigated two different mechanisms of cognitive control in face of distraction by novel sounds: modulation by working memory (WM) load and sequential adjustments in interference control after distraction. Participants performed a simple number classification task in two conditions with or without working memory load while ignoring irrelevant auditory stimulation. The unexpected occurrence of a novel sound activated bilateral superior temporal gyrus (STG) and right inferior frontal gyrus (rIFG) and resulted in behavioural distraction on the visual task in both conditions. Activity in rIFG was reduced when the task required WM. When participants were distracted by the occurrence of a novel sound, subsequent adjustments in the level of control were exerted in the following trial. This was evidenced by an increase in activation in task-relevant visual information processing areas and an inhibition of task-irrelevant auditory processing areas. These findings indicate that cognitive load reduces involuntary orienting towards novel sounds by inhibiting novelty processing areas, while interference control mechanisms respond to distraction by enhancing the processing of task-relevant sensory information and in inhibiting the processing of task-irrelevant sensory information in parallel.

Introduction

Humans are able to detect contextually novel stimuli occurring in the environment in an automatic manner. This is an important attentional function that allows the proper guidance of actions in relation to the environmental contingencies. However, orienting towards an unexpected event inevitably also leads to a disengagement from the current focus of attention, and may result in an impairment of performance whenever a task is being performed. It is therefore essential to understand how an appropriate balance between voluntarily maintaining the focus of attention on the current task and involuntarily orienting towards potentially relevant events is achieved. It was the aim of the present study to investigate mechanisms of cognitive control that operate to maintain this balance.

The involuntary orienting response (OR) has been extensively studied by presenting deviating (i.e., “novel”) auditory stimuli interspersed among a sequence of repeating (“standard”) sounds. The unexpected occurrence of a novel sound captures attention involuntarily and is accompanied by a series of electrophysiological and hemodynamic brain responses that have been described in detail. Novel sounds elicit the novelty-P3 event-related brain potential (Squires, Squires & Hillyard, 1975; Knight, 1984; Escera, Alho, Winkler, & Näätänen, 1998; (Domínguez-Borràs et al., 2008; Friedman, Cycowicz, & Gaeta, 2001) and activate a distributed network of brain areas including supratemporal (Alho et al., 1998; Downar, Crawley, Mikulis, & Davis, 2000; Downar, Crawley, Mikulis, & Davis, 2001; Kiehl, Laurens, Duty, Forster, & Liddle, 2001), prefrontal (Bledowski et al., 2004; Downar et al., 2001) and parietal cortices (Clark, Fannon, Lai, Benson, & Bauer, 2000; Downar et al., 2001), which are supposed to subserve the neural mechanisms of auditory novelty processing (Domínguez-Borràs et al., 2008; Friedman et al., 2001; Linden, 2005; Ranganath & Rainer, 2003). Moreover, if the deviating sound is presented during the performance of an unrelated task, it results in temporary distraction, as indicated by a decrease in accuracy and slowing of responses to subsequent targets (Berti & Schröger, 2001; Escera et al., 1998; Escera, Alho, Schröger, & Winkler, 2000; Escera & Corral, 2007; Schröger & Wolff, 1998a; Schröger & Wolff, 1998b; Schröger, Giard, & Wolff, 2000).

Orienting towards unexpected sounds, however, might be more or less appropriate depending on contextual factors and the orienting response is therefore susceptible of top-down modulation (Pashler, Johnston, & Ruthruff, 2001). For example, when immersed in a negative emotional context, unexpected novel sounds might signal a threat, and therefore an enhanced novelty response is found in such a situation (Domínguez-Borràs et al., 2008). Conversely, several studies show that when performing a taxing task, the processing of disruptive or irrelevant stimuli is down-regulated (Gazzaley, Cooney, McEvoy, Knight, & D'Esposito, 2005; Pinsk, Doniger, & Kastner, 2004; Postle, 2005; Spinks, Zhang, Fox, Gao, & Hai Tan, 2004; Sreenivasan & Jha, 2007). Along these lines, the novelty-P3 response and the distraction effects elicited by novel sounds are attenuated by working memory (WM) load (Berti & Schröger, 2003; SanMiguel, Corral, & Escera, 2008; see review in Escera & Corral, 2007). The modulation of novelty responses in situations of high WM load might reflect an active interference function performed in order to prevent distraction in demanding task settings. Indeed, it has been proposed that the WM system plays a crucial role in the executive control of attention (Postle, 2006). Conversely, the modulation of novelty responses by WM load might be due to an exhaustion of resources in overlapping attentional control and WM maintenance areas (Linden, 2007; Mayer et al., 2007).

The modulation of novelty responses by task factors such as emotional content or WM load represents a tonic adjustment in the balance between maintaining task focus while scanning the environment for potentially relevant events. However, dynamic or more phasic adjustments in attention control based on immediate previous performance might also take place. A well defined example of such sequential adjustments in cognitive control is the case of conflict adaptation (Gratton, Coles, & Donchin, 1992). Conflict adaptation refers to the phenomenon of reduced or abolished incongruency effects during the performance of stroop-like conflict tasks in incongruent trials immediately following another incongruent trial. According to the conflict monitoring model, conflict adaptation results from a top-down bias of processes associated with the current task set that is triggered whenever a conflict is detected in the previous trial (Botvinick, Braver, Barch, Carter, & Cohen, 2001; Botvinick, Cohen, & Carter, 2004).

Cognitive control mechanisms might bias information processing after distraction in two opposed directions resulting in reduced conflict effects: through amplification of cortical responses to task-relevant information or through inhibition of responses to task-irrelevant information. Using a variant of the stroop task that used face stimuli as either target or distracter stimuli, Egner & Hirsch (2005) have shown cortical amplification of responses in fusiform face area (FFA) to face-target stimuli in incongruent trials following incongruent trials. These results give support to the hypothesis that conflict triggers an up-regulation of responses to task-relevant stimulation. Moreover, it has been shown recently that cognitive interference control after distraction is also susceptible of modulation by cognitive load. Fischer, Dreisbach, & Goschke (2008) demonstrated that conflict adaptation is reduced when control demands are high compared to low control demands in the preceding trial.

The present study aimed at investigating the cerebral mechanisms involved in regulating distraction elicited by task-irrelevant distracting sounds during the performance of a simple visual task. First, we manipulated WM load of the task and hypothesized that increasing task demands should result in diminished distraction. We aimed at localizing these distraction modulation effects to specific brain areas involved in novelty processing that would show parallel decreases in activity. Second, we hypothesized that after distraction by unexpected sounds, sequential adjustments in control similar to those of conflict adaptation might take place in order to prevent further distraction. Such adjustments in control following distraction by unexpected sounds have, to our knowledge, not been addressed directly. In order to test this hypothesis, we have examined brain responses to sounds presented immediately after distracting sounds in order to find either an inhibition of sound processing or an enhancement of visual task-relevant processing in trials immediately following distraction.

Methods

Participants

Twenty-one healthy participants aged 20-45 years (mean age 23.95 +/- 5.3, six males) were recruited among Bremen University students. All subjects but one were right-handed and all had normal or corrected-to-normal vision and reported no past or present neurological, psychiatric or hearing disorders. The study was conducted according to the Declaration of Helsinki, with endorsement of the relevant ethical committees, and all participants gave written informed consent before participation in the experiment.

Stimuli and procedure

Participants performed a modified version of a well-characterized auditory-visual distraction task (Escera et al., 1998; Escera et al., 2000; Escera, Yago, & Alho, 2001; Escera, Corral, & Yago, 2002; Escera, Yago, Corral, Corbera, & Nuñez, 2003) adapted for functional magnetic resonance imaging (fMRI, Domínguez-Borràs et al., 2008) with two conditions: a 1-back WM condition (WM1) and a 0-back condition with no WM load (WM0). Each trial consisted of a visual target preceded in 300 ms by an auditory stimulus and lasting a total duration of 1800 ms ± 300 ms. Participants were instructed to respond to visual stimuli as fast and accurately as possible and to ignore the auditory stimulation.

The auditory stimuli were presented through MR compatible headphones calibrated at 20dB sensation level (SL; Domínguez-Borràs et al., 2008)and consisted of a 600 Hz standard tone (STD; 200 ms duration) in 80 percent of the trials and a unique environmental complex novel sound (NOV) in the remaining 20 percent of the trials. Novel sound trials were always preceded by at least one standard tone trial. Novel sounds were 100 environmental unique sounds such as those produced by a drill, hammer, rain, door, telephone ringing, selected from a larger pool (Escera et al., 1998) as those more easily identifiable (Escera et al., 2003), and with similar spectrotemporal features (see Domínguez-Borràs et al., 2008). They were digitally recorded, low-pass filtered at 10,000 Hz, with a constant duration of 200 ms, including rise and fall times of 10 ms, and were equalized for root-mean-square energy to keep the energy contour of all auditory stimuli constant over time (see Domínguez-Borràs et al., 2008). Along the session, each novel sound exemplar appeared once in each task condition, and was not repeated within the same condition. The order of conditions was counterbalanced across subjects, therefore cancelling any possible effect of novel sound repetition across conditions. Visual stimuli were single digits (1-4 and 6-9) back-projected onto a mirror mounted on the MRI head coil, presented for 200 ms in white colour against a black background subtending a vertical angle of 4.17^{o} and a horizontal angle of $2.62\ ^{o}$.

In the WM0 condition, participants had to decide by a button press with their right or left hand whether the digit presented was larger or smaller than five. The WM1 condition was a 1-back task in which participants had to decide whether the digit presented was larger or smaller in value than the digit presented in the previous trial. Response hands were counterbalanced across participants.

Before the experiment, participants performed a five minute visual-only practice block outside the scanner which was repeated until a minimum hit rate of 75 percent was reached. Once inside the scanner, immediately after sound intensity calibration, participants were presented with 10 habituation trials containing only standard tones in order to allow for magnetic saturation effects and for participants to adjust to task performance with sounds under scanner noise conditions. The experiment consisted of three consecutive runs. In each run one block of each WM condition was presented, making a total of six blocks of 160 audio-visual trials (128 STD, 32 NOV) each, separated by short breaks of 20 seconds. Every block started with 10 standard tone trials that were excluded from all analyses. The order of the conditions within each run was counterbalanced across participants and remained constant across runs for each participant.

fMRI data acquisition

fMRI data was acquired on a 3T Siemens Allegra scanner (Erlangen, Germany) using a whole brain local gradient coil. Structural images were acquired with a T1-weighted MPRAGE sequence (160 slices, TR 2.3s, TE 4.38 ms, flip angle 8°, 256x256 matrix, FOV 296x296, inversion time 900 ms, 1mm^3 voxels). Functional images were obtained using a gradient echo-planar (EPI) T2* sequence optimized for BOLD (Blood Oxygenation Level Dependency) contrast. The EPI sequence comprised 38 slices of 3 mm thickness each, parallel to the AC-PC plane, covering the whole brain, with a 0.3 mm inter-slice gap (TE 30 ms, TR 2.5 s, 64x64 matrix, FOV 192 mm, flip angle 90°, interleaved ascending). A total of 800 whole-brain volumes were acquired from every subject after three dummy scans to allow for magnetic saturation. Functional images were slice time corrected, realigned, normalized spatially to the Montreal Neurological Institute (MNI) template, and smoothed with an 8 mm FWHM gaussian kernel using SPM2 (Wellcome Department of Cognitive Neurology, London, England, 2003).

Data analysis

The analytical strategy implemented here was similar to that used in a previous study to reveal modulation by negative emotional context of hemodynamic activity elicited by novel sounds (Domínguez-Borràs et al., 2008). At the first level, event types were modelled for novel (NOV), standard (STD) and first standard after novel (AFN) trials with a correct response in each WM condition. Data were high-pass filtered (1/128Hz), corrected for intrinsic autocorrelations, and convolved with a standard hemodynamic response function (HRF) and its temporal derivative modelled to sound onset. Second level analysis was performed on single-subject statistical parametric maps, serving as random effects. Auditory novelty effects were explored contrasting novel vs. standard trials, and interference control effects implemented after distraction were explored by contrasting standard trials immediately following a novel trial vs. standard trials immediately following another standard trial. Activation elicited by auditory novelty was explored by two contrasts of interest, by means of voxel-referred t-tests, comparing BOLD signal for the following conditions: STD0<NOV0 (*novelty processing in the WM0 condition*) and STD1<NOV1 (*novelty processing in the WM1 condition*).

Subsequently, modulation of auditory novelty effects by WM load was assessed by means of an interaction contrast (*WM effects on novelty processing*), examined with a one-factor ANOVA: [(STD0<NOV0)>(STD1<NOV1)]. On the other hand, four contrasts of interest were defined to explore interference control effects: STD0<AFN0 (*enhancement by interference control in WM0*); STD1<AFN1 (*enhancement by interference control in WM1*); STD0>AFN0 (*inhibition by interference control in WM0*) and STD1>AFN1 (*inhibition by interference control in WM1*). Modulation of interference control effects by WM load was assessed by means of the interaction contrast *(WM effects on enhancement by interference control)*, examined with a one-factor ANOVA:

[(STD0<AFN0)<(STD1<AFN1)] and its reverse [(STD0<AFN0)>(STD1<AFN1)]. The parallel interaction contrasts to explore WM effects on inhibition by interference control [(STD0>AFN0)<(STD1>AFN1)] and [(STD0>AFN0)>(STD1>AFN1)] will not be reported as less inhibition in WM1 is equivalent to more enhancement and vice versa due to the lack of an absolute baseline. Activation was considered significant when at least 20 contiguous voxels survived a threshold of $p<0.001$, uncorrected for multiple comparisons. Stereotactic MNI coordinates were translated into standard Talairach space (Talairach & Tournoux, 1988) following nonlinear transformations.

Behavioral performance was assessed by computing mean response time (RT) for correct trials and hit rate (HR) for each auditory stimulus type. Any trial containing a correct response after visual stimulus offset and before the end of the trial (1300+/-300 ms) was regarded as a hit. Behavioural effects for the experimental conditions were assessed by means of repeated measures analysis of variance (ANOVA) with the type of auditory stimulus (STD, NOV, AFN) and WM condition (WM0, WM1) as factors, performed on HR and RT, and post-hoc tests were conducted subsequently to establish the origin of interactions between the main factors. Greenhouse-Geisser corrections were applied to all analyses where appropriate.

Results

Behavioural data

The working memory task was more difficult to perform, as indicated by increased RT ($F(1,20) = 16.175$, $p=0.001$, $\eta^2 = 0.447$) and decreased HR ($F(1,20) = 22.317$, $p<0.001$, $\eta^2 = 0.527$) in the WM1 condition (see Fig.1). The general ANOVA on RT revealed a main auditory stimulus type effect ($F(2,40) = 7.961$, $p=0.003$, $\eta^2 = 0.285$), and an interaction between WM condition and auditory stimulus type ($F(2,40) = 3.801$, $p=0.031$, $\eta^2 = 0.160$).

Participants responded slower after novel sounds than after standard sounds (F(1,20) = 22.752, p<0.001, η^2 = 0.532), reflecting behavioural distraction caused by the occurrence of the novel sounds. The distraction effect by novel sounds did not interact with the WM condition.

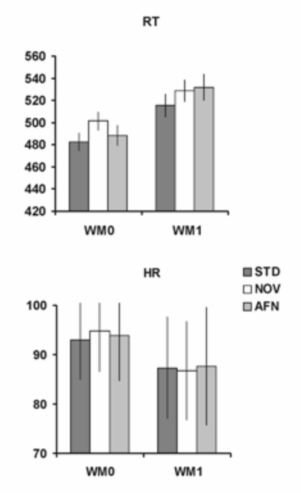

Figure 1. *RT and HR for each trial type in the WM0 and WM1 condition. Bars indicate the standard error of the mean (SEM).*

Distraction persisted in the first standard trial after a novel trial, as reflected by increased RT in AFN compared to STD trials (F(1,20) = 8.359, p=0.009, η^2 = 0.259). The increase in RT in AFN relative to STD was significant in WM1 (F(1,20)= 6.831, p=0.017, η^2 = 0.255) and showed a trend to significance in WM0 (F(1,20)= 3.316, p=0.084, η^2 = 0.142). However the interaction between WM condition and auditory stimulus type for STD vs. AFN trials failed to reach statistical significance (F(1,20) = 2.905, p=0.104, η^2 = 0.127). Moreover, the RT did not differ between standard trials immediately following a novel trial and novel trials in WM1 (F(1,20)= 0.183, p=0.674, η^2 = 0.009), but was reduced for AFN compared to NOV in WM0 (F(1,20)= 12.050, p=0.002, η^2 = 0.376). This difference between WM condition was reflected by a significant interaction between WM condition and auditory stimulus type for NOV vs. AFN trials (F(1,20) = 7.675, p=0.012, η^2 = 0.277). There was no auditory stimulus type effect or interaction between WM condition and auditory stimulus type in HR. In sum, novel sounds distracted performance as reflected in increased RT and this distraction persisted in the first standard trial immediately following a novel trial. However, the carry-over effect on novel sounds on subsequent standard trials was more prominent under higher WM load.

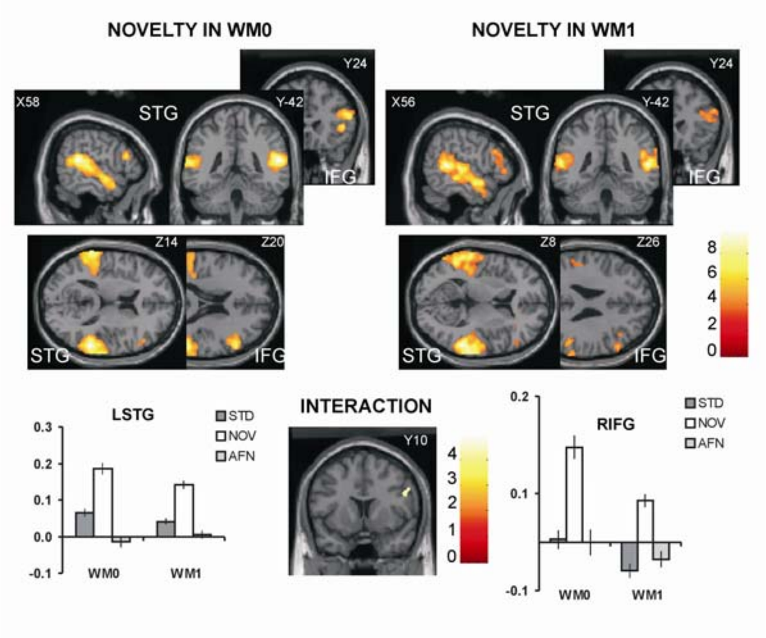

Figure 2. *Novelty processing in WM0 and WM1 and interaction contrast showing WM effects on novelty processing. Percent signal change values of all event types in both WM conditions are shown for left superior temporal gyrus (lSTG) and right inferior frontal gyrus (rIFG). Bars indicate SEM. Novel sounds activated bilateral STG and rIFG in both conditions. Activity in rIFG was reduced in the WM1 condition.*

fMRI data

Novelty processing

Activation elicited by the impact of WM load on auditory novelty was explored with the contrasts *novelty processing in WM0* and *novelty processing in WM1*. Novel sounds activated auditory cortex (superior temporal gyrus, STG), and inferior frontal gyrus (IFG) bilaterally in both WM conditions (Table 1, Fig.2). The hypothesized inhibition of novelty processing by WM load was explored in the interaction contrast *WM effects on novelty processing*. This contrast revealed reduced activity in WM1 in right IFG, reflecting an inhibition of this novelty processing area under WM load (Table 2, Fig. 2).

Table 1. *Novelty processing (STD<NOV)*

	Brain region	Brodmann area	z value	Size (voxels)	X	Y	Z
WM0	R STG	13	5.63	3310	57	-40	15
	R STG	42	5.28		67	-21	12
	R STG	42	5.21		67	-27	7
	L STG	22	5.24	2227	-55	-27	5
	L STG	22	5.21		-63	-36	15
	L STG	42	4.86		-61	-29	11
	R IFG	45	4.93	794	55	24	17
	R IFG	45	4.58		46	29	0
	R IFG	9	3.83		40	9	29
	L IFG	47	3.76	23	-42	21	-3
WM1	R STG	22	5.90	4001	55	-40	9
	R STG	38	5.87		48	-6	-11
	R MiTG	21	5.62		50	5	-19
	L STG	21	5.78	3324	-51	-21	-1
	L STG	22	5.56		-53	-46	13
	L INS	13	5.55		-46	-32	20
	L IFG	47	4.13	124	-46	31	-10
	R MiFG	46	3.99	507	55	24	23
	R IFG	46	3.93		50	26	12
	R IFG	47	3.78		55	35	-2
	L SubCG	34	3.73	42	-16	5	-12
	L Uncus	34	3.11		-18	1	-20
	R IFG	47	3.71	35	26	15	-18

All coordinates reported in Talairach space. Activations shown are based on voxelwise p<0.001, uncorrected, k=20. L = left hemisphere; R = right hemisphere; STG = Superior temporal gyrus; IFG = Inferior frontal gyrus; MiFG = Middle frontal gyrus; INS = Insula; SubCG = Subcallosal Gyrus.

Interference control after distraction

Two mechanisms of interference control following distraction were hypothesized: a possible enhancement of task-relevant stimulus processing and a possible inhibition of task-irrelevant stimulus processing in standard trials immediately following a novel trial compared to standard trials immediately following another standard trial. The *enhancement by interference control* contrasts showed increased activity in striate and extrastriate visual areas in standard trials immediately following a novel trial in both WM conditions (Tables 3 and 4, Fig. 3A), supporting the hypothesis of enhancement of task-relevant stimulus processing. Additional active areas were found for the WM0 condition in the right temporoparietal junction (TPJ; BA 39 and BA 40) as well as in prefrontal cortex (PFC; BA 8). Activation was more widespread in WM1, particularly in PFC and included also subcortical areas (Table 4).

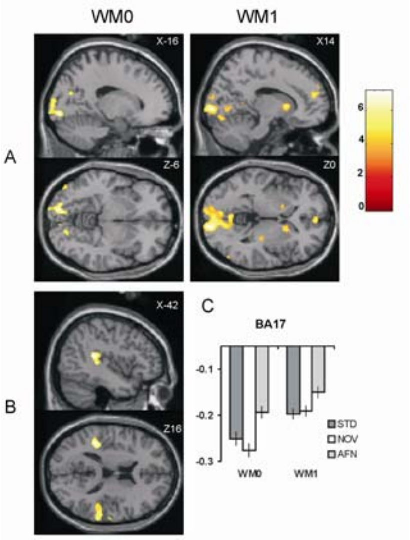

Figure 3. *A) Enhancement by interference control in WM0 and WM1. B) Inhibition by interference control in WM0. C) Percent signal change values of all event types in WM0 and WM1 in striate cortex (BA 17). Bars indicate SEM. In standard trials immediately following a novel trial activity was enhanced in visual cortex in both conditions and inhibited in auditory cortex in WM0.*

The *inhibition by interference control* contrast showed, in turn, significant activations only in the WM0 condition (Table 3, Fig 3B). Auditory cortical areas (STG) were inhibited bilaterally in standard trials immediately following a novel trial, rendering support for the hypothesis of inhibition of irrelevant stimulation processing after distraction.

Table 2. *WM effects on novelty processing*

	Brain region	Brodmann area	z value	Size (voxels)	X	Y	Z
[(STD0<NOV0) > (STD1<NOV1)]	L MiFG	46	3.73	25	-44	30	24
	L MiFG	10	3.55	27	-30	48	4
	R IFG	9	3.31	27	54	10	32

All coordinates reported in Talairach space. Activations shown are based on voxelwise p<0.001, uncorrected, k=20. L = left hemisphere; R = right hemisphere; IFG = Inferior frontal gyrus; MiFG = Middle frontal gyrus.

Table 3. *Interference control in WM0*

	Brain region	Brodmann area	z value	Size (voxels)	X	Y	Z
ENHANCEMENT (STD0<AFN0)	L LingG	17	4.49	275	-16	-87	-1
	L Cuneus	18	3.70		-20	-94	14
	L Cuneus	18	3.52		-16	-97	7
	L MiOG	19	4.14	102	-32	-82	21
	L MiOG	19	3.81		-26	-81	15
	L Cuneus	18	3.98	79	-6	-75	24
	L Precuneus	31	3.71		-18	-69	24
	R LingG	-	3.84	80	18	-76	0
	R LingG	18	3.45		12	-76	-5
	R LingG	18	3.34		6	-82	-4
	R Cuneus	19	3.60	32	16	-88	25
	R MiOG	18	3.39		12	-94	16
	L MiOG	19	3.58	29	-48	-78	-3
	R STG	39	3.52	90	48	-55	21
	R SMG	40	3.42		55	-53	27
	R SFG	8	3.50	25	20	39	50
	L IOG	19	3.42	22	-40	-74	-8
	R IPL	40	3.36	21	46	-49	36
INHIBITION (STD0>AFN0)	L STG	41	4.54	330	-42	-34	16
	L STG	41	4.00		-42	-33	7
	L STG	-	3.33		-48	-23	1
	R STG	42	4.05	483	63	-32	18
	R STG	22	3.77		61	-15	6
	R STG	41	3.66		53	-17	5

All coordinates reported in Talairach space. Activations shown are based on voxelwise p<0.001, uncorrected, k=20. L = left hemisphere; R = right hemisphere; LingG = Lingual gyrus; MiOG = Middle occipital gyrus; STG = Superior temporal gyrus; SMG = Supramarginal gyrus; SFG = Superior frontal gyrus; IOG = Inferior frontal gyrus; IPL = Inferior parietal lobule.

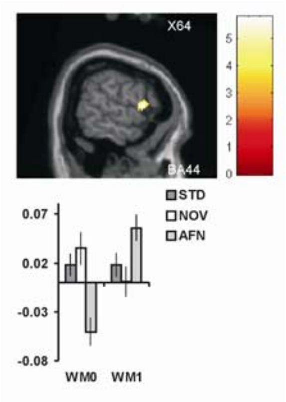

Figure 4. *WM effects on interference control [(STD0<AFN0)<(STD1<AFN1)] contrast showing areas that were more active or less inhibited following distraction in WM1 than in WM0. Percent signal change values of all event types in WM0 and WM1 for area BA44 are shown. Bars indicate SEM.*

The interaction contrasts were defined to explore possible modulations by WM load of these enhancement and inhibition effects after distraction. The interaction contrast [(STD0<AFN0)>(STD1<AFN1)] revealed no significant activation, indicating there were no areas that were significantly less active or more inhibited following distraction in WM1 than in WM0. On the other hand, the [(STD0<AFN0)<(STD1<AFN1)] contrast revealed areas that were more

active (or less inhibited) following distraction in WM1 than in WM0 (Table 5). Significant activation was found for this contrast in right frontal areas (BA44, Insula) and posterior cingulate.

Table 4. *Interference control in WM1*

	Brain region	**Brodmann area**	**z value**	**Size (voxels)**	**X**	**Y**	**Z**
ENHANCEMENT (STD1<AFN1)	R Cuneus	17	7.18	3845	14	-91	5
	L FusG	19	6.52		-32	-76	-8
	L Cuneus	19	6.47		-26	-82	32
	L Putamen	-	6.43	229	-28	0	-7
	L Putamen	-	5.11		-22	9	-7
	L Putamen	-	4.43		-18	8	1
	R MeFG	11	5.64	296	2	48	-12
	R MeFG	10	5.25		2	54	-3
	R MeFG	10	3.82		-4	51	5
	L PostCG	2	5.61	37	-44	-25	36
	R MeFG	10	5.38	133	12	51	14
	R SFG	10	4.32		20	59	19
	R SFG	9	3.95		14	58	27
	R PostCing	29	5.17	44	8	-50	8
	R Caudate	-	5.17	142	12	14	3
	R Putamen	-	4.11		22	11	-11
	R MiOG	37	5.06	84	46	-64	-5
	R ITG	-	4.19		55	-68	2
	L SubCallG	25	4.59	36	-6	19	-14
	L RectalG	11	3.95		0	18	-19
	L SFG	9	4.42	26	0	52	27
	R Precuneus	7	4.31	53	28	-63	31
	R Putamen	-	4.29	21	30	-21	1
	L ParaHipG	37	4.20	22	-30	-39	-11
	L CingG	31	4.19	48	-8	-45	41
	L Precuneus	31	3.87		-2	-47	34
	L ACC	32	4.01	42	0	36	18
	L MeFG	9	3.90		-6	43	14
	L MiOG	19	3.97	22	-38	-87	17
	L MiOG	19	3.58		-34	-93	8

All coordinates reported in Talairach space. Activations shown are based on voxelwise p<0.001, uncorrected, k=20. L = left hemisphere; R = right hemisphere; FusG = Fusiform gyrus; MeFG = Medial frontal gyrus; PostCG = Postcentral gyrus; SFG = Superior frontal gyrus; PostCing = Posterior cingulate; MiOG = Middle occipital gyrus; ITG = Inferior temporal gyrus; SubCallG = Subcallosal gyrus; RectalG = Rectal gyrus; ParaHipG = Parahippocampal gyrus; CingG = Cingulate gyrus; ACC = Anterior cingulate.

Table 5. *WM effects on Interference control*

	Brain region	Brodmann area	z value	Size (voxels)	X	Y	Z
[(STD0<AFN0) < (STD1<AFN1)]	R PreCG	44	4.91	53	63	10	7
	R PostCing	29	3.85	66	6	-48	8
	R ParaHipG	30	3.39		6	-39	6
	L Culmen	-	3.37		-4	-37	2
	R Claustrum	-	3.34	35	38	-15	8
	R Insula	13	3.17		46	-11	12
	R Insula	13	3.27	20	42	-3	13

All coordinates reported in Talairach space. Activations shown are based on voxelwise p<0.001, uncorrected, k=20. L = left hemisphere; R = right hemisphere; PreCG = Precentral gyrus; PostCing = Posterior Cingulate; ParaHipG = Parahippocampal gyrus.

Discussion

Brain regions associated with novelty processing areas were identified by comparing novel sound trials against standard sound trials. This contrast yielded activation of auditory processing areas in temporal cortex (STG) in both WM conditions. STG has been consistently associated to novelty processing (Alho et al., 1998; Domínguez-Borràs et al., 2008; Downar, Crawley, Mikulis, & Davis, 2002; Kiehl et al., 2001; Kiehl et al., 2005; Opitz, Mecklinger, Friederici, & von Cramon, 1999; Opitz, Mecklinger, Von Cramon, & Kruggel, 1999; Opitz, Rinne, Mecklinger, von Cramon, & Schröger, 2002; Strobel et al., 2008; Watkins, Dalton, Lavie, & Rees, 2007) and has been shown to subserve the novelty-P3 event-related brain potential (Alho et al., 1998; Knight, Scabini, Woods, & Clayworth, 1989; Knight, 1997; Opitz, Mecklinger, Friederici et al., 1999). Novelty responses have also been recorded from temporal cortex intracranially (Alain, Richer, Achim, & Saint Hilaire, 1989; Halgren, Baudena, Clarke, Heit, Liegeois et al., 1995; Halgren, Baudena, Clarke, Heit, Marinkovic et al., 1995). IFG was activated by novel sounds in both conditions, again in accordance with other studies showing that this region is involved in novelty processing (Bledowski, Prvulovic, Goebel, Zanella, & Linden, 2004; Domínguez-Borràs et al., 2008; Downar et al., 2000; Downar et al., 2002; Kiehl et al., 2001; Kiehl et al., 2005; Opitz, Mecklinger, Friederici et al., 1999; Strobel et al., 2008; Watkins et al., 2007). Moreover, lesion studies (Alho, Woods, Algazi, Knight, & Näätänen, 1994;

Daffner et al., 2000; Knight, 1984; Knight, 1997) and intracranial recordings (Baudena, Halgren, Heit, & Clarke, 1995) support a role for frontal areas in novelty processing. It has been proposed that STG is the basis for the novelty detection process, whereas frontal areas would be a secondary source, involved in attentional control and an additional stage of semantic analysis of the novel events (Opitz, Mecklinger, Friederici et al., 1999; Tulving, Markowitsch, Craik, Habib, & Houle, 1996).

The activation of STG and IFG was accompanied by behavioural distraction as reflected by increased RT in novel trials. Contrary to our hypothesis, behavioural distraction was not modulated by WM load. However, the processing of novel sounds in right IFG was inhibited under load, i.e., in the WM1 condition. This result supports the hypothesis of active inhibition of novelty processing under conditions of increased WM load. However, the modulation does not seem to take place in auditory cortex, over simple deviance detection processes. Rather, WM load modulated the processes subserved by IFG, which are potentially related with the analysis of the relevance of the novel event. Possibly, the analysis of the relevance influences more directly whether the attention switch is triggered towards the novel sound. IFG is part of a ventral fronto-parietal network strongly lateralized to the right hemisphere that is known to be engaged by salient and behaviourally relevant but unattended events that require an attention switch (Corbetta et al., 2008; Corbetta & Shulman, 2002).

We hypothesized that after distraction by novel sounds, sequential adjustments in interference control should take place, similarly to the case of conflict adaptation after distraction by incongruent information in Stroop-like tasks (Egner & Hirsch, 2005; Gratton et al., 1992). This hypothesis was explored contrasting standard trials immediately following a distracting novel trial to standard trials that did not follow distraction. Both, enhancement of task-relevant information processing and inhibition of irrelevant information processing were found after distraction, supporting the hypothesis of sequential adjustments in interference control after distraction. The enhancement contrasts showed an up-regulation of extrastriate visual areas following distraction in both WM conditions. This result resembles the enhancement of task-relevant information processing in trials following an incongruent trial underlying the conflict adaptation effect in stroop-like tasks (Egner & Hirsch, 2005). However, in the present study, an inhibition of task-irrelevant processing was also found in trials following distraction. In the WM0 condition, activity in STG was suppressed after distraction. The inhibition of STG was only significant in WM0, suggesting that this particular mechanism of interference control might be less effective under load, similarly to the findings of reduced conflict adaptation when control demands are increased (Fischer et al., 2008). However, this difference between WM conditions was not supported statistically by the interaction contrast, which showed no areas that were more inhibited or less active after distraction in WM0 than in WM1. The behavioral results also showed a tendency towards more interference control being exerted after distraction in WM0 than in WM1. Although distraction persisted in the first trial after a novel trial in both conditions, RTs decreased in the first trial after a novel trial in WM0 while it showed no reduction and remained as high as in the previous novel trial in WM1. This result, together with the lack of modulation of behavioral distraction in the WM1 condition, suggests that the specific load manipulation used in the present study might not have been sufficiently effective. Indeed, studies using similar paradigms have found reliable modulations of behavioral distraction by WM load (Berti & Schröger, 2003; SanMiguel et al., 2008). Possibly, in the WM0 condition, the requirement of comparing each digit to a memory representation (the digit 5) might have placed some demands on WM, rendering the comparison with the WM1 condition less effective.

The *enhancement by interference control* contrast also showed activation in prefrontal and parietal areas in both WM conditions. This contrast showed areas that were more active in trials following distraction, therefore any areas exerting interference control over lower processing areas following distraction, may also be identified by this contrast, irrespective of whether the top-down biasing is in the direction of enhancement or inhibition. Indeed, the frontal and parietal areas that showed activation in this contrast have been related to the control of attention. Frontal areas included right superior frontal gyrus (rSFG) and anterior cingulate cortex (ACC) both of which have been demonstrated to be involved in the top-down biasing of activity at sensory or association cortices (Corbetta & Shulman, 2002; Corbetta, Patel, & Shulman, 2008) and in behaviour monitoring and control adjustments (Ridderinkhof, Ullsperger, Crone, & Nieuwenhuis, 2004; Ridderinkhof, van den Wildenberg, Segalowitz, & Carter, 2004; Royall et al., 2002). Moreover, ACC was only activated in the WM1 condition. It has been proposed that this area is particularly active when there is a need for strong inhibitory control (Garavan, Ross, Murphy, Roche, & Stein, 2002), giving further support to the hypothesis that sequential adjustments in control might have been more difficult to perform when WM was loaded. Moreover, parietal areas around the right temporo-parietal junction (rTPJ) and inferior parietal lobule (IPL) that were activated in the *enhancement by interference control* contrast have also been implicated in inhibitory control (Garavan et al., 2002). However, these results should be addressed with caution, as a direct causal relationship between the activation of these areas and the reported enhancement of task-relevant information processing and inhibition of irrelevant information processing at lower perceptual processing areas cannot be inferred from the present design. Moreover, although prefrontal and parietal areas predominantly on the right hemisphere were identified with the *enhancement by interference control* contrast in both WM conditions, the specific areas differed across WM conditions. However, the interaction contrast showed that only activity in the right ventral prefrontal cortex (BA 44 and insula) and the right posterior cingulate was enhanced in WM1.

In sum, two different mechanisms of top-down control of novelty processing were found in the present study. Novel sounds activated STG bilaterally and rIFG. When participants performed a more demanding task requiring WM, novelty processing was reduced in rIFG. This result indicates that WM load might modulate the analysis of the relevance of novel events and the triggering of an involuntary attention switch. Conversely, in trials immediately following a distracting novel trial, interference control adjustments were exerted by enhancing task-relevant information processing at visual areas and inhibiting task-irrelevant information processing in STG. This data suggest that the interference control function was carried out by a right-lateralized fronto-parietal network of areas and that it was more difficult to exert under load.

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Study III.

San Miguel I., Escera C., Yabe H., Nowak R., Matsuoka T., Tomiharu, H., Sunao, K. Selective top-down modulation of recurrent novelty processing in auditory cortex.

Selective top-down modulation of recurrent novelty processing in human auditory cortex

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ABSTRACT

Involuntary orienting towards unexpected, novel events is an adaptive response as such events might be of behavioural relevance. However, orienting to such events also implies a disengagement from what was previously being attended, therefore, involuntary orienting is modulated in demanding task situations. This study explored the precise spatio-temporal dynamics of the mechanisms leading to modulation of responses towards novel sounds in demanding task situations. MEG responses to unattended, unexpected novel sounds during the performance of a visual task requiring working memory (WM) were compared to responses to the same novel sounds when the task required no WM. Novel sounds resulted in behavioural distraction and elicited N1/MMNm and P3am responses that could be modelled to adjacent areas of superior temporal gyrus (STG) in both conditions. Importantly, task demand modulated responses to novel sounds, reducing P3am responses arising from STG to roughly half their magnitude. These results indicate that during the performance of demanding tasks, involuntary orienting towards novel events is inhibited by down-regulating novelty responses in auditory cortex, but only after the initial preattentive detection of such events has been accomplished.

Introduction

Imagine you are immersed reading the last sentences of a thrilling novel. Several intricate plots that have evolved over many chapters are about to resolve in the next few statements. You are maximally focused and in expectation. As you reach the end point, a sense of relaxation expands through your body. Suddenly you realize: did the phone just ring a short while ago? Detection of salient or contextually novel stimuli that are of behavioural relevance is an essential function of the human brain. Novel stimuli generate an orienting response and capture attention involuntarily, preparing the individual for prompt action (Näätänen, 1992; Sokolov, 1963; Sokolov, 1990). However, orienting towards an unattended event necessarily implies at least partial disengagement from the current focus of attention; therefore the consequences of this disengagement must be balanced with the potential benefits. Surely, in the example above, if you would have been expecting an important call, the telephone ring would not have gone unnoticed.

It is unclear how the modulation of responses to unattended novel and behaviourally relevant events is accomplished. According to current models of attention, the selection of events for their entry into awareness seems to be attained by competition between the relative activation of the respective brain areas where these events are represented (Knudsen, 2007). Attention operates by biasing the activation in sensory and association areas, in favour of the most relevant representations (Desimone & Duncan, 1995). For example, when focusing on a visual task, such as reading a book, visual input is prioritized, whereas responses to sounds are inhibited (Chawla, Rees, & Friston, 1999; Corbetta, Miezin, Dobmeyer, Shulman, & Petersen, 1990; Johnson & Zatorre, 2005; Shulman et al., 1997; Woldorff et al., 1993). Moreover, the magnitude of the attentional modulation of activity in sensory and association areas depends on the demand of the task being performed. On one hand, the processing of irrelevant information is further down-regulated during the performance of demanding tasks, in respect to less demanding tasks (Gazzaley, Cooney, McEvoy, Knight, & D'Esposito, 2005; Pinsk, Doniger, & Kastner, 2004; Postle, 2005; Rees, Frith, & Lavie, 1997; Schwartz et al., 2005; Spinks, Zhang, Fox, Gao, & Hai Tan, 2004; Sreenivasan & Jha, 2007). On the other hand, when distraction is due to interference by conflicting stimuli, the processing of relevant information is enhanced in order to resolve this conflict (Egner & Hirsch, 2005; Weissman, Warner, & Woldorff, 2004). Moreover, this interference control function appears to be less effective during the performance of very demanding tasks (Fischer, Dreisbach, & Goschke, 2008), and conflicting stimuli lead to increased distraction in such situations (Lavie, 2005).

However, the means by which distraction caused by orienting towards novel events is modulated depending on the demands of ongoing cognitive processes are unclear. If irrelevant sensory information was to be gated completely at sensory processing areas in very demanding situations in order to prevent distraction, significant events occurring in the unattended stream –such as the important telephone ring- would go unnoticed. However, a certain attentional inhibition of irrelevant information is necessary to avoid excessive orienting towards any novel event, especially when performing demanding tasks. Therefore, we hypothesize that while primary sensory responses to irrelevant stimuli can be inhibited during the performance of demanding tasks, novel events must surpass the early attentional inhibition. Following this idea, the specific hypothesis is that orienting towards irrelevant novel events will be inhibited during the performance of demanding tasks only after initial preattentive detection and analysis of these events has taken place. That is, novel events will be processed irrespective of the task demand until the appropriateness of issuing an orienting response has been assessed. Whether an involuntary orienting response towards the novel event is finally issued will depend on the relevance of the novel event in the current situation.

Evidence from functional magnetic resonance imaging (fMRI) studies has shown that novel sounds activate a widely spread network of brain areas including supratemporal (Downar, Crawley, Mikulis, & Davis, 2000; Downar, Crawley, Mikulis, & Davis, 2001; Kiehl, Laurens, Duty, Forster, & Liddle, 2001; Kiehl et al., 2005), prefrontal (Bledowski, Prvulovic, Goebel, Zanella, & Linden, 2004; Downar et al., 2001) and parietal cortices (Clark, Fannon, Lai, Benson, & Bauer, 2000; Downar et al., 2001). This widely spread network of areas is assumed to be the substrate for novelty processing and involuntary attention control (Domínguez-Borràs et al., 2008; Friedman, Cycowicz, & Gaeta, 2001; Linden, 2005; Ranganath & Rainer, 2003). Therefore, the reduction of involuntary orienting in demanding situations could generally be assumed to be accomplished thorough the modulation of activity in this network of higher processing areas that control involuntary orienting.

We propose, however, that the same mechanisms that select information for their entry into awareness by biasing primary sensory responses could also modulate involuntary orienting towards novel auditory events. That is, the reduction of involuntary orienting will not be accomplished by modulating the activity of networks implicated in attention control, but rather by directly modulating the processing of novel stimuli in sensory cortices. If this was the case, in our example of the telephone ring, while concentrated on reading, sensory responses to sounds would be generally inhibited and visual processing enhanced. However, a novel event such as the telephone ring would be automatically processed until its relevance in the present situation was established, and the sensory responses would only be inhibited after deeming it irrelevant. Reducing the signal power arising from sensory cortices would result in fewer chances for the auditory event for entering awareness through competition with other sensory representations, and therefore involuntary orienting towards the novel event would be diminished or prevented (Knudsen, 2007).

This assumption is based on evidence from MEG recordings that have localized to adjacent areas in superior temporal gyrus (STG) three different consecutive responses that are respectively implicated in initial sensory analysis, deviance detection, and involuntary orienting (Alho et al., 1998). We therefore propose that recurrent loops of activity take place in auditory cortex after the occurrence of a novel sound, each achieving a more complex analysis of the novel sound in relation to the attentional configuration. Further, we propose that after the initial feed-forward sweep of activity, subsequent loops might be modulated from higher processing areas via feedback projections, similarly to the feedback mechanisms that have been described for visual cortex (e.g., Saalmann, Pigarev, & Vidyasagar, 2007). Event-related potential (ERP) studies have shown that the responses generated by unattended sounds that deviate from the context are attenuated during the performance of demanding tasks at circa 300 ms after sound presentation (Berti & Schröger, 2003; Harmony et al., 2000; Restuccia, Della Marca, Marra, Rubino, & Valeriani, 2005; SanMiguel, Corral, & Escera, 2008). The responses generated by novel sounds at this latency range have been related to the involuntary orienting response (Escera, Alho, Schröger, & Winkler, 2000; Friedman et al., 2001; Knight & Scabini, 1998) and depend also on the relevance of the novel events in relation to the attentional configuration (Escera, Alho, Winkler, & Näätänen, 1998; Escera, Yago, Corral, Corbera, & Nuñez, 2003; Sussman, Winkler, & Schröger, 2003). However, an earlier ERP response taking place at circa 100 ms after sound onset, which is an index of the preattentive detection of the auditory deviance, is not modulated by task demands (Muller-Gass, Stelmack, & Campbell, 2006).

The present study investigated the brain mechanisms involved in the modulation of involuntary orienting towards novel sounds and the resulting distraction effect by task demands. We hypothesized that the modulation of involuntary orienting is accomplished through inhibition of the processing of novel sounds in auditory cortex (i.e., STG) during the performance of demanding visual tasks. This inhibition of sensory processing areas will reduce the signal power of the neural representation of the novel event, resulting in fewer chances for the novel event to enter awareness through competition with other sensory representations, altogether leading to reduced distraction. Moreover, we hypothesize that the inhibition of sensory processing will not affect responses related to the preattentive change detection; rather, task demand will modulate a subsequent response arising from auditory cortex that has been related to the effective orienting of attention towards the novel event.

Materials and method

Subjects.

Seven right-handed male volunteers participated in the experiment. Participants were members of the Hirosaki University (Japan) community, ranging in age from 22 to 38 years. None reported a history of neurological illness, head trauma, auditory impairment, or psychiatric illness. All participants gave written informed consent according to institutional guidelines prior to testing. An audiometric test was administered to each subject before the experimental session, resulting in similar hearing thresholds, all below 40 dB sound pressure level (SPL). All subjects displayed normal or corrected-to-normal visual acuity.

Procedure and stimuli.

Subjects sat in a comfortable armchair in a magnetically shielded room and were presented with an adapted version of a very well-established auditory-visual distraction task (Escera et al., 1998; Escera, Yago, Polo, & Grau, 2000; Escera & Corral, 2007). The task consisted of four blocks of 250 stimulus pairs (trials) delivered at a constant rate of one trial every 1250 ms. Each trial consisted of an irrelevant auditory stimulus followed after 350 ms. (onset-to-onset) by a visual imperative stimulus. The auditory sequence consisted of repetitive standard tones (600 Hz, 200 ms; P = 0.8), occasionally replaced by an environmental novel sound selected from a sample of 100 different exemplars (P = 0.2), such as those produced by a drill, hammer, rain, door, telephone ringing, etc. The novel sounds were digitally recorded, low-pass filtered at 10,000 Hz, and edited to have a duration of 200 ms, including rise and fall times of 10 ms. 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 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 for 200 ms. The probability of appearance was equal for all combinations. Visual stimuli were of white color, subtended a visual angle of 2°x2° at 150 cm from the subject's eyes and were projected on a gray rear-projection screen in front of the subject, via a video projector placed outside the magnetically shielded room. Auditory and visual stimuli were constructed and presented with the software Stim (NeuroScan, Inc).

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 finger 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 MEG 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. 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 one practice block for each condition without any auditory stimuli. To prevent tiredness, a short rest period was allowed after each block.

MEG recordings.

Magnetic responses were collected with a whole-head helmet-shaped 204-channel magnetometer (Neuromag, Ltd., Helsinki, Finland). The MEG signals were collected using a sample rate of 0.6kHz and a band pass filter within 0.1-172Hz. The horizontal electrooculogram (EOG) was recorded simultaneously with the MEG and trials contaminated by eye movements or blinks were rejected. Before the MEG recording, the individual head coordinate system and head surface of each subject was digitally recorded using a 3D digitizer (3Space Fastrak, Inc., Colchester, VT, USA). To determine exact head position with respect to the MEG sensors, four head position indicator (HPI) coils were placed at prefrontal and preauricular sites on the subject’s scalp. At the beginning of each recording block, the position of the subject’s head with respect to the sensor array was determined by feeding current to the coils. The headbased coordinate system was defined by the x-axis passing through the preauricular points (positive to right), the y-axis passing through the nasion, and the z-axis as the vector cross product of the x-unit and y-unit vectors. These coordinates were used for the transformation of the source locations to the Talairach’s standard brain space (Talairach & Tournoux, 1988).

Analysis.

Mean response time (RT) for correct responses and hit rate (HR) were calculated separately for the standard and novel sound trials and WM conditions. Only correct responses in a time window between 150 and 1000 ms were regarded as hits. 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 and RT. Standard trials immediately following a novel trial were excluded from all analyses hereafter.

Event-related magnetic fields in response to standard and novel sounds were analyzed using ASA software (ANT, Germany). On average 7% of each subject’s data were excluded due to artifacts (SD = 0.6%). Responses related to novel sounds were estimated by separately subtracting the average response elicited by the standard stimuli from that elicited by the novel stimuli. In the difference waves, two deflections of MEG activity related to novelty processing were identified. First, an early negative deflection peaking at circa 100 ms from the onset of the novel sound was identified. According to previous studies, this early negativity reflects detection of novelty within the human auditory cortex and is presumably composed of an enhancement of the auditory N1 and a genuine mismatch negativity (MMN) response (Alho et al., 1998; Escera et al., 1998) and will therefore be termed N1/MMNm hereafter. Subsequently to the N1/MMNm, a broad positive deflection peaking at circa 300 ms from sound onset was identified. This response, termed P3am, reflects the effective orienting of attention towards the detected change (Alho et al., 1998).

N1/MMNm and P3am were subjected to source analysis separately for each task condition. Although a variety of source modeling approaches have been proposed, in the current study we decided to use a single-ECD source model (Sarvas, 1987). Alternative algorithms hold many promises as tools for magnetic source localization but have not yet been validated against invasive localization procedures. In contrast, there is currently a wealth of data testifying to the validity of the single-ECD model for reliably localizing and lateralizing neurophysiological activity associated with cognitive functions (Breier, Simos, Zouridakis, & Papanicolaou, 2000; Papanicolaou et al., 2003; Simos et al., 2001). Prior to source modeling, MEG averages were high-pass filtered at 1Hz and low-pass filtered at 40Hz. Two equivalent current dipoles (ECDs) of the N1/MMNm and P3am, one for each hemisphere, were determined by the least-squares method using a spherical head model. A set of 51 channels over temporal cortex of each hemisphere was used for ECD fittings. The ECDs computation was restricted to the 110-180ms latency period for N1/MMNm and to the 180-350ms latency period for P3am. The dipole fit was computed over successive time points within these latency intervals, and the time point in which the solution best explained the dominant source of the deflection is reported as the *fit latency*. The correlation between the recorded measurements and the values calculated using the ECD model was used to assess the goodness-of-fit of the ECD model. Only current dipoles which accounted for >70% of the field variance were accepted for the subsequent analyses.

Differences in ECD locations between components, hemispheres and WM conditions along each (x, y, z) axis, were assessed by means of analysis of variance (ANOVA) including the factors deflection (N1/MMNm, P3am), WM condition (WM0, WM1) and hemisphere (left, right). The values along the x-axis were transformed into absolute values in order to assess hemispheric asymmetries. The nature of interactions between the factors of the ANOVA was clarified by post-hoc comparisons for each hemisphere, component and WM condition. The effects of WM load on dipole strengths and best fit latencies of ECDs were examined by separate ANOVAs for each deflection with the factors WM condition (WM0, WM1) and hemisphere (left, right). In all of the ANOVAs, the Greenhouse-Geisser correction was applied when appropriate, and ε values and corrected p values are reported.

Results

Participants performed a number classification task in two conditions of WM load (WM0 and WM1) while ignoring irrelevant auditory stimulation. The behavioural data (Table 1) showed that the WM1 was more difficult to perform, as reflected in a reduced overall percentage of correct responses in WM1 (F=13.834, p=0.01, η^2=0.697). There were no other significant effects on accuracy. The higher difficulty of the WM1 condition was also confirmed by the response times, as they were longer for WM1 than WM0 (F=95.649, p<0.001, η^2=0.941). In addition, novel sounds resulted in an increase of response time in WM0 (F=11.18, p=0.016, η^2=0.651) but not in WM1 (F=1.12, p=0.331; η^2=157), reflecting distraction by novel sounds only in the WM0 condition.

Table 1. *Behavioral measures*

Hit rate (%)	*Standard*	*Novel*
WM0	95 ± 1	94 ± 1
WM1	85 ± 3	83± 4
Response time (ms)		
WM0	449 ±20	464±16
WM1	493±16	500±19

Hit rate (HR) and response time (RT) for standard and novel trials in WM0 and WM1. Data are presented as means ± standard error of the mean (SEM).

The equivalent current dipoles for N1/MMNm and P3am were successfully modelled in all 7 subjects in both hemispheres and conditions. Table 2 shows the mean best fit latencies, Talairach coordinates and dipole magnitude values for the N1/MMNm component for both hemispheres and conditions. Figure 1 shows source locations on a selected subject's individual anatomy. Talairach coordinates of N1/MMNm dipoles suggest bilateral sources in the superior temporal gyrus (STG) (BA22). There were no significant differences in N1/MMNm ECDs latencies, locations and source strengths between WM conditions. Therefore, modelling of the N1/MMNm fields elicited by novel sounds indicated that responses to novel sounds were similar in both conditions at the early stage of deviance detection (see Fig. 3).

Table 2. *Best fit latencies, Talairach's coordinates and dipoles magnitudes values for N1/MMNm component for both hemispheres in WM0 and WM1 conditions.*

	Hemisphere	***Best Fit Latency [ms]***	***x [mm]***	***y [mm]***	***z [mm]***	***Magnitude [nAm]***
WM0	**L**	121.12 ±5.21	-54.71 ±3.99	-21.49 ±3.16	5.19 ±0.38	23.12 ±8.54
	R	125.25 ±12.23	56.11 ±3.29	-26.11 ±2.19	4.39 ±1.24	23.70 ±6.35
WM1	**L**	124.09 ±11.25	-55.30 ±3.87	-22.86 ±3.59	4.83 ±0.60	25.52 ±7.28
	R	130.17 ±9.65	57.11 ±3.27	-25.87 ±2.75	3.93 ±0.69	22.25 ±4.26

Data are presented as means ± standard deviation (SD)

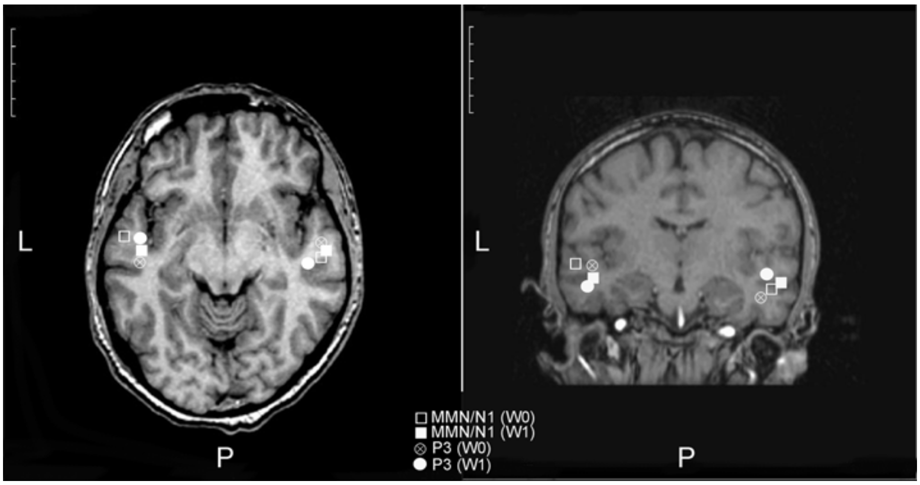

Figure 1*. Anatomic images of sample individual showing the locations of the MMN/N1m and P3am dipoles in both hemispheres for the WM0 and the WM1 conditions.*

Table 3 summarizes the mean values of best fit latencies, Talairach coordinates and dipole magnitudes for the P3am component for both hemispheres in the WM0 and WM1 conditions. Dipole modelling of the

P3am fields elicited to novel sounds also suggested bilateral sources in the STG (BA22, see Fig. 1). It is worth noting that the N1/MMNm and P3am sources were located in neighbouring albeit clearly separated areas in STG in both hemispheres. Figure 2 shows the locations of the N1/MMNm and P3am dipoles of all subjects in a three-dimensional cube covering a restricted region of the temporal lobe in both hemispheres. Location differences between components, hemispheres and conditions along each axis (x, y, z) were tested by means of ANOVA.

Table 3. *Best fit latencies, Talairach's coordinates and dipoles magnitudes values for P3am component for both hemispheres in WM0 and WM1 conditions.*

	Hemisphere	***Best Fit Latency [ms]***	***X [mm]***	***y [mm]***	***z [mm]***	***Magnitude [nAm]***
WM0	**L**	228.43 ±21.37	-51.47 ±3.47	-21.90 ±2.96	6.56 ±0.31	19.87 ±6.11
	R	236.86 ±29.09	52.61 ±3.39	-30.06 ±3.95	2.44 ±0.77	19.10 ±3.33
WM1	**L**	225.29 ±14.60	-48.14 ±2.46	-27.11 ±2.60	5.11 ±0.76	9.58 ±3.11
	R	238.86 ±17.53	53.09 ±5.96	-22.71 ±2.04	4.46 ±0.60	10.96 ±3.25

Data are presented as means ± SD.

A main effect of the deflection factor in the x-axis indicated that the P3am source was located more medial in respect to the N1/MMNm in both hemispheres and WM conditions (F(1,6)=38.184, p=0.001, η^2=0.864; average 4 mm distance). Significant interactions between deflection, WM condition and hemisphere factors were present for both the y-axis (F(1,6)=17.160, p=0.006, η^2=0.741) and the z-axis (F(1,6)=18.480, p=0.005, η^2=0.755). Post-hoc comparisons indicated that in the WM0 condition, the P3am source was located dorsal to the N1/MMNm source (F(1,6)=34.734, p=0.001, η^2=0.853, average 1 mm distance) in the left hemisphere, and more caudal (F(1,6)=7.068, p=0.038, η^2=0.541, average 4 mm distance) and ventral (F(1,6)= 20.229, p=0.004, η^2=0.771, average 2 mm distance) to the N1/MMNm source in the right hemisphere. Furthermore, in the WM1 condition, the P3am ECD was displaced posteriorly along the y-axis

(F(1,6)=19.28, p=0.005, η^2=0.763) in the left hemisphere, and to more rostral and dorsal locations in the right hemisphere (y-axis: F(1,6)=22.241, p=0.003, η^2=0.788; z-axis: F(1,6)=51.505, p<0.001, η^2=0.896).

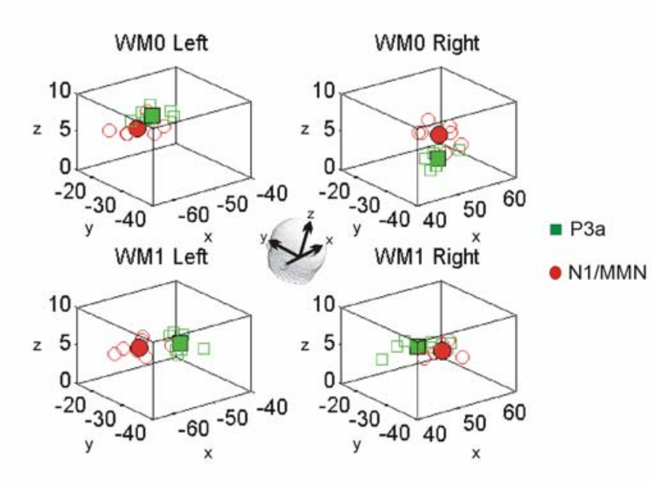

Figure 2. *Locations of N1/MMNm and P3am ECDs for each hemisphere and WM condition. Empty circles and squares indicate individual subjects (n=7), filled circles and squares represent mean location across all subjects. Axis values indicate Talairach coordinates. Cubes cover a reduced area of the temporal lobe comprising STG in each hemisphere.*

Moreover, magnetic responses to novel sounds showed a clear modulation of the P3am dipole moment as a function of WM load. Figure 3 depicts the dipole magnitudes and event-related magnetic field scalp distributions of N1/MMNm and P3am in the two WM conditions. The P3am dipole moment was reduced to half of its magnitude under WM load compared to the no load condition, in both hemispheres similarly (main WM effect: F(1,6)=21.886, p=0.003, η^2=0.785; left hemisphere: 19.87 nAm vs. 9.58 nAm F(1,6)=13.488, p=0.01, η^2=0.692; right hemisphere: 19.1 nAm vs. 10.96 nAm F(1,6)=37.202, p=0.001, η^2=861; no hemisphere or WM x hemisphere effects). There were no significant effects of WM condition or hemisphere on best fit latencies of P3am.

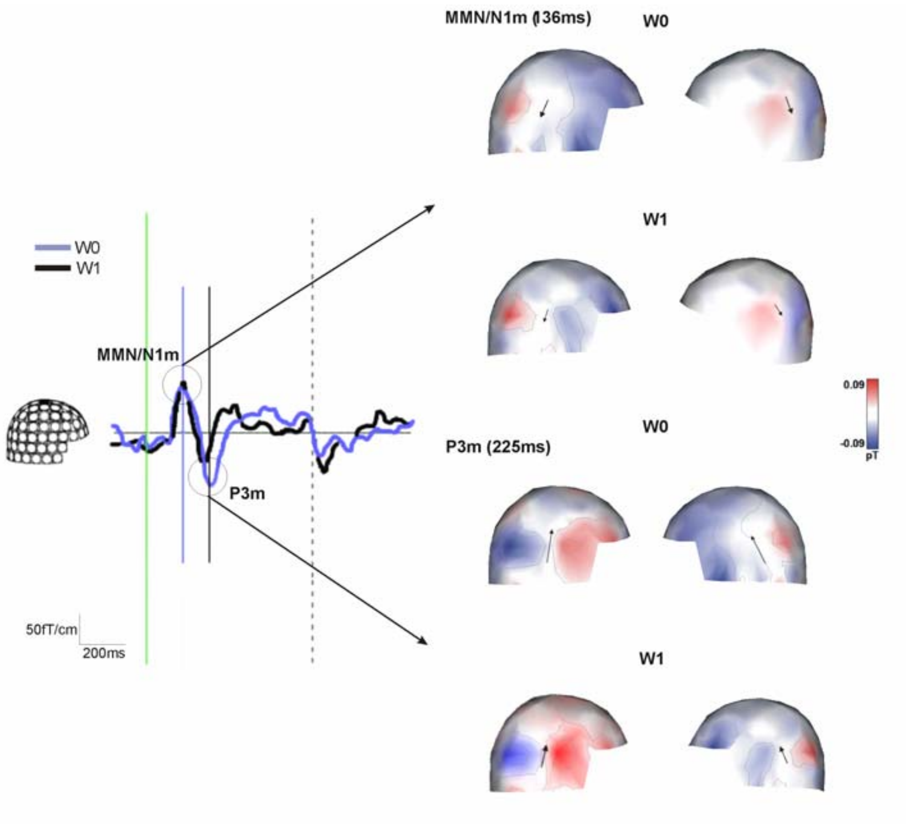

Figure 3. *Left: Novel-Standard event-related field waveforms at a selected sensor position for WM0 and WM1. Right: Fitted dipoles and event-related field scalp distributions for each component. Arrow size indicates dipole magnitudes.*

Discussion

Novel events hold a special status in the human brain as they are prioritized for their entry into awareness through involuntary orienting. However, demanding situations require that attention stays maximally focused on task-relevant information. Attention biases the selection process in such demanding situations, enhancing activation related to relevant representations and inhibiting activation related to irrelevant representations. However, it is unclear how orienting towards novel events that involuntarily capture attention is prevented. The present results replicate previous findings showing that involuntary attention switching to novel sounds is suppressed by task demands (Berti & Schröger, 2003; SanMiguel et al., 2008). Neurophysiologically, the correlate of this suppression was found in reduced activity arising from auditory cortices at circa 230 ms when the visual task required holding information in WM.

Novel sounds accompanied by behavioral distraction resulted in the sequential activation of two adjacent areas in auditory cortex. The initial response, corresponding to N1/MMNm is considered to reflect pre-attentive change detection in the acoustic environment at the level of auditory sensory memory (Näätänen, Gaillard, & Mantysalo, 1978; Näätänen & Alho, 1997). Simple deviance detection appears to be accomplished in the tonotopically organized primary auditory cortex, possibly through stimulus-specific adaptation of single neuron responses (Schonwiesner et al., 2007; Ulanovsky, Las, & Nelken, 2003). In addition, when compared to standard tones, complex novel sounds might also activate non-refractory populations of neurons, resulting in an enhanced auditory N1 response recorded at scalp, and likely contributing to the deviance detection process (Alho et al., 1998).

Subsequent to the N1/MMNm response, the P3am was obtained. This component reflects a more profound evaluation of the change, as it can be influenced by the familiarity or relevance of the deviating stimulus (Escera et al., 2003; Friedman et al., 2001), and is related to the involuntary switch of attention towards the deviating event. The present results suggest, in accordance with previous studies (Alho et al., 1998; Opitz, Mecklinger, Friederici, & von Cramon, 1999), that this response also arises at least partially from auditory cortices. However, studies of patients with cerebral lesions, intracranial recordings in humans and imaging studies suggest that the generation of the P3a engages a largely distributed cerebral network (reviews in Linden, 2005; Ranganath & Rainer, 2003). The areas forming this network are likely implicated in the control of attention and might mediate the involuntary attention shift towards the novel sound and accompanying executive control processes.

The finding that modelling of the N1/MMNm fields elicited to novel sounds yielded no WM modulation on this early attention capture process suggests that the initial change detection system is determined in a bottom-up manner. Although a certain controversy exists on the issue (see e.g., Yucel, Petty, McCarthy, & Belger, 2005a; Yucel, Petty, McCarthy, & Belger, 2005b), the present results are compatible with the view emerging from other studies that suggest that top-down processes do not affect the deviance-detection process itself (Alho, Woods, Algazi, & Näätänen, 1992; Harmony et al., 2000; Muller-Gass et al., 2006; Otten, Alain, & Picton, 2000; Rinne, Antila, & Winkler, 2001; Ritter, Sussman, Deacon, Cowan, & Vaughan, 1999; Sussman et al., 2003) and supports the automatic, bottom-up nature of MMN, confirming that higher-level cognitive processes do not play a role in the MMN generation. This result confirms our hypothesis that although attention can inhibit primary sensory responses in demanding situations (Johnson & Zatorre, 2005; Shulman et al., 1997), the initial detection of potentially relevant events must surpass any early attentional inhibition in order to allow further processing of the relevance of these events.

A modulation of the P3am dipole moment as a function of task demand was found, the P3am dipole moment being smaller under WM load. The current dipole strength is hypothesized to be an indicator of the net strength of cortical activation which reflects the total number of synchronously firing neurons contributing to the stimulus-driven cortical response. Our finding of task demand reducing the current dipole strength implicate either a decrease in the extent or a decrease in the activation of the neuronal population contributing to the signal evoked by novel sounds in STG. These changes in the magnitude of the dipole might have also resulted in a change in its centre of gravity, therefore leading to small location shifts in the WM1 condition.

The reduction of the P3am dipole strength in WM1 indicates that involuntary orienting towards the novel sounds and the consequent disengagement from the visual task was prevented in the demanding task situation by reducing the signal power elicited by the novel sound in auditory cortices, therefore diminishing the chances of this event to gain access to WM and become the focus of attention through competition with the task-relevant representations (Knudsen, 2007). However, this inhibition of responses in auditory cortex only took place at a late stage of processing, likely after a certain amount of semantic analysis of the event had taken place, in order to assess whether issuing an orienting response would be appropriate in the present situation. Possibly, the analysis of the relevance of the novel event might take place in other areas of the widely distributed network that these events activate. Specifically, it has been proposed that such analysis is subserved by inferior frontal gyrus (IFG, Opitz et al., 1999; Tulving, Markowitsch, Craik, Habib, & Houle, 1996), an area that is consistently activated in fMRI studies of novelty responses (Bledowski et al., 2004; Domínguez-Borràs et al., 2008; Downar et al., 2000; Downar, Crawley, Mikulis, & Davis, 2002; Kiehl et al., 2001; Kiehl et al., 2005; Opitz et al., 1999; Strobel et al., 2008; Watkins, Dalton, Lavie, & Rees, 2007).

However, the analysis of the relevance of the novel event might take place also in STG. Although we lack a comprehensive model of the functional organization of auditory cortex, it is known to be organized in several adjacent functional areas, each responding to increasingly more complex features of sounds (Rauschecker, 1998; Read, Winer, & Schreiner, 2002; Scott, 2005; Talavage, Ledden, Benson, Rosen, & Melcher, 2000; Wessinger et al., 2001). Moreover, primary auditory cortex (A1), contrary to primary visual cortex (V1), seems to achieve a more complex level of processing than simple feature extraction, as several important sound features seem to be extracted much earlier, already at the level of subcortical structures (Braun, 1999; Joris, Schreiner, & Rees, 2004; Nelken, 2004; Schreiner & Langner, 1997; Shackleton, Skottun, Arnott, & Palmer, 2003; Wiegrebe & Winter, 2001; Zhang, Tan, Schreiner, & Merzenich, 2003). A great deal of semantic analysis of the sounds seems to take place in auditory areas along superior temporal gyrus (STG) with a progressively increasing level of complexity in each adjacent functionally segregated area. For example, STG areas are progressively more responsive to intelligible speech moving from posterior to anterior locations and extending to superior temporal sulcus (STS, Scott, Blank, Rosen, & Wise, 2000) and separate regions in STG are responsive to both syntactic and semantic violations in sentences (Friederici, Ruschemeyer, Hahne, & Fiebach, 2003). Therefore, auditory areas in STG seem to have sufficient processing capacity to reach a semantic analysis of novel auditory events and in turn assess the relevance of these events after the simple deviance detection process has taken place.

Therefore, we propose that several recurrent loops of activity take place in auditory cortex after the occurrence of a novel sound, each reflected in the N1, MMN and P3a responses respectively. Early attentional modulation of sound processing may inhibit the initial sensory (N1) responses (e.g., Woldorff et al., 1993), however, involuntary orienting is modulated only after the preattentive change detection stage has taken place and is evidenced in a reduced P3am response in the present study. This modulation may be attained via feedback projections from higher processing areas, similarly to mechanisms of attentional modulation that have been described for early visual processing areas (e.g., Saalmann et al., 2007).

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Study IV.

SanMiguel, I., Linden, D., Escera, C. Attention capture by novel sounds: Distraction vs. facilitation. (*submitted*).

Title: Attention capture by novel sounds: Distraction vs. facilitation

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ABSTRACT

Unexpected sounds have been shown to capture attention, triggering an orienting response. However, opposing effects of this attention capture on the performance of a concomitant visual task have been reported, in some instances leading to distraction and in others to facilitation. Moreover, the orienting response towards the unexpected stimuli can be modulated by working memory (WM) load, but the direction of this modulation has been another issue of controversy. In four experiments, we aimed to establish the critical factors that determine whether novel sounds facilitate or disrupt task performance and the modulation of these effects by WM load. Depending on the overall attentional demands of the task, novel sounds led to faster or slower responses. WM load attenuated novel sound effects, independent of their direction (facilitation or distraction). We propose a model by which the unexpected stimuli always generate the same orienting response but result in distraction or facilitation depending critically on the attentional focusing induced by the task at hand and the temporal relationship between the irrelevant and task-related stimuli.

Introduction

The unexpected occurrence of abrupt auditory stimuli or those deviating from an auditory homogenous background capture attention involuntarily as they elicit the orienting response. This response is characterized by at least two components: a "physiological" burst of arousal resulting from a sudden transient increase in reticular activation, and a "psychological" reflexive orienting of attention towards the eliciting stimulus (Näätänen, 1992). Several lines of research have investigated the involuntary orienting response in humans by means of the so-called auditory "oddball" paradigms (Escera, Alho, Winkler, Näätänen, 1998; Escera & Corral 2003; Schröger & Wolff, 1998a, 1998b; Friedman, Cycowicz, Gaeta, 2001). In these oddball paradigms, a homogeneous auditory context is generated by presenting auditory stimuli that follow a specific regular pattern. Once this auditory context is established, its implicit regularity is broken by presenting an unexpected and task-irrelevant deviating sound. The automatic detection of the irrelevant deviation leads to the involuntary orienting of attention towards the eliciting sound. If a task is performed while the irrelevant stimuli occur, the involuntary orienting of attention towards the irrelevant stimulus results in distraction from the current task and thus in a momentary impairment of performance (Escera et al., 1998; Escera, Alho, Schröger, Winkler, 2000; Escera, Yago & Alho, 2001; Escera, Corral, Yago, 2002; Escera, Yago, Corral, Corbera & Nuñez, 2003; Escera & Corral, 2007, Domínguez-Borràs, Garcia-Garcia & Escera, 2008).

However, other lines of research have reported facilitation rather than distraction caused by the occurrence of auditory stimuli. The most straightforward example of auditory stimulus facilitation is when the auditory stimulus acts as a precue that conveys some information about the forthcoming visual stimulus (e.g., its location or time of appearance) (Posner & Petersen, 1990). However, uninformative cues, or even accessory stimuli (auditory stimuli presented at roughly the same time as the visual stimulus) can also facilitate visual task performance. These uninformative stimuli have been shown to shorten RT (Valls-Solé et al., 1995; Hackley & Valle-Inclán, 1998, 1999), increase response force (Stahl & Rammsayer, 2005), enhance the detectability (d’) of a visual stimulus (Stein et al., 1996; McDonald et al., 2000), produce temporal order judgement effects (McDonald, Teder-Sälejärvi, Di Russo, Hillyard, 2005), and shorten the latency of reflexive reactions such as the eye blink reflex to a reflexogenic stimulus (Low, Larson, Burke, Hackley, 1996; Carlsen, Chua, Inglis, Sanderson, et al., 2004).

Irrelevant, attention-capturing sounds can thus have very different effects on the performance of simple visual tasks. It will be the aim of this paper to explore conditions that determine whether distraction or facilitation occurs. A factor that might play a functional role in determining the effects of task-irrelevant, unexpected auditory stimuli is their attentional contingency with the task being performed. Indeed, although involuntary, the orienting response has been proposed to be not fully automatic (Pashler, Johnston, Ruthruff, 2001). The presence and magnitude of the orienting response can be affected by the *attentional or task set*. Previous information about the upcoming stimuli, the current state of cognitive control, or preparation related to the task at hand may all modulate the orienting response towards the distracting stimuli (Pashler, 1998).

A range of experimental results also shows that concomitant cognitive processing produces quantitative modulations of the orienting response (e.g., enhancing or attenuating its magnitude). When participants have to keep information online, responses to distractors may be attenuated. For example, during the performance of an arithmetic task, behavioural distraction elicited by irrelevant novel visual stimuli was reduced with increasing difficulty of the task (Spinks, Zhang, Fox, Gao, Tan, 2004). Furthermore, distraction generated by deviating auditory stimuli was reduced when working memory (WM) demands were imposed in a simple classification task (Berti & Schröger, 2003; SanMiguel, Corral, Escera, 2008). However, there is also ample evidence for the opposite effect of WM load on distraction. When participants performed a selective attention task during the delay of a WM task, distraction by an attention-capturing visual stimulus was enhanced with increasing WM load in a number of studies (De Fockert, Rees, Frith, Lavie, 2001; Lavie & De Fockert, 2005; Lavie, 2005; Lavie, Hirst, De Fockert, Viding, 2004). The conflict between distraction enhancement and distraction attenuation by WM load has so far not been resolved.

Two main questions arise from the findings summarized above and were addressed in the present study. First, there is evidence that similar irrelevant, non-informative auditory stimuli facilitate performance of simple visual tasks in some instances but have a distracting effect in others. Therefore, the series of experiments to be reported here was aimed at establishing the critical factor(s) that more directly determine the direction of the effects that irrelevant novel sounds have on visual task performance. The second aim of the present study was to test the effects of WM load on involuntary orienting. Several studies have shown that WM load modulates the effects of attention-capturing, irrelevant stimuli, but the direction of this effect (attenuation or enhancement) has remained a matter of some controversy. We therefore manipulated WM load in the present tasks and expected to find a quantitative modulation of the distracting or facilitating effects.

In order to achieve these purposes, in Experiments 1 and 2 we manipulated the type of WM task used and the type of comparison between WM conditions, as possible variables influencing the direction of the modulation effects of WM load on involuntary orienting. In Experiment 2 we directly contrasted conditions leading to distraction and conditions leading to facilitation, and we manipulated the position of the sounds in respect to the task stimuli to assess the influence of their temporal relationship. In Experiment 3, we tested whether the implicit predictive value of the irrelevant auditory stimuli is responsible for the distraction effect. Finally, in Experiment 4, we tested whether task demand determines the direction of the effects of irrelevant auditory stimuli on performance.

EXPERIMENT 1

Specific goals: There is an unresolved controversy in the literature between studies showing enhancement of distraction by WM load and those showing the opposite effect, i.e., attenuation of distraction by WM load. The paradigms differ across studies in a number of factors that might play an important role in determining the direction of the effects reported. Thus, to better understand the reasons of these discrepancies, the aim of the present experiment was to replicate the previously described auditory novelty distraction effects and their attenuation by WM load (SanMiguel et al. 2008, Berti & Schröger, 2003) in a similar setting to where distraction enhancement was found elsewhere (De Fockert et al., 2001; Lavie & De Fockert, 2005; Lavie, 2005; Lavie et al. 2004). In the present experiment, we used a delayed memory recognition paradigm rather than an n-back task, to rule out the possibility that the type of WM task used determined the direction of the modulating effects of WM on distraction.

Previous studies on the effects of WM load on attention capture have employed different types of comparisons across WM conditions. Whether the type of comparison employed between conditions is of a quantitative (low WM load vs. high WM load) or qualitative (no WM load vs. WM load) nature may also play an important role in determining the results. Comparing a condition without WM load to a condition with WM load will provide information about how involving the WM system affects the processing of irrelevant stimulation. However, a parametric manipulation of the amount of load will only provide information about the effects of the amount of information to be held in WM, which is not necessarily the only function of the WM system (Baddeley, 2003). Thus, both qualitative and quantitative comparisons were used in the present experiment, aiming to elucidate possible differences in the results obtained with each type of comparison.

Methods: Nine healthy students of the University of Wales Bangor and five healthy students of the University of Barcelona (18-39 years; mean age 22.4; 5 male) participated in the experiment. One participant abandoned the task and thus the corresponding data was eliminated. Participants gave informed consent after the nature of the experiment was explained to them and either received course credits or were reimbursed for their participation in all experiments hereafter. They were presented with an auditory-visual working memory task with three conditions of WM load: no-load, load-1 and load-3. Trials corresponding to the load-1 and load-3 conditions were randomized within the same block, whereas the no-load condition was presented in a separate block. All participants performed the no-load condition first, in order to be equally familiarized with the stimuli prior to performing the conditions involving memory of the same stimuli. Each trial (Figure 1) consisted of an initial black fixation cross for 1.2 s, which then turned red for 1s. This was followed by the encoding array presented for 2 s, consisting of four images organized around a black fixation cross, which could either be three different faces and a scrambled image in the load-3 condition, one face and three scrambled images in load-1, or four scrambled images in the no-load condition. Faces were randomly selected from a set of six black and white male faces (Ekman & Friesen, 1976) and eight scrambled images, and their location among the four possible positions was randomised. A one second retention interval was presented after the encoding array and finally a target face in the load-1 and load-3 conditions (or a target stimulus which could be alternatively a face or scrambled image in the no-load condition) was presented for 2 s. The total trial length was

7.2 s. Only responses within 900 ms from the target stimulus were accepted. In the load-1 and load-3 conditions participants had to indicate, as accurately and fast as possible, whether the target face was present or absent on the encoding array; in the no-load condition, they had to indicate whether the target stimulus was a face or a scrambled image. Participants responded by pressing either one of two response buttons with the index and middle finger of the preferred hand. Half of the trials in the load-1 and load-3 conditions had a face present in the encoding array whereas the other half did not. In the no-load condition, half of the trials had a face and half of them a scrambled image. Auditory stimuli were presented through headphones along the whole duration of each trial, with a stimulus onset asynchrony (SOA) of 1.2 s. These auditory stimuli were either repetitive “standard” (STD) tones (600 Hz, 200 ms) or environmental novel (NOV) sounds of 200 ms length selected from a sample of 100 different exemplars, such as those produced by a drill, hammer, rain, door, telephone ringing, etc (see Escera et al., 1998, 2003 for technical details of novel sounds). Fifty percent of the trials had only standard tones, in the number of six, and were therefore called “standard” trials. The remaining trials were called “novel”, as they contained five standard tones and one novel sound, so that the actual probability of a novel sound was p=1/12. The novel sound in these latter trials was presented 300 ms prior to the target stimulus (the “test” position). Randomly, one out of nine trials was a “catch trial” in which the novel sound was presented at a different position, 300 ms after the start of the encoding array, to avoid predictability. Each condition consisted of 150 trials and the total duration of the experiment was 60 minutes, allowing for pauses every 3.5 minutes. Ten practice trials were performed before the start of each condition.

General analysis procedure. In all further experiments, mean response time (RT) for correct responses and hit rate (HR) were calculated separately for the different auditory stimulus type trials and task conditions. Effects caused by auditory stimulus type and task condition effects were analyzed by means of repeated measures analysis of variance (ANOVA) with the type of auditory stimulus and specific task condition as factors, performed on HR and RT. Subsequent paired comparisons were performed whenever needed to clarify the origin of interactions found on the main analysis. Greenhouse-Geisser correction was applied whenever suited and corrected p values are reported.

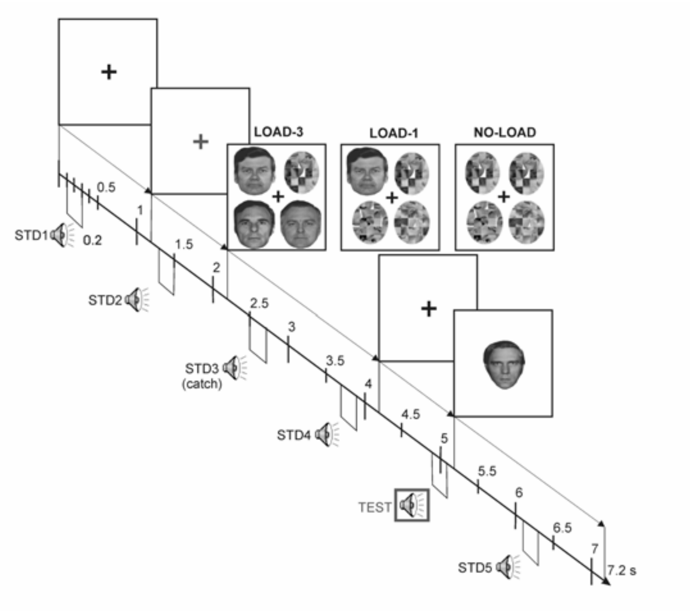
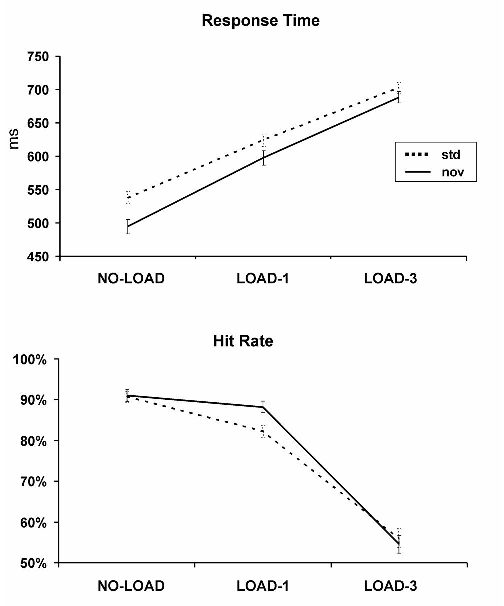


Figure 1. Trial structure of Experiment 1. STD: standard auditory stimulus, TEST: test auditory stimulus (50% novel/standard). In the no-load condition participants responded whether the target stimulus presented was a face or a scrambled image. In load-1 and load-3 participants responded whether the target face presented was present in the encoding array or not.

Results: The repeated measures ANOVA on RT with WM load (no-load, load-1, load-3) and auditory stimulus type (novel, standard) as factors revealed a main effect of WM load (F(2,24)=105, p<0.001, ε=0.756, η^2=0.897) (Figure 2). RT increased with increasing load. There was also a main effect of auditory stimulus type (F(1,12) = 36, p< 0.001, η^2=0.751), due to shortened RT (facilitation) in novel sound trials. Moreover, we found a significant WM load x auditory stimulus type interaction (F(2,24)=4.6 p=0.022, ε=0.98, η^2=0.276). Paired comparisons revealed that the facilitation effect was significant in the no-load (F(1,12)=51.61, p<0.001, η^2=0.811) and load-1conditions (F(1,12)=9.54, p=0.009, η^2=0.443), and showed a trend to significance in the load-3 condition (F(1,12)=5.68, p=0.051, η^2=0.281). However, the facilitation effect was smaller with WM load and it differed significantly between the no-load and the load-3 conditions (F(1,12)=8.62, p=0.012, η^2=0.418). The magnitude of the facilitation effect did not differ significantly between no-load and load-1 and between load-1 and load-3.

Figure 2*. RT and HR in the no-load, load-1 and load-3 conditions for novel and standard trial types in Experiment 1. Bars indicate standard error of the mean (S.E.M.).*



The repeated measures ANOVA on HR revealed a main effect of WM load (F(2,24)= 45, p<0.001, ε=0.667, η^2=0.791) (Figure 2). HR decreased progressively with load. There were no main auditory stimulus type effects but there was a significant WM load x auditory stimulus type interaction (F(2,24)= 5.263, p=0.013, ε=0.977, η^2=0.305). Paired comparisons revealed that this interaction was due to a higher HR (facilitation) in novel sound trials only in the load-1 condition (F(1,12)=11.7, p=0.005, η^2=0.494).

Discussion: Novel sounds facilitated task performance as opposed to the distraction effects of novel sounds reported in several previous studies with other types of working memory tasks (SanMiguel et al., 2008, Berti & Schröger, 2003) and other non-mnemonic tasks such as number classification (Escera et al., 1998). This suggests that task settings dramatically determine the effects of irrelevant sounds on performance. Interestingly, this facilitation effect was of large magnitude when the task required no WM, whereas imposing WM load on the task reduced the effect without making it disappear totally (Figure 2). The effects were similar when comparing no WM vs. WM conditions and when comparing low WM load vs. high WM load conditions. Thus WM load had a graded effect on the facilitation that was similar to the effects of WM load on distraction reported previously (SanMiguel et al., 2008, Berti & Schröger, 2003), but in the opposite direction.

In the subsequent experiments we investigated the nature of this novel sound facilitation effect and the critical factors in the relationship between the task-irrelevant auditory stimuli and the current attentional or task set that determine the direction (facilitating vs. distracting) of the irrelevant novel sound effects as well as their modulation. In Experiment 2, the same participants performed the task leading to novel sound facilitation and a control task in which the typical distraction effect by novel sounds was expected, to allow for a direct comparison of the effects.

EXPERIMENT 2

Specific goals: In the present experiment, we aimed at obtaining the two opposed novel sound effects (facilitation and distraction) in the same session and for the same participants. We therefore compared the task used in Experiment 1, with minor variations, to a control condition in which only the trial structure was varied while keeping the auditory-visual task stimulus relationship and the task instructions (the simple classification task of the no-load condition) equal. This control condition also allowed us to relate the present experiments to previous studies in which distraction was elicited by novel sounds. We hypothesized that with this simplified trial structure, a distraction effect by novel sounds should be observed as previously described (Escera et al., 1998).

A second aim of the present experiment was to test the role of the specific temporal relationship between the irrelevant stimuli and the task-relevant stimuli. For this purpose, we manipulated the position of the novel sound within the auditory sequence and in respect to the delayed recognition task. At least three phases can be differentiated within the delayed recognition task according to the cognitive operations being performed: encoding, retention and retrieval. We hypothesized that the facilitation or distraction effects of novel sounds would depend on the specific phase of the task in which they are presented, as the attentional set differs between the phases.

Methods: Eight healthy students of the University of Wales Bangor and five healthy students of the University of Barcelona (17-47 years; mean age 21.8; 3 male) participated in the present experiment. One participant was eliminated due to a very low HR on the task, and one of the participants only performed the three experimental conditions. The experiment consisted of a block of three experimental conditions and a control condition performed in counterbalanced order across participants. The three experimental conditions (no-load, load-1 and load-3) were the same as described in Experiment 1 (see methods for Experiment 1 for further details), but the timing of the trial was slightly modified to introduce a novel sound 300 ms prior to the encoding phase on 1/3 of the trials. Each trial in the three experimental conditions (Figure 3) consisted of an initial black fixation cross for 1 s, which then turned red for 600 ms. The red fixation cross was followed by the encoding array presented for 2.3 s. After the encoding array, a 1.3 s retention interval was introduced. Finally a target face in the load-1 and load-3 conditions, or a target stimulus which could be alternatively a face or a scrambled face in the no-load condition was presented for 2 s. The total trial length was thus 7.2 s, as in Experiment 1. Auditory stimuli were presented through headphones every 1200 ms. Three types of trials were defined depending on the type of auditory stimuli presented and their position in respect to the delayed memory recognition task. One third of the trials were standard trials containing six standard tones, one third were encoding novel (nov-E) trials, in which a novel sound was presented 300 ms prior to the encoding array and the remaining five auditory stimuli were standard tones, and finally one third of the trials were retrieval novel (nov-R) trials, in which a novel sound was presented 300 ms prior to the target stimulus and the remaining five auditory stimuli were standard tones. The overall probability of a novel sound in the experimental conditions was thus p=11%. Each experimental condition consisted of 225 trials and the total duration of this block was 84 minutes, allowing for pauses every 3 or 4 minutes. The response window was 900 ms. Ten practice trials were administered before the start of each condition.

In the control condition, participants performed a visual discrimination task (Figure 3) in which they had to respond as accurately and fast as possible whether the target stimulus presented at the centre of the screen was a face or a scrambled image by making the corresponding button press with the index and middle finger of the preferred hand. Response buttons were counterbalanced across participants. Half of the trials were faces and the remaining half were scrambled images, arranged in random order. Each trial lasted 1.1 s. Only responses within 800 ms from the presentation of the visual stimulus were accepted. In each trial, either a standard tone (p=0.8) or a novel sound (p=0.2) was presented through headphones 300 ms before the visual stimulus. Auditory and visual stimuli were identical to those used in Experiment 1 and in the experimental conditions of the present experiment, and lasted 200 ms. Total duration of the control condition was 7 min., divided into three blocks allowing a short rest between blocks. The first four trials of each block were always standard tone trials, and standard tone trials immediately following a novel sound trial were automatically discarded from any analysis. All participants performed ten practice trials without sounds before the start of the control condition.

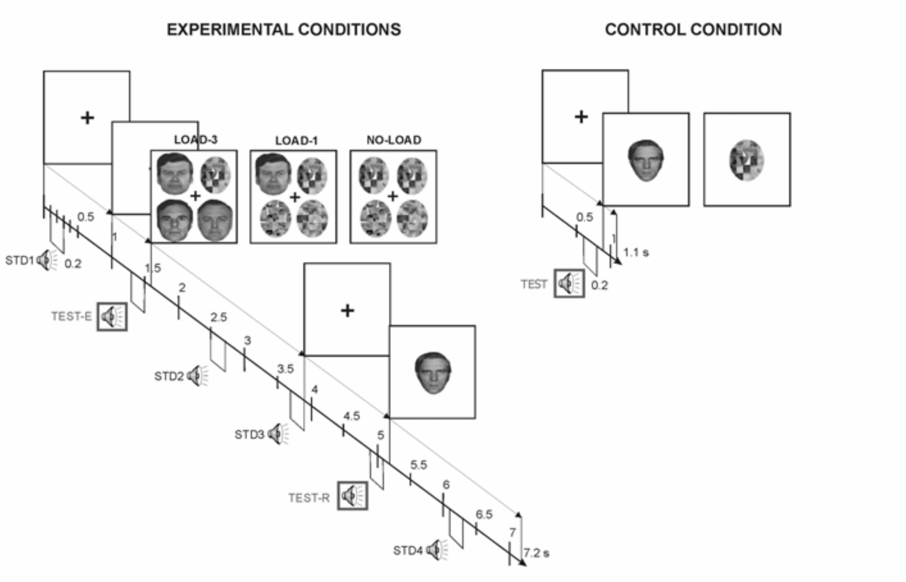


Figure 3. *Trial structure for Experiment 2. STD: standard auditory stimulus, TEST: test auditory stimulus (novel/standard) at encoding (TEST-E) and retrieval (TEST-R). In the no-load experimental condition and in the control condition participants responded whether the target stimulus presented was a face or a scrambled image. In the experimental conditions load-1 and load-3, participants responded whether the target face presented was present in the encoding array or not.*

Results:

Experimental conditions

The ANOVAs performed on RT and HR including WM load (no-load, load-1, load-3) and auditory stimulus type (Std, Nov-E, Nov-R) as factors showed main effects of WM load on HR and RT (Figure 4). RT increased progressively with increasing WM load ($F(2,22)=80$, $p<0.001$, $\varepsilon=0.662$, $\eta^2=0.880$) and HR decreased progressively ($F(2,22)=58.7$, $p<0.001$, $\varepsilon=0.577$, $\eta^2=0.842$). Further effects were present in the ANOVA for RT measures. There was a main effect of auditory stimulus type ($F(2,22)=29.5$, $p<0.001$, $\varepsilon=0.960$, $\eta^2=0.728$) on RT, and a significant interaction between WM load and auditory stimulus type ($F(4,44)=8.1$, $p<0.001$, $\varepsilon=0.730$, $\eta^2=0.423$). Therefore, subsequently, the effects on RT of encoding and retrieval novels were analysed separately against the standard trials in each WM condition. Encoding novels (nov-E in Figure 4) had a distracting effect in the no-load condition (F(1,11)=8.4, p=0.014, η^2=0.434). RT to target stimuli was increased after the occurrence of a novel sound during the “encoding” phase (note, however, that no encoding was required in the no-load condition). The apparent RT increase in load-1 was non-significant (average 9 ms increase, F(1,11)=2.7, p=0.1, η^2=0.195) and there was no effect of encoding novels in load-3.

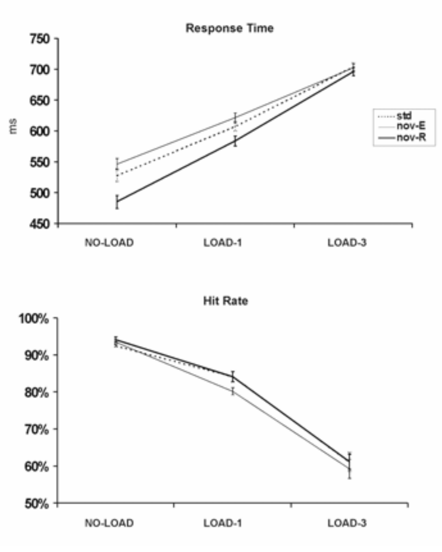


Figure 4. *RT and HR in standard, novel-E (encoding) and novel-R (retrieval) trials for the no-load, load-1 and load-3 experimental conditions in Experiment 2. Bars indicate S.E.M.*

Facilitation effects caused by retrieval novels (nov-R in Figure 4) roughly replicated those of Experiment 1. There was a significant facilitation effect in the no-load condition (F(1,11)=74.9, p<0.001, η^2=0.872) and in the load-1 condition (F(1,11)=8.3, p=0.015, η^2=0.430) (Figure 4). The facilitation effect was reduced and failed to reach significance in load-3 (F(1,11)=3.1, p=0.1, η^2=0.222). Neither encoding nor retrieval novels had any significant effects on HR to target stimuli.

Control condition

The ANOVA performed on HR and RT contrasting novel sound and standard tone trials showed that participants were distracted by the novel sounds (Figure 5). This was reflected in an increased RT in novel compared to standard trials (F(1,10)=5.2, p=0.045, η^2=0.343). No differences in HR were found between standard and novel trials (F(1,10)=0.015, p=0.9).

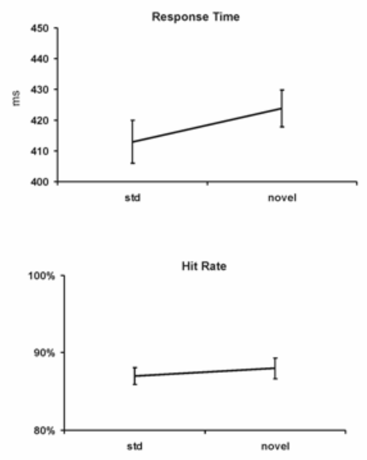


Figure 5*. RT and HR for standard and novel trials in Experiment 2, control condition. Bars indicate S.E.M.*

Discussion: In the experimental conditions, the facilitation effects caused by novel sounds presented before the target stimulus (Nov-R) were similar to those found in Experiment 1 (Figure 4). Novel sounds in this phase reduced RT to the target stimuli, and this facilitation effect was attenuated with WM load. Encoding novels, however, had the opposite effect, as they increased RT to the target stimuli in the no-load condition. Neither encoding nor retrieval novels had an effect on HR. The opposite effects found for encoding and retrieval novels show that the specific temporal relationship between the auditory stimuli and the task at hand plays a key role in determining the direction of the auditory stimulus effects.

However, it is possible that novel sounds at the encoding phase (Nov-E) still had the same facilitation effect as when they were presented shortly before the target (Nov-R), but the temporal distance between the novel sound and the target stimulus resulted in the facilitation effect being lost and even reverted. The facilitation effect is probably due to the alerting component of the orienting response, resulting in a non-specific state of readiness to respond. However, an optimal state of preparation cannot be maintained indefinitely and would probably not last until the time when a response was required, 3.6 seconds later (Los & Schut, 2008). On the contrary, after a period of optimal preparation to respond, an inhibition of the prepared response has been reported under different circumstances. For example, somatic reflexes elicited by a reflexogenic stimulus appear to be facilitated by a warning signal presented up to 500 ms prior to that stimulus. However, the reflex is inhibited if the warning precedes the reflexogenic stimulus by more than 500 ms (Scheirs & Brunia, 1985, reviewed in Requin, Brener, Ring, 1991). A similar phenomenon in visual attention has been termed inhibition of return (IOR: Posner, Rafal, Choate, Vaughan, 1985). IOR refers to a small impairment of performance after a momentary facilitation on a detection or discrimination task. The initial facilitation, lasting approximately 300 ms, is caused by a cue providing information on the upcoming target. IOR is a robust effect for approximately 3 s after cue presentation and appears to disappear after this point. This limit however, varies as a function of how it is measured (Samuel & Kat, 2003). Also, it has been demonstrated that IOR is a supramodal phenomenon (Spence, Lloyd, McGlone, Nicholls, Driver, 2000). Thus, the apparent distraction by novel sounds presented at the encoding phase could be due to a similar inhibition mechanism after an initial facilitation period. The effect found for novel sounds presented during the encoding phase was reduced to the point of becoming non-significant under WM load. This is congruent with the similar attenuation by WM load found on the facilitation effects when novel sounds were presented shortly before the target.

The results of the control condition show that when the trial structure was simplified, the effect of the irrelevant novel sounds on task performance was reverted for the same subjects, paralleling the well-established distraction effect of previous related studies (Escera et al., 1998, 2000, 2001, 2002, 2003; SanMiguel et al., 2008). This discards the possibility of the facilitation effect being specific to the face classification task, and it shows that some yet undefined specific characteristic of the delayed memory recognition trial structure prompts facilitation as opposed to distraction. With the subsequent experiments we thus aimed to identify more specifically the critical factors that determine the direction of the novel sound effects whenever the auditory stimuli are presented shortly before a target stimulus. We considered the following variables, which differed between the memory tasks of experiments

1 and 2 and previous studies: *predictive value of the auditory stimulus in respect to the target stimulus* (present in the distracting task but not in the facilitating task), *target stimulus duration* (very short in the distracting task - 200 ms- and much longer in the facilitating task -around 2 s-), and trial duration, which also implies *event rate* (short trial: 1200 ms in the distracting task, and thus higher event rate; long trial: of about 6-7 s in the facilitating task, and thus lower event rate). The first variable was investigated in Experiment 3 and the two latter ones in Experiment 4.

EXPERIMENT 3

Specific goals: There is one critical difference between Experiment 1 and the experimental conditions of Experiment 2, where novel sounds presented shortly before the target stimulus yielded facilitation, and the control condition of Experiment 2, where they induced distraction. In this latter condition, all auditory stimuli always appeared with an unequivocal temporal relation to the task stimuli: an auditory stimulus was presented always and only 300 ms before the target stimulus. Therefore the auditory stimuli had a predictive value and most probably, participants made use of them as a warning signal to prepare for the subsequent stimulus requiring a response (Escera et al., 1998, 2003). An unexpected change in this warning signal may thus have resulted in distraction. In the conditions that yielded facilitation, however, the irrelevant auditory stimuli and the task stimuli did not hold this strict temporal relationship. Here, the occurrence of an auditory stimulus was not predictive of the subsequent task stimuli, since auditory stimuli occurred throughout the trial, apparently holding no relation to the task. Consequently, we designed a further experiment to test whether the predictive value of the auditory stimulus in relation to the target stimulus accounts for the difference in the direction of the auditory stimulus effects. We imposed a predictive value to the auditory stimulus in respect to the target stimulus in the memory task by presenting auditory stimuli exclusively before the target stimulus, eliminating all the remaining auditory stimuli. A control no-sound condition was introduced to control for sound effects, irrespective of novelty.

Methods: Eleven healthy students of the University of Barcelona participated in the present experiment (18-22 years; mean age 19.8, all female). One participant's data was eliminated due to a very low HR on the task. A modification of the task used in Experiment 1 was employed in the present experiment, including the three WM load conditions (no-load, load-1, load-3). Additionally, as a control condition, the same task was performed without any auditory stimuli in a separate block. The order of the sound and no sound blocks, as well as the order of the WM load conditions within each block, was counterbalanced across participants. The timing of the trial was slightly modified in order to present a single auditory stimulus in each trial, providing a predictive value to it. Each trial (Figure 6) consisted of an initial black fixation cross for 1 s, which then turned red for 0.6 s. This was followed by the encoding array presented for 2 s. A one second retention interval was presented after the encoding array and finally a target face in the load-1 and load-3 conditions (or a target stimulus which could be alternatively a face or scrambled image in the no-load condition) was presented for 2 s. Therefore the total trial length was 6.6 s. Participants responded whether the target face was absent or present in the encoding array in the load-1 and load-3 conditions and they responded whether the target stimulus was a face or a scrambled image in the no-load condition as accurately and fast as possible. Only responses within 900 ms from the presentation of the visual target stimulus were accepted. In the block in which auditory stimuli were presented, either a standard tone (p=0.7) or a novel sound (p=0.3) was presented through headphones 300 ms before the visual stimulus (the "test" position) on each trial. Auditory stimuli and visual stimuli were identical to those used in Experiments 1, 2 and 3 and had a duration of 200 ms. Each load condition consisted of 100 trials and the total number of trials was 600, half of them with auditory stimuli and the other half without. The total duration of the experiment was 72 minutes, allowing for pauses every 4 minutes. Ten practice trials were performed before the start of each condition.

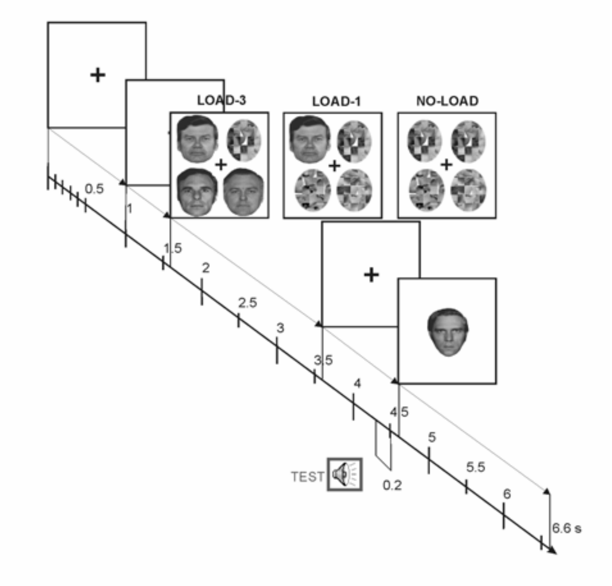


Figure 6. *Trial structure of Experiment 3. TEST: test auditory stimulus (novel/standard). In the no-load condition participants responded whether the target stimulus was a face or a scrambled image. In the WM conditions load-1 and load-3, participants responded whether the target face presented was present in the encoding array or not.*

Results: The repeated measures ANOVA on RT revealed a main effect of WM load (no-load, load-1, load-3) ($F(2,20)= 56.2$, $p<0.001$, $\varepsilon=0.749$, $\eta^2=0.849$). RT increased progressively with load (Figure 7). Both novel sounds and standard tones facilitated (shorter RT) with regard to the no-sound condition in the no-load condition (NOV: $F(1,10)=8.4$, $p<0.016$, $\eta^2=0.458$; STD: $F(1,10)=12.2$, $p<0.006$, $\eta^2=0.550$). In load-1 and load-3, only novel sounds facilitated significantly (load-1: $F(1,10)=10,9$, $p<0.008$, $\eta^2=0.520$; load-3: $F(1,10)=14.1$, $p<0.004$, $\eta^2=0.585$). Facilitation by standard tones failed to reach significance in these conditions (load-1: $F(1,10)=1.6$, $p=0.2$; load-3: $F(1,10)=2.9$, $p=0.1$). RT in novel sound trials was significantly decreased in comparison to standard tone trials as well in load-1 and load-3 (load-1: $F(1,10)=13.4$, $p=0.004$, $\eta^2=0.573$; load-3: $F(1,10)=9.7$, $p=0.011$, $\eta^2=0.493$). RT in novel sound trials did not differ significantly from that of standard tone trials in the no-load condition.

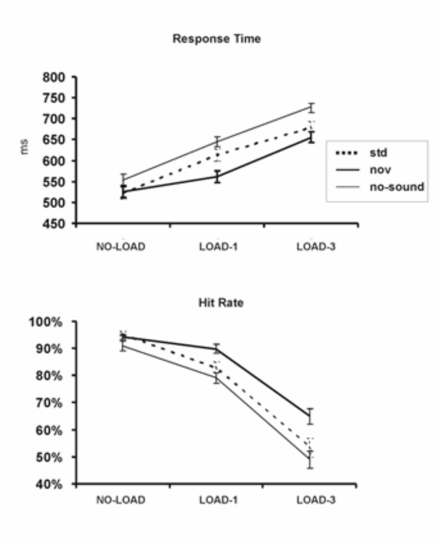


***Figure 7**. RT and HR in the no-load, load-1 and load-3 conditions for no-sound, novel and standard trial types in Experiment 3. Bars indicate S.E.M.*

The repeated measures ANOVA on hit rate (HR) revealed a main effect of WM load ($F(2,20)=46.6$, $p<0.001$, $\varepsilon=0.730$, $\eta^2=0.823$): HR progressively decreased with WM load (Figure 7). Also, a main effect of auditory stimulus type was found ($F(2,20)=7.4$, $p=0.01$, $\varepsilon=0.738$, $\eta^2=0.425$), as well as a marginally significant interaction between the two factors ($F(4,40)=3$, $p=0.059$, $\varepsilon=0.611$, $\eta^2=0.231$). Paired comparisons revealed that there was a facilitation effect by novel sounds respect to the no-sound condition in load-1 ($F(1,10)=15.9$, $p=0.003$, $\eta^2=0.614$) and load-3 ($F(1,10)=11$, $p=0.008$, $\eta^2=0.524$). HR in novel sound trials was also significantly larger than HR in standard tone trials in load-1 ($F(1,10)=5.2$, $p=0.046$, $\eta^2=0.341$) and load-3 ($F(1,10)=12.9$, $p=0.005$, $\eta^2=0.563$). Standard tones had no effect on HR.

Discussion: The presence of auditory stimuli (both standard and novel) generally facilitated performance in the task. This replicates previous findings (Escera et al., 2000; Escera & Corral, 2007). Facilitation by standard auditory stimuli however was only significant in the no-load condition. Novel sounds facilitated in all WM load conditions and this facilitation effect did not differ from that of standard auditory stimuli in the no-load condition. The facilitation effects found here are composed of two different effects. First, the presence of the auditory stimulus (both standard and novel) acted as a warning signal for the upcoming visual stimulus, as it was unequivocally related to it. Second, the sudden occurrence of the auditory stimulus (of any type) also leads to an orienting response towards it, and thus it has a non-specific alerting component. Here probably both standard and novel sounds generated this orienting response, as the distance between one auditory stimulus and the next was of 6.6 s. Additionally, novel sounds should generate a novelty response resulting from a mismatch between the trace (the repeating standard auditory stimuli) and the present stimulus. Here, the trace of the standard auditory stimuli might have been lost or attenuated due to the long silent periods between one auditory stimulus and the next, and thus this novelty response might have been attenuated. However, any differences found between the effects generated by the standard tones and the novel sounds could still be due to a difference in general sound energy, the novel sounds covering a wider range of spectral frequency than the standard tones. In the no-load condition, both standard tones and novel sounds facilitated equally. Most probably, as both novel and standard tones acted as a similar warning and alerting signal, the facilitation effect was at ceiling and thus no novelty effect, that is, no difference between standard tones and novel sounds, was apparent here. In the load-1 and load-3 conditions, only novel sounds facilitated, while facilitation by standard tones failed to reach significance. As in the previous experiments, this indicates that imposing WM load attenuated the processing of the auditory stimuli. Thus, possibly more stimulus energy was needed here in order for the auditory stimulus to produce any effect, and therefore only novel sounds facilitated in conditions of WM load. Most importantly, the facilitation effect was not eliminated, nor did it revert when auditory stimuli had a predictive value in relation to the target stimulus. Experiment 3 thus showed that the predictive value of auditory stimuli is not the crucial factor in determining the direction of the novelty effect.

EXPERIMENT 4

Specific goals: Experiment 3 discarded the possibility that the predictive value of the auditory stimuli in relation to the target stimuli was the critical variable determining the distraction effect of the auditory stimulus. However, there was a second important factor that differed between tasks with distraction by novel sounds and those with facilitation. In the experiments leading to facilitation a much less demanding task, with longer trials and thus a lower event rate was used. Also, the duration of the target stimuli was significantly longer in this task. Indeed, in simple tasks leading to distraction by irrelevant deviating stimuli, RT is typically in the order of 400-500 ms (see Escera & Corral, 2007 for a review), whilst here, where facilitation was found, a much slower pace was induced by the task (RT in the order of 500-700 ms in Experiments 1-3). We thus designed a further experiment to test whether target stimulus duration or trial length were the critical factors in determining whether the novel sounds result in distraction or facilitation. We employed the simple trial structure of the control condition of Experiment 2, in which distraction was found, and manipulated trial duration and target stimulus duration. We hypothesized that the amount of task demand determined the direction of the novel sound effects, with higher demands leading to distraction. Therefore, we expected to observe facilitation or distraction, depending on our manipulations of event rate and target stimulus duration.

Methods: Twelve healthy students of the University of Barcelona participated in the present experiment (18-32 years; mean age 23.9, 4 male). As in Experiment 3, they were presented with a visual discrimination task (Figure 8) in which they had to respond as accurately and fast as possible whether the image presented at the centre of the screen was a face or not by making the corresponding button press with the index and middle finger of the preferred hand. Response buttons were counterbalanced across participants. Randomly, in half of the trials there was a face and in the other half there was a scrambled image. Only responses within 800 ms from the presentation of the visual target stimulus were accepted. The total duration of the experiment was 25 min, divided into 4 different condition blocks: Short trial-Short face; Short trial-Long face; Long trial-Short face and Long trial-Long face, allowing a short rest between conditions. Visual stimulus duration was 200 ms in the “short face” conditions and 700 ms in the “long face” conditions. SOA for the visual stimuli was 1500 ms in short and 4500 ms in long trials. In both long and short trials auditory stimuli were presented every 1500 ms, thus, one auditory stimulus was presented in each short duration trial and three auditory stimuli in each long duration trial. The overall probability of appearance of a novel sound was of p=0.17 in both short and long trial duration conditions. Thus in the short trial condition, either a standard tone (p=0.83) or a novel sound (p=0.17) was presented 300 ms before the visual target stimulus (“test” position). Standard trials immediately following a novel trial were excluded from the analysis in this condition. In the long trial conditions, 50% of the trials were standard trials (containing three standard tones), 35% were novel trials (a novel sound was presented 300 ms prior to the visual stimulus –the “test” position-, and two standard tones at the other two positions) and 15% were catch trials, which also contained a novel sound and two standard tones. However, in the catch trials, the novel sound was not presented at the “test” position but randomly at any of the other two positions. Catch trials were introduced to avoid predictability and were excluded from all analyses. All condition blocks started with 6 standard tones. All participants performed ten practice trials without auditory stimuli before the start of each condition.

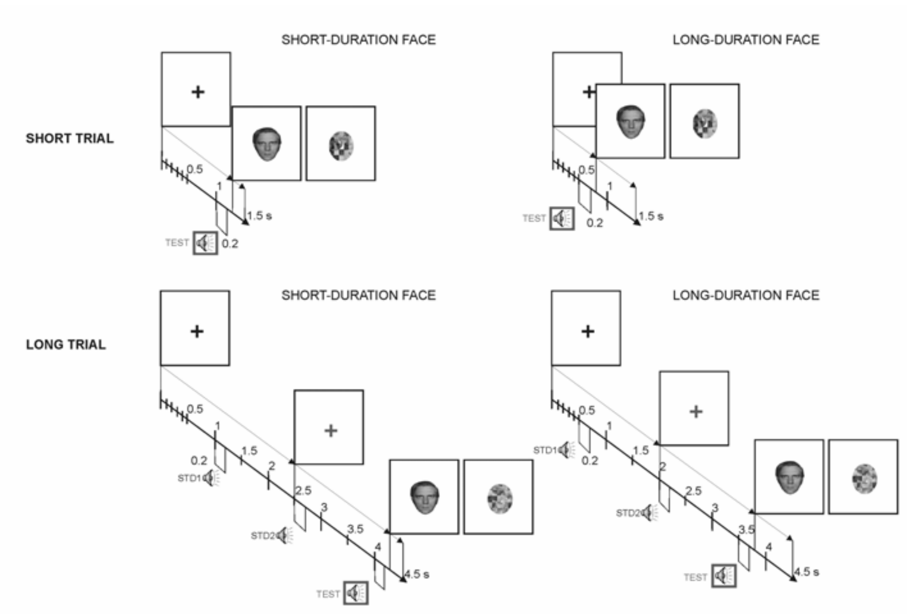


Figure 8. *Trial structure of Experiment 4. Trials and target visual stimuli of short and long duration were combined in 4 blocked conditions. In long trials, novel sounds could appear in any of the auditory stimulus positions. Only standard trials (all auditory stimuli were standard) and novel trials (a novel sound appeared on the TEST position and the other two auditory stimuli were standard) were taken into account. Participants responded whether the target stimulus was a face or not.*

Results: The three-way repeated measures ANOVA on RT with the factors trial length (short, long), face duration (short, long) and auditory stimulus type (novel, standard) revealed a main effect of trial length (F(1,11)=10.3, p=0.008, η^2=0.483), a main effect of auditory stimulus type (F(1,11)=19, p=0.001, η^2=0.632) and a significant interaction between these two factors (F(1,11)=53.6, p<0.001, ε=1, η^2=0.830) (Figure 9). Paired comparisons revealed that there was an effect of trial length only on standard trials (long face: F(1,11)=17.1, p=0.002, η^2=0.608; short face: F(1,11)=19.2, p=0.001, η^2=0.636), with longer RT in the long trials than in the short trials. There were opposed novel sound effects in the short and long trial types. While in the long trials novel sounds facilitated performance (shorter RT compared to standard; long face: F(1,11)=46.6, p<0.001, η^2=0.809; short face:

F(1,11)=22, p=0.001, η^2=0.667), in the short trials they induced a distracting effect (longer RT after novel sounds than after standard tones), although this effect was only marginally significant in trials where the face was present for a long period (long face: F(1,11)=4.1, p=0.068, η^2=0.272; short face: F(1,11)=5.1, p=0.045, η^2=0.317). There was no main effect of face duration on RT, nor any interactions of face duration with trial duration or auditory stimulus type.

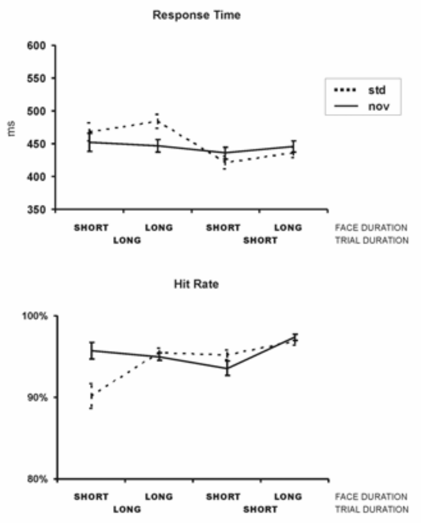


***Figure 9**. RT and HR in novel and standard trials for all combinations of visual stimulus and trial duration in Experiment 4. Bars indicate S.E.M.*

The three-way repeated measures ANOVA on HR with the factors trial length (short, long), face duration (short, long) and auditory stimulus type (novel, standard) revealed a main effect of face duration (F(1,11)=7.6, p=0.019, η^2=0.409) and a three way interaction between face duration, trial duration and sound type (F(1,11)=9.2, p=0.011, ε=1, η^2=0.455) (Figure 9). There were no main effects of auditory stimulus type or trial duration on HR. Paired comparisons revealed that face duration had an effect on HR, with increased HR for long faces compared to short faces, in short trials both for standard tones (F(1,11)=7.7, p=0.018, η^2=0.413) and marginally for novel sounds (F(1,11)=3.9, p=0.075, η^2=0.260), and in long trials only marginally for standard tones (standard: F(1,11)=4.5, p=0.058, η^2=0.288; novel: F(1,11)=0.3, p=0.6, η^2=0.025).

Discussion: Varying the trial duration in the task dramatically affected the effects of irrelevant auditory stimuli on visual task performance. When novel sounds were presented during the short trial conditions of the visual discrimination task, they caused distraction as reported in previous studies (Escera et al. 1998, 2000, 2001, 2003) and in Experiment 2 of the present paper. Conversely, when the event rate was reduced, giving rise to a slow paced task rhythm, novel sounds caused facilitation instead of distraction. Visual stimulus duration generally affected the performance of the task, with higher HR to longer visual stimuli, but did not play a role in the novel sound effects. A lower rate of events, in the long trial conditions, caused participants to respond more slowly, suggesting that the task was less demanding or attention engaging when a long trial was used. Indeed, an increase in event rate generates a more pronounced vigilance decrement and thus event rate is one of the critical variables most often manipulated in vigilance tasks (Davies & Parasuraman, 1982, Parasuraman, 1979). A higher event rate thus consumes more attentional demands and generally induces a higher state of arousal or preparation (Kahneman, 1973). This indicates that the attentional demands of the task are the critical factor influencing the direction of the effects caused by irrelevant novel sounds on task performance. When performing a task that demands constant and highly focused attention, novel sounds presented prior to the target stimulus disrupted performance, whereas when participants were performing a task that did not require constant attention, novel sounds seemed to act as alerting stimuli to facilitate performance.

GENERAL DISCUSSION

With the series of experiments reported here we aimed to examine the effects of task set on the processing of irrelevant auditory stimuli and their effects on the performance of visual tasks. It has been long claimed that the unexpected occurrence of a task-irrelevant auditory stimulus captures attention automatically, resulting in a disruption of ongoing concomitant activity. However, recent studies have demonstrated that these effects depend on top-down factors, such as the current cognitive load (Pashler et al., 2001; Lavie, 2005). The present experiments have shown not only that the capture of attention by irrelevant novel sounds is modulated by these top-down factors, but also that the impact of the auditory stimuli on concurrent task performance can be completely reversed by manipulating task parameters. Surprisingly, when the irrelevant novel sounds were presented shortly before the target stimulus in a delayed memory recognition task, a facilitation effect, rather than a distraction effect was observed (Experiments 1 and 2). This was even true when the same trial structure was used but no WM was required to perform the task. When the same subjects performed this latter simple visual classification task with no WM requirement but with a simplified trial structure, the well-established pattern of distraction by novel sounds was obtained (control condition of Experiment 2). Moreover, the observed facilitation effect was modulated by working memory load, in the same fashion as previously described for the distraction effect (SanMiguel et al., 2008; Berti & Schröger, 2003).

Novel sound effects depend on task demands

Which factors can then account for the opposite effects of novel sounds on task performance? In Experiment 3 the importance of the predictive value of the irrelevant stimuli in respect to the relevant aspects of the task stimulation was tested, by modifying the task of Experiments 1 and 2 in order to create an unequivocal temporal relationship between the task-irrelevant and task-relevant stimuli. Under these conditions, no distraction emerged so that we could disregard the implicit predictive value of the irrelevant sounds as a critical variable determining whether novel sounds result in facilitation or distraction. In Experiment 4, we tested whether the trial duration and/or the target stimulus duration were the critical variables influencing the direction of the novel sound effects. The results of this experiment were striking: trial duration dramatically affected the effects of irrelevant auditory stimuli on task performance, resulting in distraction when the trial duration was short and facilitation when the trial duration was long. Most likely, trial duration determined the attentional demands of the task. Indeed, response time was generally slower in the long trial conditions in which the event rate was lower, indicating that this condition was less attentionally engaging. This result suggests that the attentional demands of the task are the critical factor in determining the direction of the effects of irrelevant auditory stimuli on visual task performance.

Nature of facilitation and distraction effects

Several mechanisms can explain facilitation caused by auditory stimuli. Facilitation might occur due to the auditory stimuli acting as informative cues. In the present experiments, however, the auditory stimuli were completely irrelevant to the task and did not convey any information about the upcoming visual stimulus as they were presented throughout the trial with no apparent relation to the visual stimulation (with the exception of Experiment 3 where the predictive value was imposed). Implicitly, the standard tones could have conveyed some temporal information, as they were presented at a regular SOA. Indeed, in Experiment 3 general auditory stimulus effects were observed most likely due to the auditory stimuli acting as a temporal cue to the upcoming visual stimulus. We differentiated these possible expectancy effects from the specific effects of the unexpected occurrence of a novel sound. In all of the experiments described here, the appearance of a novel sound could not be predicted and did not convey any information about the visual task. Thus, the novel sound could not have acted as a precue, and an expectancy explanation is not plausible for the facilitation effect in any of the present experiments.

Facilitation by auditory stimuli has also been explained from a multisensory integration perspective (Stein et al., 1996) when it results in enhanced perceptibility of a visual stimulus; although other explanations such as energy summation or statistical facilitation have also been proposed (for review see Diederich & Colonius, 2004). However, in the present task the facilitating auditory stimulus was presented 300 ms prior to the visual stimulus, which rules out a possible multisensory integration explanation (Meredith, Nemitz, Stein, 1987).

Finally, the facilitation of reflexive actions is best explained by a brief surge of arousal caused by the facilitating stimulus. Indeed, the neurophysiological mechanism behind accessory stimulus effects on monosynaptic reflexes appears to be a noradrenergic modulation of motor neuron excitability (Stafford & Jacobs, 1990). Although these mechanisms explaining facilitation of reflexive reactions and perceptibility might play a role in response time shortening in tasks requiring a cognitive operation (i.e., response selection), here, higher order, more cognitive mechanisms also need to be taken into account. The locus of the RT facilitation effect has been extensively studied, and according to Hackley and Valle-Inclan's model (2003), the accessory signal speeds up response selection processes that take place after sensory-perceptual analysis and before the onset of the response-specific motor processes reflected by the *lateralized readiness potential* (LRP). Therefore, the exact locus of the RT facilitation effect would be an early phase of the response selection process.

The most plausible explanation is therefore that the novel sound acted as an unspecific alerting signal. An alerting effect is part of the orienting response generated towards attention-capturing auditory stimuli (Näätänen, 1992). The orienting response is present both when the auditory stimuli are presented as an accessory signal, due to their sudden appearance, and when they are presented in the context of an oddball paradigm as a deviating auditory stimulus. Therefore, facilitation effects might be explained by the alerting component of the orienting response triggered by the attention-capturing stimuli, which may result in a general and unspecific state of readiness to respond. Conversely, distracting effects have been mainly explained by the attention component of the orienting response, as a result of temporarily drawing attention away from the main task towards the disrupting stimulus (Parmentier, Elford, Escera, Andrés, SanMiguel, 2008)

A model of novel sound effects

The results obtained in the present experiments lead us to suggest a model in which the novel sounds always generate the same orienting and alerting response but result in distraction or facilitation, depending critically on the baseline level of attentional focusing induced by the task at hand (Figure 10). That is, whenever a novel sound occurs, the attentional resources are momentarily drawn towards the auditory stimulus in order to process it, resulting in an impaired visual stimulus processing, its response being slightly delayed (Parmentier et al., 2008). Thus, there is an “orienting cost” (OC) associated with the occurrence of the novel sound. At the same time, however, the novel sound acts as an alerting signal, resulting in a burst of arousal and refocusing the attentional resources, and possibly leading to optimum performance after the initial distraction. Therefore there should be also an “alerting benefit” (AB) of the novel sound. This model would explain the results of Experiment 4 (Figure 9). In this experiment, when the attentional demands of the task were high, due to a high event rate, participants were performing at an optimum level of highly focused attention (“F” conditions in Figure 10). Due to the high attentional demands, the alerting component of the novel sounds might not have had a consequence on performance in this case, as performance probably was at ceiling. Thus, in the highly focused situation, the unexpected appearance of the novel sound resulted in a small impairment in performance, caused by the orienting cost (OC). However, when the attentional demands of the task were low, the attentional resources were not focused at maximum (“U” conditions in Figure 10), and there was an “unfocused attention cost” (UAC) on baseline performance, relative to the situation in which the attentional demands of the task were high. This was reflected in a general increase in RT when the attentional demands were low (long vs. short trials on Figure 9, upper panel). In this unfocused attention situation, novel sounds generated the same responses: orienting and alerting. Again, there should be a small cost on performance due to the orienting component (OC). However, whereas in the previous situation the alerting component did not have any consequences on performance, here it should have an impact, as attention was at an unfocused state and performance was not at ceiling. The novel sound here would generate a burst of arousal, refocusing the attentional resources and eliminating the unfocused attention cost present at baseline (“alerting benefit”, AB in Figure 10). As a result, since the orienting cost (OC) was smaller than the unfocused attention cost (UAC), the novel sounds resulted in facilitation due to their alerting benefit (AB) in the less demanding conditions. This can be stated as follows, where “stimulus processing” (SP) stands for the time it takes to process the visual stimulus and select and execute a behavioural response:

$$
\begin{array}{l}
RT_{(Std)} = SP + UAC \\
RT_{(Nov)} = SP + OC + UAC - AB \\
where \\
UAC = AB \\
Therefore \\
RT_{(Std)} - RT_{(Nov)} = AB - OC \\
\left\{ \begin{array}{lll}
if & RT_{(Nov)} \rangle RT_{(Std)} & distraction \Leftrightarrow AB < OC \Leftrightarrow UAC < OC \\
if & RT_{(Nov)} \langle RT_{(Std)} & facilitation \Leftrightarrow AB > OC \Leftrightarrow UAC > OC
\end{array} \right.
\end{array}
$$

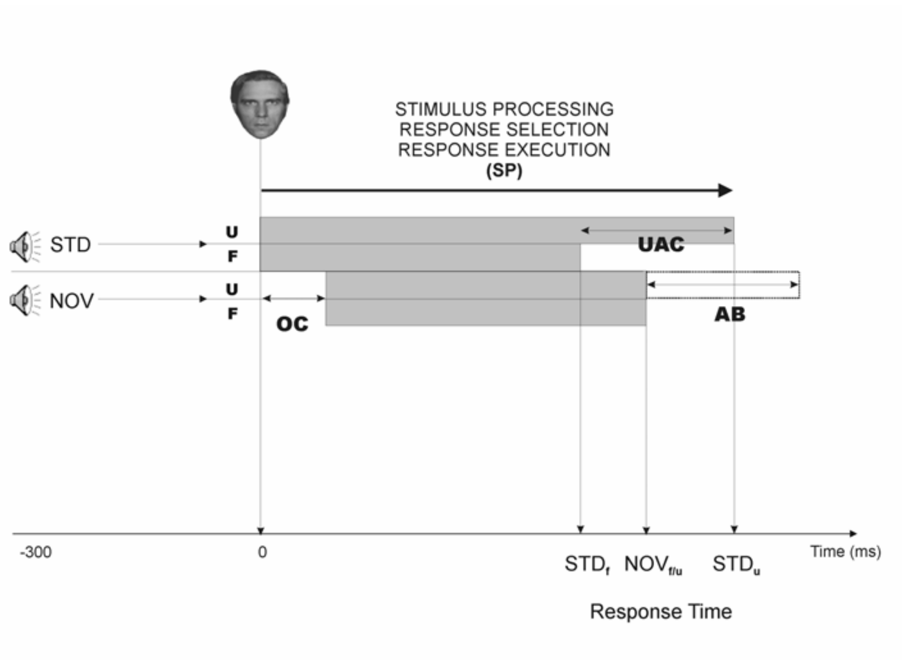


Figure 10. *A model of novel sound effects. Novel sound effects depend on the attentional demands of the task. F: task inducing focused attention, U: task inducing unfocused attention. RT to novel sounds and standard tones in the unfocused and focused situations are shown. RT is longer when performing a task that induces an unfocused attention state, due to an "unfocused attention cost" (UAC) which results in a slower processing of the visual target (SP). Novel sounds generate an orienting cost (OC) due to a momentary orienting of attention towards the novel sound, which results in a delay of visual stimulus processing (SP); and an alerting benefit (AB) that eliminates the UAC when present. Novel sounds cause distraction in the focused situation, as UAC=0; and facilitation in the unfocused situation, as OC<AB.*

In summary, according to the proposed model, whenever performance is at ceiling (UAC = 0), the appearance of a novel sound should always result in a small impairment in performance due to its "orienting cost". However, when performance is not at ceiling (UAC > 0) the effect of the novel sounds will depend on the baseline level of performance. Whenever the "orienting cost" (OC) is larger than the "alerting benefit" (AB), the novel sound will result in distraction; however, if OC is smaller than AB facilitation should result. It is important to point out that this model of the effects of irrelevant, attention-capturing novel sounds on task performance will only apply when the auditory stimulus is presented shortly before the stimulus requiring a response.

Attenuation of irrelevant stimulus processing by WM load

The second aim of the present experiments was to study the effects of WM load on the processing of task-irrelevant, attention-capturing auditory stimuli and their consequences on performance. We observed a modulation of the facilitation effect by WM, and this modulation was similar to the WM effects found previously in distraction tasks (Berti & Schröger, 2003; SanMiguel et al., 2008). As WM load increased, the novel sound facilitation effect decreased as well. Thus, the modulation by WM load was found irrespective of whether the irrelevant stimuli had a distracting or facilitating effect.

An active mechanism of protection from distraction might be activated when WM is loaded, in order to preserve the information held in WM from interference (Postle, 2005, 2006; Sakai, Rowe, Passingham, 2002). In the present experiments, orienting towards the auditory stimuli could be attenuated in order to avoid interference with the task-relevant information that is being maintained or manipulated. Moreover, previous distraction attenuation results (Berti & Schröger, 2003; SanMiguel et al., 2008) support this proposal. The biased competition model advances a possible mechanism through which this modulation by WM load could be achieved as an active function (Desimone & Duncan, 1995; Miller, Erickson, Desimone, 1996).

Alternatively, the suppression of auditory stimulus processing in the present experiments could be the result of a capacity limitation, in the overlapping fronto-parietal systems for working memory encoding and attention (Linden, 2007; Mayer, Bittner, Nikolic, Bledowski, Goebel et al., 2007).

WM effects might depend on task-relevance of the attention-capturing stimuli

A number of studies have found increases in distraction when WM is loaded. These results have motivated a theoretical model proposing that when a task is loaded cognitively less resources become available to suppress interference by the distracters and thus distraction is increased (Lavie et al., 2004). The results discussed here of both distraction and facilitation attenuation by WM load, possibly due to a general attenuation of the processing of irrelevant stimuli, appear to be in contradiction with the predictions of this model. However, this apparent contradiction might be due to differences in the type of distractors used.

Generally, whenever distraction enhancement has been found, the distracters were presented in the frame of a selective attention task and imposed a response conflict (see Lavie et al., 2004). However, in the present experiments, participants did not perform a specific selective attention task; rather, the effects of the irrelevant auditory stimuli were measured on the responses given to the WM task. That is, the auditory stimuli were completely task-irrelevant and could not generate a response conflict with the task. It is unlikely, thus, that these two types of tasks engage the same kind of executive control processes of active suppression of the irrelevant stimuli. Rather, we propose that WM load narrows the “attentional spotlight”, attenuating the processing of any task-irrelevant stimuli that fall outside this spotlight, in order to avoid interference with the contents of the WM store. This would explain why the processing of the auditory stimuli appears to be attenuated in the present experiments. However, the same mechanism would not result in an attenuation of distracters presented within the frame of a selective attention task, as in such task the distracters would be part of the task display. On the contrary, processing of the distracters could be enhanced as they would be in the attentional spotlight. In this case, as WM load increases fewer resources would be available to suppress responses to distracters that generate a response conflict.

Conclusions

Whether attention-capturing auditory stimuli facilitate or disrupt performance depends on the attentional demands of the task and the temporal relationship between the unexpected stimulus and the task. Furthermore, the processing of stimuli that fall outside the attentional spotlight attenuates with working memory load, possibly to protect the contents of the WM store. This attenuation might be an active function of the WM system, or could be the result of an exhaustion of resources. The discrepancy of results with studies showing an increase in distraction by WM load might be owed to the differences in task-relevance of the distracters employed. In sum, the results reported in the present series of experiments indicate that unexpected, novel auditory stimuli may facilitate or distract performance depending on the task set. We developed a model which allows the operationalisation of the critical variables affecting facilitation and distraction in order to design optimum alerting signals.

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Study V.

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On the functional significance of Novelty-P3: Facilitation by unexpected novel sounds

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ABSTRACT

The unexpected occurrence of a change in auditory context has been shown to result in distraction due to a momentary attention shift. These unexpected sounds elicit the Novelty-P3 (NP3) response which has been proposed as an electrophysiological index of distractibility, and used as such in the evaluation of several clinical populations. However, unexpected sounds also result in facilitation in certain conditions. Here, we investigate the electrophysiological concomitants of novel sounds in a task in which these sounds facilitate visual task performance. Novel sounds elicited NP3 and resulted in an enhancement of the visual P300 response to subsequent visual targets. This result clearly argues against the use of NP3 as an index of distractibility and asks for a reformulation of the functional significance of this response. We suggest that the NP3 is a complex signal that comprises alerting, orienting and executive control processes triggered by the novel sound. The present facilitation seems to take place at late stage of processing and might be due to a phasic increase in alertness.

Introduction

Humans permanently scan the environment in order to filter out the information that might be relevant for guiding actions. Without salient cues, this process can be very unreliable, as in the case of change blindness (Simons & Rensink, 2005). Conversely, salient changes of the sensory environment, for example a colour that pops out or an unexpected sound, capture attention involuntarily and generate an orienting response (OR). This OR, which serves the purpose of analysing the potential relevance of the change (Näätänen, 1992), comes at a behavioural cost. If the unexpected stimulus occurs during an unrelated task, the OR generally results in an impairment of task performance (Escera, Alho, Winkler, Näätänen, 1998).

Several lines of research have investigated the OR by means of auditory oddball paradigms (see reviews in Escera & Corral 2003, 2007; Friedman, Cycowicz, Gaeta, 2001; Knight & Scabini, 1998; Ranganath & Rainer, 2003). In these studies, a stable auditory context is generated by presenting repeating sounds following a specific pattern. In most cases, an identical tone, referred to as the standard sound, is repeated at a regular stimulus onset asynchrony (SOA). Once the auditory context is established, this regularity is broken by the unexpected occurrence of a deviating sound. The deviation can be small, e.g., a subtle change in duration or pitch, or large, as when a completely novel environmental sound is presented. The automatic detection of the deviation leads to the involuntary orienting of attention towards the eliciting sound. This orienting response results in distraction on a concomitant simple classification task, increasing response time (RT) and decreasing hit rate (HR) to the target stimulus (Escera et al., 1998; Escera, Alho, Schröger, Winkler, 2000; Escera, Yago & Alho, 2001; Escera, Corral & Yago 2002; Escera, Yago, Corral, Corbera, Nuñez, 2003, Berti & Schröger, 2001; Schröger & Wolff, 1998a, 1998b; Schröger & Berti, 2000; Schröger, Giard, Wolff, 2000)

Recently, we have described in a behavioural study (SanMiguel, Linden, Escera, 2008b) that novel sounds can result in facilitation rather than in distraction when presented in the same type of oddball sequence but during the performance of a delayed memory recognition task, involving memory for faces. The evidence suggests that the direction of the novel sound effect (facilitation vs. distraction) depends on the attentional demands of the visual task being performed (SanMiguel et al., 2008b). The nature of the facilitation effect, however, is unclear. Possibly, it results from a burst of arousal generated as part of the OR towards the unexpected sound. However, specifically how this arousal response would interact with the processing of the visual stimulus, and which phase in the processing of the visual target would be facilitated is unknown.

Benefits from unexpected, non-informative auditory stimuli (neutral warnings or accessory stimuli) presented shortly before or simultaneously with the visual task stimuli have been reported by a different stream of research (Valls-Solé, Valldeoriola, Muñoz, Gonzalez, et al., 1995; Hackley & Valle-Inclán, 1998, 1999). In these studies, a sudden sound shortens RT to a visual stimulus. These neutral warning sounds are assumed to generate a burst of arousal mediated by the noradrenergic system (Fernandez-Duque & Posner, 1997); however, the exact mechanism of facilitation remains unclear. The unexpected sound does not appear to facilitate the sensory processing of the target; rather, it speeds up response selection processes that take place after the initial sensory-perceptual analysis has taken place but before the onset of the response-specific motor processes (Hackley & Valle-Inclan, 2003).

Similar to the neutral warning facilitation effect, McDonald, Teder-Sälejärvi and Hillyard (2000) found that a spatial non-predictive auditory cue enhances detectability (d') of a subsequent visual stimulus presented at the same location. This facilitation is presumably due to involuntary orienting in space to the sound location. By means of ERP recordings it was established that the initial sensory-evoked visual responses are unaffected by the validity of the unpredictive auditory cue. However, a sustained negativity emerged thereafter in valid trials (McDonald & Ward, 2000). Inverse electrical source modelling of this negativity suggested that feedback from multimodal to unimodal brain areas underlies the cross-modal spatial attention effect on visual perception (McDonald, Teder-Sälejärvi, Di Russo, Hillyard, 2003).

In the same vein, the nature and locus of the facilitation effect by novel sounds on face recognition that we have obtained using the auditory oddball paradigm (SanMiguel et al., 2008b), can be investigated by means of ERP recordings. A predefined sequence of electrophysiological markers follows the presentation of a visual stimulus upon which a classification task needs to be performed. First, visual P1 and N1 sensory-evoked responses are elicited upon the perception of the visual stimulus. These initial responses are known to be modulated by spatial attention, indicating enhanced sensory processing of the visual target at visual extrastriate areas, which results in faster and more accurate responses at the attended location (Luck, Woodman, Vogel, 2000). Therefore, a modulation of early components such as the visual P1 and N1 would indicate that novel sounds facilitate early sensory processing, similar to the spatial attention effect.

Subsequent to sensory-evoked components, recognition of specific content of the visual stimulus may elicit related content-specific components. The N170, a negative wave over occipitotemporal areas, is elicited by the presence of a face. This component is thought to reflect structural encoding (Bentin, Allison, Puce, Perez, McCarthy, 1996; Carmel & Bentin, 2002) and it has likely sources in occipito-temporal cortex, particularly in the fusiform gyrus (Latinus & Taylor 2006; Schweinberger, Pickering, Jentzsch, Burton, Kaufmann, 2002; Horovitz, Rossion, Skudlarski, Gore, 2004; Iidaka, Matsumoto, Haneda, Okada, Sadato, 2006). The N250r, on the other hand, is a relative negativity over inferior temporal sites for repeated compared to new faces, and therefore likely indexes face recognition (Begleiter, Porjesz, Wang, 1995; Boehm & Paller, 2006; Schweinberger & Burton, 2003; Schweinberger, Huddy & Burton, 2004; Morgan, Klein, Boehm, Shapiro, Linden, 2008). Finally, these early components are followed by a P300 response, that indexes higher level cognitive processing such as event categorization or context updating. The elicitation of the P300 response seems to be related to completion of stimulus evaluation rather than to response selection processes (Duncan-Johnson & Donchin, 1982; Donchin, 1981; Kok, 2001). Looking for a modulation by novel sounds of specific ERP components related to the processing of the visual target might ascertain which specific level of processing is facilitated by them, and give some indication of the brain areas involved.

In the oddball paradigm, the appearance of a novel sound and the involuntary orienting of attention are accompanied by a well-defined pattern of electrophysiological responses. These responses are generally observed in the difference waves that result from subtracting the response generated by the standard sound from that generated by the deviating one (Escera et al., 1998, 2000; Escera & Corral, 2003, 2007). In the first 100-200 ms from sound onset, a predominantly frontal negative deflection termed the mismatch negativity (MMN; Näätänen, Paavilainen, Rinne, Alho, 2007) indexes the detection of the change in the auditory context. In addition to the MMN, an enhancement of the auditory N1 may be observed when the deviating sound is more complex than the repeating standard sound (Escera et al., 1998, 2001; Alho, Winkler, Escera, Huotilainen, Virtanen, et al., 1998).

If the deviation is evaluated as relevant, the MMN/N1-enhancement is followed by an involuntary orienting of the attentional resources towards the eliciting sound. The effective orienting of attention is accompanied by the novelty-P3 (NP3) or P3a component, a fronto-central positive deflection appearing in the 200-400 ms latency range (Friedmann et al., 2001; Knight 1984; Squires, Squires, Hillyard, 1975; Knight & Scabini, 1998; Courchesne, Hillyard, Galambos, 1975). In the psychophysiological literature, the NP3 has been taken as a cerebral signature of the OR (Friedmann et al 2001; Knight 1984; Squires et al., 1975; Knight & Scabini, 1998). Indeed, NP3 amplitude is correlated with the phasic skin conductance response that reflects the OR (Lyytinen, Blomberg, Näätänen, 1992; see also Knight, 1996). Therefore, according to the most accepted view, the NP3 indeed reflects the orienting of attention towards the unexpected deviating or novel sound (Escera et al, 1998, 2000; Friedmann et al 2001; Herrman & Knight, 2001; Knight, 1984).

Finally, whenever the involuntary attention capture occurs during the performance of a concomitant task, the ERP shows a frontal negative deflection time-locked to the task stimuli that has been proposed to index the reorientation of the attentional resources back to the task after the evaluation and processing of the deviation has been completed, i.e., after a momentary "distraction" (reorienting negativity, RON, Schröger & Wolff 1998b; Schröger, Giard & Wolff, 2000; Berti & Schröger, 2001; Berti, Roeber & Schröger, 2004, Escera et al., 2001; SanMiguel et al., 2008a; Munka & Berti 2006).

The NP3 and RON components have been specifically associated with the distracting consequences of the irrelevant sounds. Schröger & Wolff (1998a) formally investigated whether the distraction effects found at the behavioural level relate to the same phenomenon as the deviance-related effects concomitantly present at the electrophysiological level, yielding support for this hypothesis. Subsequently, a series of studies demonstrated parallel modulations of the behavioural distraction effect and the underlying ERP components (Berti et al., 2004; Rinne, Särkkä, Degerman, Schröger, Alho, 2006; Jääskeläinen, Hirvonen, Kujala, Alho, Eriksson et al., 1998; Escera et al., 2003; Berti & Schröger, 2003; SanMiguel et al., 2008a; Jääskeläinen, Schröger, Näätänen, 1999). Additionally, when no behavioural distraction was obtained, either due to the predictability of the oddball sequence (Sussman, Winkler, Schröger, 2003) or to the use of a very small deviance (Berti et al. 2004), no NP3 and RON were elicited.

On the basis of the evidence pointing towards a relationship particularly between NP3 and behavioural distraction, it was suggested that the auditory oddball paradigms could be used to study in a reliable way the phenomenon of distraction and electrophysiological indices of the underlying cerebral processes (Escera, 2000; Schröger and Wolff, 1998a). Escera & Corral (2003, 2007) went a step further in this direction and named the three-peak waveform elicited by novel sounds the "distraction potential". They suggested that it reflects activation of the cerebral network underlying involuntary attention control. Following this proposal, increased amplitude of the NP3 component has been interpreted as an index of distractibility in the evaluation of several clinical populations, for example patients with closed head injury (Kaipio, Alho, Winkler, Escera, Surma-aho, Näätänen, 1999; Kaipio, Cheour, Ceponiene, Ohman, Alku et al., 2000), children with depression (Lepistö, Soininen, Ceponiene, Almqvist, Näätänen et al., 2004), autism (Ferri, Elia, Agarwal, Lanuzza, Musumeci et al., 2003) and dyslexia (Rüsseler, Kowalczuk, Johannes, Wieringa, Münte, 2002). However, one important caveat with these studies resides in the general absence of behavioural measures of distractibility. A thorough investigation of the conditions under which the NP3 is increased is therefore paramount, if we want to make reverse inferences about psychological states or traits, e.g. distractibility, from changes in the NP3 amplitude. Our paradigm is suited to this investigation because we found facilitation rather than distraction by novel sounds (SanMiguel et al., 2008b). If novel sounds are found to generate the same sequence of electrophysiological responses when they have a facilitating rather than a distracting effect on task performance, we will need to re-evaluate the psychological events often assigned to the NP3 and RON components and their use as clinical markers of distractibility.

The orienting of attention towards an unexpected stimulus is an involuntary response, but it can be modulated by top-down factors such as working memory (WM) load (De Fockert, Rees, Frith, Lavie, 2001; Lavie & De

Fockert, 2005; Lavie, 2005; Lavie, Hirst, De Fockert, Viding, 2004; SanMiguel et al., 2008a; Berti & Schröger, 2003) and therefore it cannot be regarded as fully automatic (Pashler, Johnston & Ruthruff, 2001). Particularly, the amplitude of the NP3 generated by deviating auditory stimuli was reduced when WM load was imposed in the task, accompanied by a reduction of behavioural distraction (SanMiguel et al., 2008a; Berti & Schröger, 2003). This has led to the conclusion that cognitive load attenuates the process indexed by the NP3, i.e., the effective orienting of attention towards the distracting stimulus. However we have recently also found a modulation by short term memory load of the behavioural facilitation effect caused by novel sounds presented in an oddball sequence (SanMiguel et al., 2008b). This finding indicates that memory load might modulate the processing of irrelevant auditory stimuli per se, rather than a specific distraction effect caused by them. The recording of electrophysiological responses can ascertain which particular process is modulated by memory load.

In sum, the present experiment served three main purposes: First, to investigate, by means of ERPs, the nature and locus of the facilitation effect produced by novel sounds in specific task settings. To that aim, we compared electrophysiological responses generated by the visual stimulus after the presentation of standard and novel sounds. The precise timing of the ERP components allows identifying the specific phase of the processing of the visual stimulus that is facilitated. Second, the NP3 and RON components have been commonly used as an electrophysiological index of distraction caused by unexpected auditory deviant or novel stimuli. Thus, we investigated whether these components are also elicited when novel sounds result in facilitation rather than distraction. The elicitation of NP3 under conditions of behavioural facilitation would undermine its use as an electrophysiological marker of distractibility. And third, the evidence suggests that WM load modulates both distracting and facilitating effects caused by novel sounds. The distracting effect of novel sounds has been associated with the NP3. With the present paradigm we can identify the locus of the memory load effects in the case in which the novel sounds result in facilitation, in order to learn whether the same mechanism is responsible for both types of modulation. The overall aim of the study was to provide a better understanding of the impact of auditory novelty on visual performance and the underlying cerebral processes.

Methods

Subjects and procedure

Twelve healthy students of Bangor University, Wales (18-32 years; mean age 22.5; 5 male; all right-handed) with normal or corrected to normal vision participated in this experiment. Participants gave informed consent after the nature of the study was explained to them and were reimbursed for their participation. The study was conducted according to the declaration of Helsinki. The participants sat inside a Faraday cage during the experiment to minimize electrical interference and were presented with an auditory-visual task with two conditions: a high short term memory load condition (STM1) and a low short term memory load condition (STM0). We presented these two conditions in separate blocks and their order was randomised across participants. Stimuli were presented in the centre of a screen on a 19 inch TFT monitor using E-Prime software running on a PC, and appeared on a white background. Each trial (fig. 1) started with a fixation cross for 1.7 s. This was followed by a 2.3 s sample presentation period, consisting of a face in the STM1 condition and a scrambled image in the STM0 condition. Faces were randomly selected from a set of six neutral expression black and white male faces (Ekman & Friesen, 1976) and eight scrambled face images each of which subtended a visual angle of 3°30’ vertically and 3° horizontally approximately (see fig. 1 for example). A 1.3 s retention interval was presented after the sample presentation period and finally a target stimulus was presented for 1.9 s, which was always a face in the STM1 condition and either a face or scrambled image in the STM0 condition. In the STM1 condition participants had to respond, as accurately and fast as possible, whether the target face was the same or different as the one presented previously on the sample presentation period. In the STM0 condition, participants had to respond whether the target stimulus was a face or not. Only trials with responses within 900 ms after target stimulus onset were accepted. Participants pressed one of two response buttons on a standard mouse with the index and middle finger of the right hand. In half of the trials in the STM1 condition the target face matched the sample face and on the other half of the trials a different face was presented as a target. In the STM0 condition a target face was presented in half of the trials and in the other half the target was a scrambled image. During the whole duration of the trial, a sequence of sounds was presented through headphones. Sounds were either repetitive standard tones (600 Hz, 200 ms) or environmental novel sounds selected from a sample of 100 different exemplars, such as those produced by a drill, hammer, rain, door or telephone ringing. The novel sounds were digitally recorded, low-pass filtered at 10,000 Hz, and edited to have a duration of 200 ms, including rise and fall times of 10 ms (see Escera et al., 2003 for details on novel sound editing). Six sounds were presented in each trial using an SOA of 1.2 s. Fifty percent of the trials were standard trials, in which all 6 sounds were standard tones; the other half of the trials were novel trials. In these latter trials, a novel sound was presented 300 ms prior to the target stimulus while the other five sounds of the novel trial were standard tones, thus the actual probability of a novel sound was 1/12. Randomly, one out of nine trials was a "catch trial" in which the novel sound appeared at a different position to avoid predictability, 300 ms before the start of the sample presentation period. Each condition consisted of 200 trials and the total duration of the experiment was 68 minutes, allowing for pauses every 4 minutes. Participants performed ten practice trials for each condition before starting the experiment.

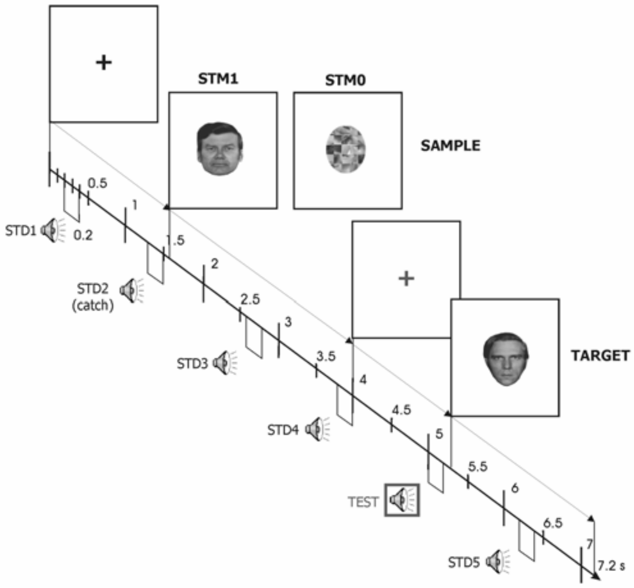


Fig. 1. *Trial structure of the task. Participants performed a memory task (STM1) and a simple visual classification task (STM0). In STM1 a sample face had to be matched to the target face after a retention period. In STM0 a scrambled image was always presented during the sample presentation period. Participants had to respond whether the target stimulus was a face or a scrambled image. Standard tones were presented throughout the trial with an SOA of 1.2 s. The test sound (50% novel, 50% standard) was presented 300 ms before the target stimulus. In 1/9 trials a catch novel sound was presented 300 ms before the sample presentation period.*

Data acquisition and analysis

We recorded the electroencephalogram (EEG) from 64 ring electrodes placed in an elastic cap (Easy Cap; FMS, Munich) in the following 10-10 positions (American Encephalographic Society, 1991): Nz, FP1, FPz, FP2, AF7, AFz, AF8, F9, F7, F5, F3, F1, Fz, F2, F4, F6, F8, F10, FT9, FT7, FC3, FC1, FCz, FC2, FC4, FT8, FT10, T7, C5, C3, C4, C6, T8, TP9, TP7, CP3, CP1, CPz, CP2, CP4, TP8, TP10, P9, P7, P5, P3, P1, Pz, P2, P4, P6, P8, P10, PO9, PO7, POz, PO8, PO10, O1, Oz, O2, Iz. Two infraorbital channels (IO1 and IO2) were located vertically below each eye. All channels were referenced during recording to a reference electrode positioned at Cz, and an electrode positioned at AF4 served as ground. Electrode impedances were kept below 5 kΩ. The EEG was recorded with two BrainAmps DC amplifiers (Brain Products, Munich, Germany) and sampled at 500 Hz with a 250 Hz low-pass filter. EEG data were re-referenced offline to the average reference.

Eye artifact correction was accomplished using BrainVision Analyzer (Brain Products, Munich, Germany) software separately for each participant. In order to do so, during the experiment we instructed participants to fixate on a cross and blink naturally when needed and then we subjected the corresponding recorded EEG blink segments to independent components analysis (ICA; Makeig, Westerfield, Jung, Covington, Townsend et al., 1999). We then identified components related to blinks by their topography, and removed these components from the experimental data. All further analyses were conducted on Eprobe software (ANT, Eschede, The Netherlands). The EEG data was filtered offline between 0.1 and 30 Hz and all epochs exceeding ± 100 μV on any electrode were rejected from further analysis.

Two epochs were used for the trial averaging, a long and a short one. The short epoch was used to study effects related to the auditory test stimulus and the visual target stimulus in order to improve signal quality of the average. This epoch was time locked to the appearance of the test sound, comprising a 200 ms pre-stimulus baseline and lasting for 1.2 s, including up to 900 ms after the onset of the target stimulus. The long epoch lasted for 5 s, from the onset of the second auditory stimulus (catch position) until the onset of the fourth auditory stimulus, which was presented 900 ms after the target stimulus onset. A 300 ms pre-stimulus baseline was used when computing this epoch. The goal of using this epoch was to allow a comprehensive view of all trial events and to analyze memory effects during the encoding/retention interval.

We averaged separately standard and novel sound trials within each condition and only used trials with a correct response. Trials were also sorted according to whether the target was a face or a scrambled image in STM0, and whether the target face was repeated or new in STM1. Difference waves (novel-standard) were computed for both memory conditions in order to identify MMN/N1-enhancement (115-165 ms), the early (220-270 ms) and late (320-370 ms) phases of NP3 and RON (465-565 ms). Memory and novelty effects were tested by means of repeated measures analysis of variance (ANOVA) on the mean amplitude of the corresponding time windows for each component with the factors condition (STM0, STM1), stimulus type (novel, standard) and electrode (FC1, FCz, FC2, CP1, CPz, CP2) for the MMN/N1-enhancement and RON components and the additional factor phase (early, late) for the NP3 component.

Additionally, we identified by visual inspection of grand average waveforms the following components in the short epoch average: Visual P1 (420-450 ms) and N1 (480-500 ms), and P300 (600-1000 ms). Note that the epoch starts at auditory stimulus onset, and therefore 300 ms must be subtracted from all latencies to calculate the distance from visual stimulus onset. Analysis of memory condition and novelty effects was performed on the N1, P1 and P300 components by means of a three way ANOVA (condition x auditory stimulus type x electrode) on the mean amplitude of the defined time windows on the following electrodes: PO7, PO8, PO9, PO10, O1, O2, Oz, Iz for the N1 and P1 components and P5, P6, P3, P4, P1, P2, Pz for the P300 component. A concomitant novelty effect on frontal and occipital electrodes was apparent on the waveforms in the P300 time range, and thus a second, more comprehensive analysis to include these distributed effects was performed. The P300 time window was divided into 4 consecutive shorter 100 ms time windows, from 600-1000 ms. A 4-way ANOVA was performed on each time window including condition (STM1, STM0), auditory stimulus type (Std, Nov), coronal row (3 levels: frontal, parietal and posterior parietal/occipital electrodes) and sagittal row (5 levels from left to right) as factors, on the following electrodes: F3, F1, Fz, F2, F4, P3, P1, Pz, P2, P4, PO7, O1, Oz, O2, PO8.

Difference waves obtained by subtracting trials in which the target stimulus was a scrambled image from those in which the target stimulus was a face were computed to identify the N170 (490-510 ms) component in the STM0 condition. In the STM1 condition, trials in which the target was a new face were subtracted from those in which the target was a repeated face to identify the N250R (600-700 ms) component. Novelty effects on these components were assessed by means of ANOVA on the mean amplitude of the corresponding time windows on the difference waves with the factors stimulus type (novel, standard) and electrode (N170: P7, P8, P9, P10, PO8, PO9, PO10, O1, Oz, O2; N250R: P9, TP9, P10, TP10, PO9, PO10).

Finally, sustained memory effects over the retention period were assessed for the long epoch on 10 consecutive 300 ms time windows over the duration of the retention, starting 300 ms after the onset of the sample stimulus and ending with the onset of the test sound, 300 ms before the presentation of the target stimulus. The effects were assessed by means of ANOVA on the mean amplitude of each consecutive time window with the factors memory condition x stimulus type x electrode (P9, P10, PO7, PO8, P7, P8).

We calculated mean RT for correct responses and HR, separately for the standard and novel sound trials and memory conditions. We analysed effects on visual task performance caused by the novel sounds and memory condition effects by means of ANOVA with the type of auditory stimulus (standard, novel) and condition (STM0, STM1) as factors, performed on HR and RT. Greenhouse-Geisser corrections were applied to all analyses where appropriate.

Results

Behavioural data

The high short term memory task was more difficult to perform, as indicated by a reduced HR ($F_{(1,11)}$=13.922, p= 0.003, η^2=0.559) and slower RT ($F_{(1,11)}$=20.679, p< 0.001, η^2=0.653) in the STM1 condition compared to the STM0 condition (see fig.2). Participants responded significantly faster to the visual target after novel sounds compared to standard tones ($F_{(1,11)}$=21.817, p=0.001; η^2=0.665) in both conditions (STM0: $F_{(1,11)}$=14.212, p=0.003, η^2=0.564; STM1: $F_{(1,11)}$=7.332, p=0.020, η^2=0.4), and also showed a higher HR after novel sounds in STM0 ($F_{(1,11)}$=6.769, p=0.025, η^2=0.381). There was a non-significant increase in HR after novel sounds in STM1 ($F_{(1,11)}$=0.766, p=0.4, η^2=0.065). The memory condition and sound type effects did not interact.

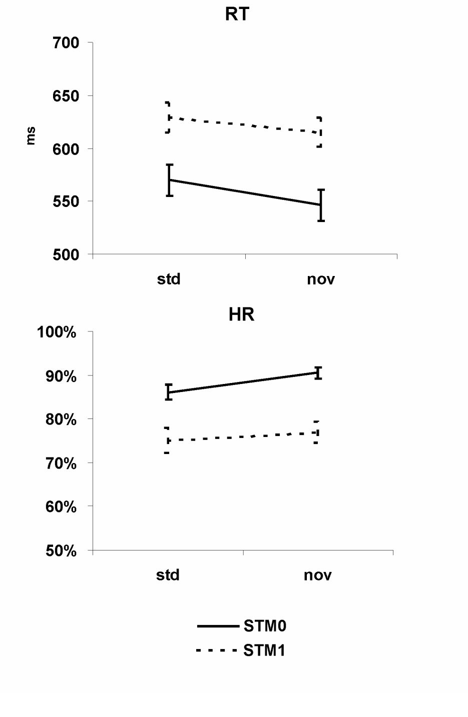


Fig. 2. *RT and HR for standard and novel trials in both conditions. The high short term memory load task (STM1) was harder to perform than the visual classification (STM0) task. Novel sounds facilitated task performance, resulting in shorter RT in both conditions and in more accurate responses in STM0. Bars indicate S.E.M.*

ERP data

Novel – Standard difference waveform

In both standard and novel trials a complex waveform comprising responses to the auditory stimulus and visual target related responses could be observed (fig. 3). Novel sounds elicited the typical three-peak waveform characterised by MMN/N1-enhancement, NP3 and RON deflections as revealed in the novel-standard difference waveforms (fig. 3). ANOVA performed on each of these peaks' time windows revealed significant main effects of the stimulus (novel, standard) factor for MMN/N1-enhancement ($F_{(1,11)}=4.79$, $p=0.051$, $\eta^2=0.303$) and NP3 ($F_{(1,11)}=40.93$, $p< 0.001$, $\eta^2=0.788$) and a significant stimulus x electrode interaction for RON ($F_{(5,55)}=16.45$, $p< 0.001$, $\varepsilon=0.305$, $\eta^2=0.599$). Subsequent post-hoc tests revealed that the stimulus effect was present for RON on CP2 ($F_{(1,11)}=11.846$, $p= 0.006$, $\eta^2 = 0.519$), CPz ($F_{(1,11)}=10.527$, $p=0.008$, $\eta^2=0.489$) and FC1 ($F_{(1,11)}=8.333$, $p=0.015$, $\eta^2=0.431$). Thus the significant differences between the novel and standard waveforms support statistically the identification of these three deflections. No memory condition effects or condition x stimulus type interactions were found, indicating that these components were not modulated by the type of task.

Early visual responses

The analysis of the P1 and N1 visual responses (fig. 3) revealed no main effects of novelty or WM condition. Significant memory condition x electrode ($F_{(7,77)}=5.266$, $p=0.006$, $\varepsilon=0.520$, $\eta^2=0.324$) and auditory stimulus x electrode ($F_{(7,77)}=4.117$, $p=0.025$, $\varepsilon=0.403$ $\eta^2=0.272$) interactions were found for the P1 component, and a significant auditory stimulus x electrode ($F_{(7,77)}=6.845$, $p=0.003$, $\varepsilon=0.449$ $\eta^2=0.384$) interaction was found for the N1 component. Subsequent post-hoc tests at each electrode location revealed significant effects only at PO8, showing a reduced P1 amplitude in the STM1 ($F_{(1,11)}=6.445$, $p=0.028$, $\eta^2=0.369$) condition and a reduced N1 amplitude for novel sounds ($F_{(1,11)}=7.910$, $p=0.017$, $\eta^2=0.418$) at this location. No interactions between auditory stimulus and memory condition were found.

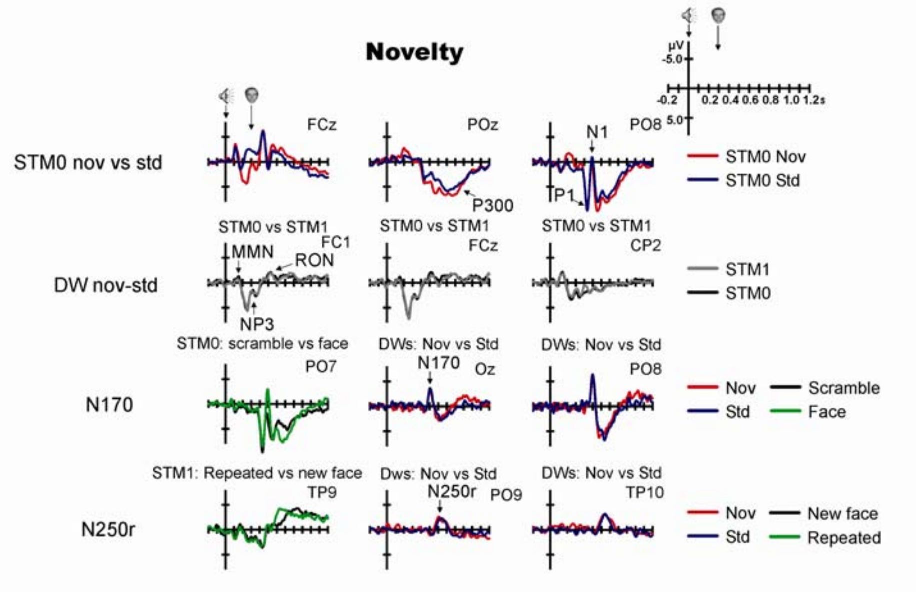


Fig. 3. *Novelty effects evaluated over the short averaging epoch. Averages are time-locked to test auditory stimulus presentation. Top row: Novel and standard waveforms in the STM0 condition. The visual P1, N1 and P300 responses to the target stimulus are identified. P300 was enhanced by novel sounds. Second row: MMN/N1-enhancement, NP3 and RON were clearly identified in the novel-standard difference waves (DW) to the sound preceding the target stimulus. These components were not modulated by memory load. Third and fourth row, N170 and N250R: Conditions subtracted to visualize the component are presented on the left diagram. Novel and standard ERPs for the resulting difference waveforms are presented on the centre and right diagrams. No effects of novelty were found on N170 and N250R.*

N170

The N170 component was isolated by subtracting the target face from the target scrambled image trials on the STM0 condition (fig. 3). Novelty effects on the N170 were explored by contrasting the novel and standard trials. No effect of the type of auditory stimulus was found for this component ($F_{(1,11)}$=0.54, p=0.479, η^2=0.046).

N250R

This component was identified as a negative going deflection present for repeated faces as compared to new faces on inferior temporo-parietal sites (fig. 3). It was isolated by subtracting the new face trials from the repeated face trials on the STM1 condition. Novelty effects on the N250R were explored by contrasting the novel and standard trials. No effect of the type of auditory stimulus was found for this component ($F_{(1,11)}$=0.006, p=0.939, η^2=0.001).

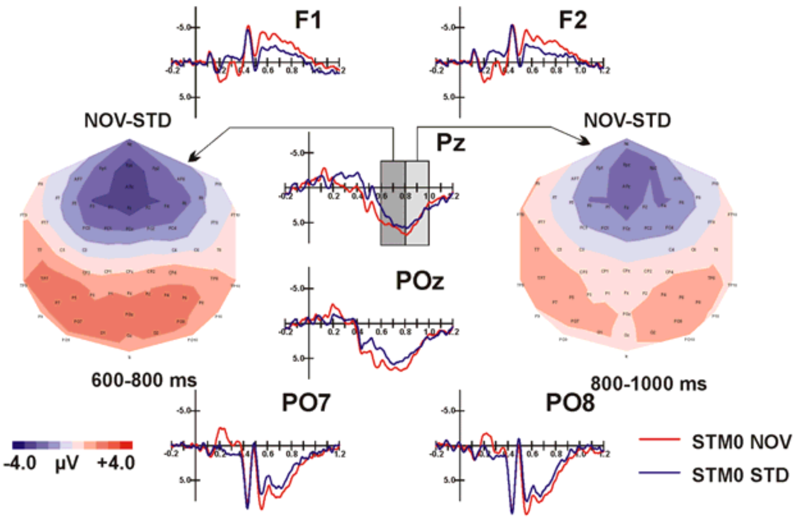
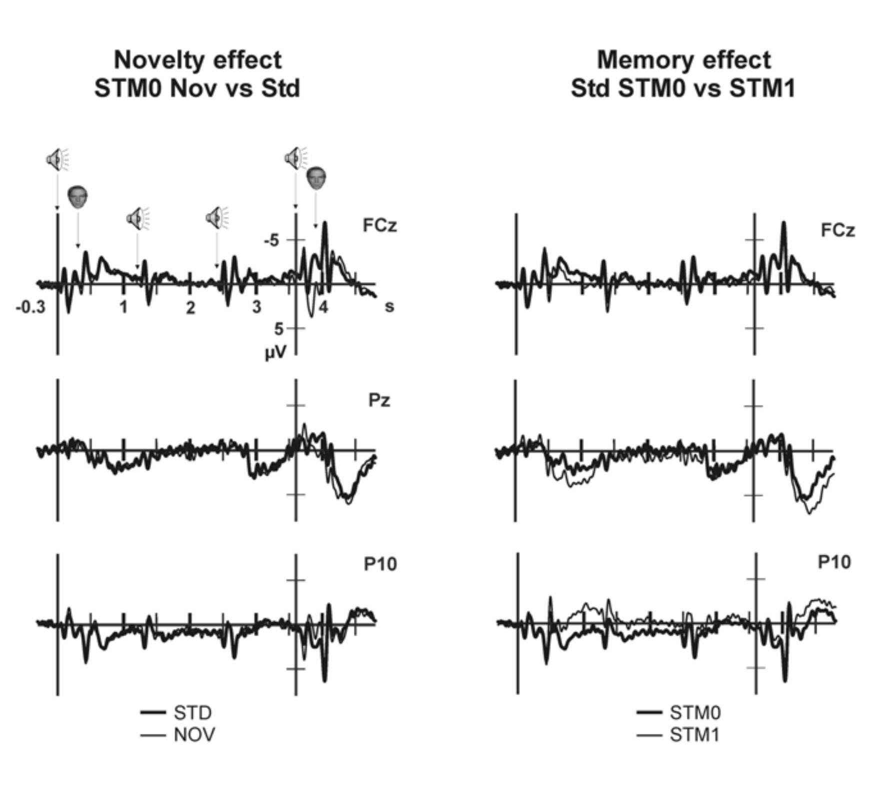


Fig. 4. *Novelty effects on the P300. Averages are time locked to presentation of test auditory stimulus. Novel sounds enhanced the P300 response to subsequent visual stimuli. A concomitant frontal negativity for novel sounds was also found. Maps show the distribution of the novelty effect, obtained from novel minus standard difference waveforms in the P300 time range, from 600-800 and from 800-1000 ms (300-500 and 500-800 ms from visual stimulus onset).*

P300

Novel sounds produced a significant enhancement ($F_{(1,11)}$=9,718, p=0.010, η^2=0.469) of the visual P300 (fig. 3, first row). A concomitant frontal negativity was also found for novel trials in the P300 time range (see fig. 4 for scalp distribution of these novelty effects). A more detailed analysis revealed a main auditory stimulus effect on the first analysis time window

(600-700 ms, $F_{(1,11)}$=6.354, p=0.028, η^2=0.366). No significant main effects of auditory stimulus were found for the subsequent three time windows (700-1000 ms), but significant auditory stimulus x coronal row interactions were present in two of these subsequent windows (window 2, 700-800 ms: $F_{(2,22)}$=7.723, p=0.015, η^2=0.412; window 3, 800-900 ms: $F_{(2,22)}$=7.388, p=0.012, η^2=0.402).


Novelty effect
STM0 Nov vs Std

Memory effect
Std STM0 vs STM1

Fig 5. *Trial events visualized over the long averaging epoch. Averages are time-locked to presentation of the second auditory stimulus (catch position). LEFT: Novelty effects on the STM0 condition. The waveforms begin to differ after test sound presentation. RIGHT: Memory load effects on standard trials. A posterior parietal negativity was found during encoding/retention in STM1. The P300 component was larger in the STM1 condition.*

Subsequent post-hoc tests showed significant auditory stimulus effects on all three levels of the coronal row (frontal, parietal and posterior parietal/occipital electrodes) in both time windows (all $p<0.05$). There were no interactions with the sagittal row factor in any time window at any of the coronal row levels. Finally, the P300 component was larger in STM1 compared to STM0 ($F_{(1,11)}=5.431$, $p=0.040$, $\eta^2=0.331$) (fig. 5). No interactions between novelty and memory condition effects were found.

Retention interval

A posterior parietal negativity was related to the memory encoding/retention in condition STM1. This sustained effect was significant in time windows 1-8 (all $p<0.05$); from 300 ms after the presentation of the sample stimulus, and lasted for 2.4 s (fig. 5, right panel).

Discussion

Novel sounds presented in an oddball sequence during the performance of a simple visual classification task generally produce a distraction effect. Whenever electrophysiological measures are recorded, novel sounds in this situation generate a series of responses indexing three main stages of attention capture: MMN/N1-enhancement, NP3 and RON (Escera et al., 1998; Escera 2000; Escera & Corral 2003, 2007). In the present study, these same novel sounds resulted in facilitation when a different visual task structure was employed. This facilitation effect was present both during the performance of a short term memory and a simple visual classification task. Novel sounds facilitated a late stage of processing, enhancing the visual P300 response to the target. The facilitating novel sounds elicited the same pattern of electrophysiological responses that is usually described when these same sounds result in distraction, comprising MMN/N1-enhancement, NP3 and RON. Short term memory load modulated neither the behavioural facilitation effect nor the NP3 and RON components. All this findings will be discussed in turn.

Nature of facilitation effect

The facilitation effect was mainly paralleled by an enhancement of the visual P300 component and a concomitant frontal negativity, indicating that the effects took place at a late stage of processing. However, a small reduction of the early visual N1 component was found to be significant at the PO8 location. Novel sounds may have led to more expectancy activity in visual cortex (Kastner & Ungerleider, 2001), possibly through cross-modal connections between auditory and visual cortices (Eckert, Kamdar, Chang, Beckmann, Greicius et al., 2008), and thus the relative increase after the visual stimulus – the N1 – was smaller. Note however, that the N1 component appeared in the same latency range as the early part of the RON component that is revealed in the novel–standard difference waves. The RON was negative at frontal electrode sites but was mirrored in positive polarity at posterior sites. Thus the apparent reduction of the visual N1 could be a residual effect of this overlapping positivity at the parieto-occipital sites where visual responses were measured.

The main correlate of the facilitation effect was localized to the P300. This indicates that novel sounds resulted in a greater amount of attentional capacity being invested in the categorization of the target (Kok, 2001). Furthermore, it suggests that, similar to the neutral warning sound facilitation effect (Hackley & Valle-Inclan, 2003), the novel facilitation effect took place after the initial perceptual-sensory processing of the target, and before response selection processes. The P300 enhancement was mirrored by a frontal negativity which could not be dissociated from the P300 effect on the basis of the present analyses. This negativity, therefore, might just represent a mirror image of the P300 enhancement. However, it is also possible that it is a processing negativity induced by the novel sound facilitation.

The facilitation effect by novel sounds can be explained by the arousal component of the OR that they generate. Generally, the arousal component of the OR has been largely ignored in oddball studies in which deviating sounds resulted in distraction. The distracting effects of the eliciting stimulus in these studies have been mainly explained by the attention component of the OR, as a result of temporarily drawing attention away from the main task towards the disrupting stimulus (Parmentier, Elford, Escera, Andrés, SanMiguel, 2008). However, the present facilitation effects could be explained by the arousal component, which may result in a general and unspecific state of readiness to respond. The mechanism leading to the facilitation effect would therefore resemble the burst of arousal that is proposed to underlie the facilitation caused by neutral warning sounds (Fernandez-Duque & Posner, 1997).

NP3 as an index of distraction

The MMN/N1-enhancement, NP3 and RON components were clearly present in the novel-standard difference waves. The NP3 and RON components have been frequently interpreted as an index of distraction and subsequent reorientation towards the task after distraction (Berti et al., 2004; Kaipio et al., 1999, 2000; Lepistö et al, 2004; Ferri et al, 2003; Rüsseler et al., 2002; Polo et al., 2003; Van Mourik, Oosterlaan, Heslenfeld, Konig, Sergeant, 2007; Gumenyuk, Korzyukov, Alho, Escera, Näätänen, 2004; Gumenyuk, Korzyukov, Escera, Hämäläinen, Huotilainen et al., 2005; Wetzel, Widmann, Berti, Schröger, 2006; Schröger & Wolff 1998b). However, the novel sounds in the present experiment resulted in facilitation rather than in distraction. This result asks for a more parsimonious explanation of the processes that these two components index. Indeed, dissociations between behavioural measures of distraction and the amplitude or elicitation of the NP3 and RON components have been frequently reported when attempting to use these electrophysiological traces as a measure of distractibility or attention deficits in different patient populations (e.g., see Polo et al., 2003; Van Mourik et al., 2007; Gumenyuk et al., 2005) or in developmental studies (Gumenyuk et al., 2004; Wetzel et al., 2006). Further dissociations have been found when using frequency deviations of increasing magnitude (Yago, Corral, Escera, 2001) and intensity decrements (Rinne et al., 2006).

The dissociation between behavioural distraction and the NP3 and RON components has led to alternative explanations of the psychological events that these components index (Munka & Berti, 2006; Escera & Corral, 2007; Ranganath & Rainer, 2003; Barceló, Periánez, Knight, 2002; Barceló, Escera, Corral, Periáñez, 2006; Berti, 2008; Polich, 2007). Different proposals have stressed the implication of different processes in NP3 generation, such as attention switching and orienting, evaluation of contextual novelty of the event and reconfiguration of task set and updating. Evidence from brain imaging, patient data and intracranial recordings suggests that a broad network of areas is activated by stimulus novelty, some of which contribute to NP3 generation (Linden, 2005; Ranganath & Rainer, 2003). This broad pattern of activation suggests that indeed the NP3 is a complex signal that probably reflects the summation of activation of several distinct functional areas. Therefore, possibly all of the processes stressed by different interpretations of the NP3 response might be implicated in it to different degrees, depending on the specific context in which it is elicited and resulting in slightly different patterns of activation of the underlying network that anyhow elicit a similar summated NP3 scalp potential.

A dissection of the different processes underlying NP3 generation might therefore be a more suitable approach to understand this complex signal, rather than a unifying interpretation. The processes thought to be implicated in NP3 generation can be separated according to the three fundamental components of attention: alerting, orienting and executive control (Fan, McCandliss, Sommer, Raz, Posner, 2002). All current interpretations of NP3 generation include to a certain degree a component of orienting. The orienting is towards an event, an object, or even an internal representation (Berti, 2008; Barceló, 2006) that was outside the focus of attention and has been evaluated as currently relevant, whether this orienting is triggered exogenously (e.g. Escera et al., 1998) or is a voluntary response to an external cue (Berti, 2008; Barceló, 2006). Interpretations of NP3 as an electrical sign of the OR have stressed the orienting component and have neglected the alerting component of the OR. Orienting, however, is always accompanied by a certain alerting component (Posner, 2008; Näätänen, 1992), as detection and orienting towards a relevant event implies the system must be ready to act upon it. Finally, more recent interpretations of the NP3 response include executive processes related to reconfiguration and updating of the task set, resulting from the attention switch to the new information (Escera & Corral, 2007; Berti, 2008).

In sum the NP3 seems to imply to a certain degree alerting, orienting and executive control processes. Indeed, NP3 has contributions from areas of the prefrontal cortex, temporo-parietal cortex and cingulate (Linden, 2005; Ranganath & Rainer, 2003), which participate in the alerting, orienting and executive control networks respectively (Fan, McCandliss, Fosella, Flombaum, Posner, 2005). The relative contributions of each of these networks to the NP3 might vary according to the particular situation in which it is elicited, therefore resulting in some cases in opposite behavioural outcomes (i.e. distraction vs. facilitation). The decomposition of the NP3 signal might allow the identification of subcomponents that can be more directly related to the behavioural responses, providing a more precise index of distraction.

Memory effects

When the task involved a higher memory load, it became more difficult to perform. This behavioural effect was accompanied by an enhancement of the visual P300 component in the memory task. Generally, the P300 amplitude decreases with memory load (Bledowski, Kadosh, Wibral, Rahm, Bittner et al., 2006; Klaver, Smid, Heinze, 1999; Watter, Geffern, Geffen, 2001; McEvoy, Smith, Gevins, 1998; see also review in Kok, 2001). Thus, it might seem surprising to find an enhancement of the P300 in the high memory load condition. However, note that here load was not increased in a parametric manner, but rather a memory task was compared to a simple visual classification task. Thus, the relative enhancement of the P300 component in the memory task might be due to a higher investment of attentional resources or a more detailed processing in this type of task. Indeed it is plausible to assume that if the P300 reflects event categorization processes (Kok, 2001), the categorization will be more demanding in the memory task in which the target stimulus had to be matched to a representation held in memory, than in the simple face/no face categorization condition. Additionally, a sustained posterior parietal negativity was present during the retention interval in the high memory load task. 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 (Rämä, Paavilainen, Anourova, Alho, Reinikainen et al., 2000; McEvoy et al., 1998; Vogel & Machizawa, 2004). Indeed, these negative slow waves have been related to continued processing in WM (Kok, 2001)

The memory load effects did not interact with the novelty effects, contrary to previous reports (SanMiguel et al., 2008a,b; Berti & Schröger, 2003). Indeed, the behavioural facilitation effect was not reduced in the high memory load task. This might suggest that memory load effects differ between facilitation and distraction; as deviating sounds generated distraction in these previous reports of memory modulation. However, it is possible that the memory load of only one face was insufficient to produce a modulation of the facilitation effect. Using a similar task, SanMiguel et al. (2008b) found that memory load reduced the facilitation effect; however, this modulation only became significant when a load of three faces was employed and capacity limits of short term memory appeared to be exceeded. On the other hand, distraction caused by novel sounds was reduced by working memory when a 1-back task involving the maintenance of only one digit was employed (SanMiguel et al. 2008a). However, n-back tasks are more taxing than delayed memory recognition tasks due to the updating required. Possibly, memory load might only have a significant effect on novelty when placing significant demands on executive processing or otherwise when approaching capacity limits.

Conclusion

In the present experiment novel sounds resulted in facilitation of visual task performance and elicited NP3. This result argues against the use of NP3 as an electrophysiological index of distractibility. Novel sounds facilitated a late stage of processing, as reflected by an enhancement of the visual P300 response. This facilitation might be due to novel sounds acting as alerting signals.

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5. General discussion

5.1. The impact of novel sounds on behaviour

The results of the present studies show that sounds are processed preattentively. Although participants were instructed to ignore the sounds in all studies, novel sounds captured attention involuntarily. Across all studies, whenever novel sounds were presented shortly before visual targets, they had a significant impact on behaviour, and were accompanied by a specific pattern of brain responses.

The study of how cues in the environment guide actions has been more thoroughly researched through the use of visual tasks; however, sounds might be more potent attention-capturing signals. Indeed the auditory channel is always open for stimuli reaching the ear from all directions in space, while gaze has to be directed to particular objects in order to perceive them. Moreover, auditory stimuli are processed faster than visual stimuli in the human brain. Also, in real life situations, humans tend to focus on visual tasks while monitoring the environment for relevant events or threats through the auditory channel. Therefore, the detection of novel or potentially relevant auditory events appears to be an attentional process of fundamental significance for cognitive function.

In the present studies, involuntary orienting towards novel sounds had a different impact on behaviour depending on specific task settings, in some cases resulting in facilitation and in some other cases resulting in an impairment of subsequent task performance. Distraction caused by novel sounds was found in studies I, II, III and IV (experiment 2). In these studies, novel sounds increased response time to subsequent targets, while HR was only significantly reduced by novel sounds in study I. Conversely, in studies IV and V novel sounds resulted in a decrease in response time and also in an increase in HR in study V, although this latter effect was less consistent across the different experiments of study IV. In study V, facilitation by novel sounds was accompanied by an enhancement of the visual P300 component to subsequent targets. In general, distraction effects were rather small (around 20 ms increase in RT) compared to the facilitation effects (around 50 ms decrease in RT).

Different lines of research have emphasized either detrimental or beneficial effects of unexpected sounds on behaviour using different paradigms. In study IV, we have shown that both effects can be obtained modifying task parameters using the same sequence of sounds. The research on facilitating effects of unexpected sounds has mainly focused on the alerting effects of these sounds (Fernandez-Duque & Posner, 1997), while the line of research showing distraction by deviating sounds has mainly made use of the oddball paradigm and has focused on the involuntary orienting of attention triggered by the sounds (Escera et al., 1998; Parmentier et al., 2008).

However, it has long been known that novel sounds trigger an orienting response that is composed of both of these alerting and orienting factors (Näätänen, 1992; Sokolov, 1963). Therefore, in study IV we proposed a model to explain the differential effects of novel sounds on behaviour based on the relative contribution of the alerting and orienting factors in specific task situations, mainly depending on the level of task demand. We suggest that a significant alerting effect will only take place when the task does not already induce a highly focused state. Whenever the alerting effect is significantly larger than the orienting effect, facilitation will occur. On the other hand, novel sounds will trigger an obligatory orienting of attention in all situations; whenever this orienting effect is larger than the alerting effect, distraction will occur.

In studies IV and V, reducing the event rate on the task led to an unfocused attentional state and therefore novel sounds produced a significant alerting effect that resulted in an overall facilitation of task performance. However, in studies I, II and III the task was very demanding due to the fast presentation rate of task-relevant stimuli, and therefore novel sounds did not result in a significant increase in alertness, leading to distraction due to a momentary orienting of attention towards the novel sound. These differences in task demand across studies were reflected in slower response times in the tasks in which facilitation was induced by novel sounds while response times were very fast, probably at ceiling, in the tasks in which distraction was obtained.

The interpretation that distraction is caused by a momentary orienting of attention towards the disrupting event and that facilitation is caused by a sudden increase in arousal is supported by other findings. Notably, distraction was reflected almost exclusively in an increase in response time, while, with the exception of study I, novel sounds did not deteriorate accuracy. This finding indeed indicates that target processing was mainly delayed rather than impaired by novel sounds and is in general agreement with previous studies where response times are consistently increased by novel sounds, while effects on accuracy are rather inconsistent accross studies (see Escera & Corral, 2007 for a review).

Very little research has been devoted to investigate the nature of the distraction effects caused by novel sounds. However, a study by Parmentier et al. (2008) directly investigated the issue and shed some light into the nature of these effects. In this study, Parmentier et al. (2008) searched for the cognitive locus of distraction by increasing the difficulty of visual processing of target stimuli and of target categorization and response selection in different conditions. The manipulation was based on the general assumption that if novel sounds interfere with any of these processes, increasing their difficulty would result in larger distraction effects.

However, although the general level of performance on the task dropped when either visual processing or response selection were made harder, the magnitude of distraction remained constant across conditions. Therefore, they hypothesized that distraction was due to a delay in target processing resulting from a momentary switching of attention towards the novel sounds. In order to test this hypothesis, an attention-capturing visual stimulus was introduced between the novel sound and the visual target in order to "re-capture" attention back to the visual task before the appearance of the visual target. Indeed, this manipulation resulted in the effective termination of the distraction effect, confirming that distraction was due to a momentary orienting of attention towards the sounds, resulting in a delay in target processing until attention had returned to the visual task.

Conversely, facilitation effects found in studies IV and V resemble those obtained in previous studies that used alerting signals such as unpredictive neutral cues (Fan et al., 2005), or accessory stimuli (Valls-Sole et al., 1995), indicating that the facilitation effect was indeed due to a general burst of arousal.

5.2. Brain indices of involuntary orienting: What does the NP3 reflect?

It has been repeatedly shown that involuntary orienting towards a novel sound is related to the elicitation of the NP3 component. The co-occurrence of these two events with behavioural distraction has led to the proposal that NP3 can be used as an index of distraction and distractibility (Escera et al., 2000), and NP3 has been used as such in several clinical populations that present attention problems, including dyslexia, alcoholism, autism, closed head injury, ADHD and schizophrenia (Cortiñas et al., 2008; Ferri et al., 2003; Gumenyuk et al., 2005; Kaipio et al., 1999; Kaipio et al., 2000; Lepisto et al., 2004; Polo et al., 2003; Russeler et al., 2002; van Mourik et al., 2007).

However, in study V we have shown that the same series of electrophysiological responses is elicited by novel sounds irrespective of whether they result in facilitation or distraction. This finding poses an important problem to the current, most widely accepted, interpretation of the functional significance of the NP3. Indeed, numerous dissociations between the amplitude or elicitation of the NP3 and the amount of distraction are present in the literature (e.g., see Gumenyuk et al., 2005; Polo et al., 2003; van Mourik et al., 2007). In an illustrative example, Rinne et al. (2006) manipulated the intensity of deviant sounds and found behavioural distraction caused by both deviants of increased and decreased intensity in respect to the standard sounds. However, NP3 was only elicited to intensity increments, when it was preceded by a combined N1-enhancement and MMN response and it was not elicited to intensity decrements in which case it was only preceded by MMN. Rinne et al. (2006) proposed that two different processes might trigger an attention switch: an enhancement of the N1 auditory response or the elicitation of MMN; and that NP3 is related solely to the first mechanism. However, studies finding behavioural distraction and NP3 responses without a preceding N1-enhancement challenge this interpretation (Bendixen, Roeber, & Schröger, 2007; Schröger, Bendixen, Trujillo-Barreto, & Roeber, 2007).

Several other views on the functional significance of the NP3 have emerged in the last years. Escera & Corral (2007) reviewed dissociations between NP3 amplitude and behavioural distraction indices and proposed that rather than reflecting orientation of attention per se, the NP3 signifies the evaluation of the contextual novelty of unexpected sounds (see also Ranganath & Rainer, 2003). Furthermore, they suggested that NP3 might reflect the reconfiguration of a cerebral network involved in updating task set information for goal-directed action selection. This interpretation is partly based on evidence from recent studies showing that NP3 and RON can be elicited in studies that did not aim to investigate the novelty response.

For example, Barceló, Periánez, Knight (2002) and Barceló, Escera, Corral, Periáñez (2006) found that feedback cues prompting the participant to accomplish a task-switch during the performance of a modified version of the Wisconsin Card Sorting Test (WCST) elicit NP3. This suggests a role of the frontally distributed NP3 response in the executive control of cognitive set shifting. Following this idea, Barceló et al. (2006) further proposed that NP3 responses could be seen as a transient activation in a neural network involved in solving response uncertainty in the face of either a novel event or a new task context. The larger the uncertainty conveyed by an environmental event, the larger the demands of control for response selection, and the larger the NP3 response elicited. Indeed, novel sounds in the oddball paradigm could be implicitly associated with an uncertain no-go response.

Berti (Berti, 2008b) used a memory updating paradigm in which an arithmetic operation had to be performed on one of a series of digits maintained in working memory. Each digit was assigned to a spatial location. The operation had to be performed either on a recently updated item (no switch of attention is required) or it should be performed on a different item (requiring an attention switch to this item). In this task, voluntary object switching within WM elicited NP3 and RON, therefore this result challenges the interpretation that the NP3 reflects *involuntary* attention switching. Rather, it was suggested that NP3 mirrors the re-configuration of a cerebral network in order to update task relevant information. According to Berti (2008b), RON may more closely reflect the allocation of the focus of attention than the NP3 response. The interpretation of Berti (2008b) resembles the view proposed by Polich (2007) suggesting that the NP3 is the manifestation of a frontal attention mechanism engaged to evaluate incoming stimuli. Processing of such stimulus events may then produce parietal (P3b) activity related to context-updating operations and subsequent memory-storage.

In summary, different views on the functional significance of the NP3 have stressed mainly the following processes: evaluation of relevance, attention orienting and executive processes such as context updating or task set reconfiguration. All of these processes can be combined in a holistic interpretation of NP3 elicitation in which different processes can contribute to the NP3 response and might be implicated in it to different degrees depending on the specific context in which it is elicited.

Indeed we can consider the following sequence of events. First, a relevant event is detected. This event might be a novel event that is detected by a preattentive change detection mechanism (e.g., in Escera et al., 1998) or it can be based on voluntary guidance relative to task instructions or expectancies (e.g., in Barceló et al., 2006; Berti, 2008b). Second, in order to evaluate the significance of this event attention is –either voluntarily or involuntarily- oriented towards it. Generally orienting is understood as orienting in space; however it is possible to orient to objects, features, orient to a certain time moment or orient towards an internal representation such as rule held in memory. This orienting will always be accompanied by a certain alerting component, as detection and orienting towards a relevant event implies the system must be ready to act upon it. Finally, the evaluation of the event leads to executive control processes based on it such as a reconfiguration of the task set, an updating of contextual contingencies or a general adaptation in cognitive control.

The complexity of the NP3 signal is reflected in the widely distributed activation pattern that underlies its generation (see Linden, 2005; Ranganath

& Rainer, 2003 for reviews). Indeed the areas that have been identified as potential sources for the NP3 signal in different studies participate in networks of alerting, orienting and executive control (Fan et al., 2005). Therefore, it appears that a dissection of the different processes underlying NP3 generation in different task settings is needed, rather than a unifying interpretation. Moreover the finding that NP3 is elicited both in conditions of distraction and conditions of facilitation indicates it cannot be directly related to the behavioural outcomes of this involuntary orienting.

In the present thesis, we found that WM load reduced both behavioural distraction (studies I and III) and behavioural facilitation (study IV) generated by novel sounds. This finding might shed some light into the nature of the processes engaged by novel sounds that are reflected in the NP3 component. The modulation of both behavioural effects indicates that WM load results in reduced processing of the novel sounds per se, at least after the initial preattentive stage of processing. The reduced processing of novel sounds was reflected in an attenuation of NP3 by WM load in studies I and III. This suggests that the NP3 reflects, at least partly, a more profound processing of novel events, after the initial preattentive processing has taken place. Indeed, we will argue in the following sections that WM load should only inhibit the processing of potentially relevant novel events at the stage at which their relevance is evaluated.

5.3. Top-down modulations of involuntary orienting towards novel sounds

The results of the present studies show that involuntary orienting towards novel sounds is largely dependent on the attentional or task set and as such can be modulated by several top-down factors. Notably, WM load attenuated behavioural and/or cerebral indices of involuntary orienting towards novel sounds in studies I-IV. Moreover, the direction of novel sound effects was also found to be dependent on the attentional demands of the concomitant task, leading to facilitation when the event rate was low (studies IV and V). Irrelevant sounds also had different effects depending on their temporal relationship with the task and whether they could be used as predictive signals for the task-relevant aspects of stimulation (study IV). Finally, executive control processes were triggered by the occurrence of novel sounds that resulted in distraction, in order to dynamically adjust the level of control exerted over novel sound processing in subsequent performance.

These results all represent good evidence of the importance of the attentional or task set in novel sound processing and of how voluntary and involuntary attention mechanisms interact in order to achieve an appropriate balance in each different situation, based on the relative relevance of different events, specific plans and goals and expectancies.

5.3.1 Dynamic adjustments in interference control

The results of study II indicate that after distraction by a novel sound has occurred, subsequent adjustments in the level of control are triggered, likely in order to avoid further distraction by the irrelevant sounds. This finding resembles the conflict adaptation effect that is found when distraction is induced by incongruent information in stroop-like tasks (Gratton et al., 1992).

To our knowledge, this is the first study that has directly investigated adjustments in interference control occurring after distraction by deviating sounds in the oddball paradigm. However, a few studies have reported behavioural and ERP measures to the first standard after a deviating sound (Ahveninen et al., 2000; Berti, 2008a; Roeber, Widmann, & Schröger, 2003). Generally, these studies indicate that distraction, albeit weaker, persists in the next trial after a novel or deviant trial and that a positive deflection can be observed in the ERPs that resembles the NP3. These results can be interpreted as a long lasting distraction effect. However, another possibility is that the occurrence of a novel sound effectively triggers a reconfiguration of the expectancies which are based on the memory trace of the preceding sounds. Therefore, a standard tone immediately following a novel sound might be acting, to a certain extent, as a deviant stimulus, at least until it is repeated a sufficient amount of times so that the expectancy of standard tone repetition is reinstated. It has indeed been demonstrated that the first standard stimulus following a deviant tone is at least partly processed as a deviant (Sams, Alho, & Naatanen, 1984).

In either case, the results of study II clearly indicate that actions are taken in order to potentiate performance in face of distracting stimulation after distraction has occurred, providing further evidence of top-down modulation of involuntary orienting. Activity in task-relevant information processing areas was enhanced, while auditory processing areas were inhibited. Using a stroop task, Egner & Hirsch (2005) showed that conflict adaptation is accomplished via the enhancement of task-relevant information, while irrelevant information processing was not modulated. The results of study II, however, support that both an enhancement of task relevant processing and an inhibition of task irrelevant processing take place in parallel after distraction is elicited by novel sounds.

5.3.2. Working memory load modulates involuntary orienting

In general, in the present studies, introducing WM load in the visual task resulted in a modulation of behavioural effects elicited by novel sound presentation and the related brain indices, in accordance with previous studies (e.g., Berti & Schröger, 2003). In studies I and III behavioural distraction was reduced when participants performed an n-back task. Reduced distraction was accompanied by an attenuation of NP3. In study IV, we observed that facilitation caused by novel sounds was also attenuated when participants had to hold three face stimuli in memory during a delay.

The results of studies II and III showed that WM load attenuated the activation of novelty processing areas in inferior frontal and superior temporal cortex. In the following sections, these findings will be discussed in detail.

5.3.3. How much working memory load is needed?

The results of studies I, II and IV show that involuntary orienting can be modulated by WM load, reducing both distraction and facilitation exerted by these sounds. However, no modulation by WM load was found in studies II and V. This discrepancy leads us to speculate that WM load might only modulate involuntary orienting when significant executive processing demands are placed by the WM task or otherwise when approaching capacity limits.

In study IV, although there was an overall significant interaction between the amount of load and the facilitation effect, this interaction was mainly driven by the load 3 condition. Paired comparisons revealed that the magnitude of the facilitation effect did not differ significantly between the no load and load 1 conditions and facilitation was only significantly reduced in the load 3 condition compared to the no-load condition. That is, in this particular task, a load of one face item was insufficient to modulate the novel sound effect. The same result was found in study V, were no significant interaction between auditory stimulus type and WM condition was found when a single face stimulus was maintained in memory. Therefore, it appears that WM load might only significantly modulate involuntary orienting when approaching capacity limits. Face stimuli are complex stimuli that contain many relevant features. The capacity limits for such items is reduced in comparison to simple items (Alvarez & Cavanagh, 2004). Indeed, participants were performing in the load 3 condition barely above chance level.

However, in studies I and III a load of one digit was sufficient to significantly reduce the distraction effect caused by novel sounds. This discrepancy might indicate that facilitation and distraction are not equally modulated by WM load. However, a more plausible explanation is that this discrepancy is due to differences between the specific WM tasks used. In studies I and III an 1-back task was implemented in the WM condition, while in study IV the memory task was a short term memory recognition task. N-back tasks are more taxing as they place more demands on executive processing. In such tasks, each item requires at least three operations: encoding, comparison in WM and updating of WM, operations which all need to be performed in rapid succession. Indeed, participants find it hard to maintain more than one item in WM in this kind of tasks. Therefore, a load on only one digit in an n-back task might be comparable to a load of two or three face stimuli on a short term memory recognition task.

However, in study II a 1-back task was also employed and no WM modulation over involuntary orienting was found. The format of the 1-back task in study II was slightly different from that of studies I and III. While in studies I and III the specific instruction was to compare whether two digits were the same or different, in study II participants had to assess whether the present digit was numerically larger or smaller than five in the no memory condition and whether the present digit was numerically larger or smaller than the previous digit in the WM condition. Therefore, while in studies I and III in the no memory condition the comparison could be executed based on visual features and needed no access to the memory representations of the digits, in study II the digit five had to be maintained and accessed in memory to be able to execute the comparison.

Moreover, the comparison between memory conditions could have also been confounded in study II by a numerical distance effect (Dehaene, Dupoux, & Mehler, 1990; Moyer & Landauer, 1967). That is, numerical comparisons between numbers that are far apart (e.g. 1 vs. 9) are easier to perform than numerical comparisons between numbers that are close together (e.g. 4 vs. 5). In the no memory condition the maximum numerical distance between two numbers was four (e.g. in 5 vs. 9) whereas in the 1-back memory condition the maximum numerical distance between two digits was eight (in 1 vs. 9). Therefore, altogether, in respect of the numerical distance effect, the 1-back memory condition was easier to perform. The numerical distance effect and the requirement to compare each digit to the number five might have shortened the difference in difficulty between the memory and no memory conditions in study II, leading to a weaker modulation of involuntary orienting by WM load that did not reach statistical significance.

In sum, the findings indicate that WM load reduces the processing of novel sounds whenever the WM task places significant demands on executive processing, such as when an n-back task is used, or otherwise when approaching capacity limits, which here required the maintenance of three face stimuli in memory.

5.3.4. Where and when does the modulation take place?

In both studies I and III the modulation by WM load on brain indices of involuntary orienting took place on the novelty-P3 component. Conversely, the initial preattentive change detection mechanism indexed by MMN/N1-enhancement was unaffected by WM load. This result is in agreement with a large body of research. MMN has been shown insensitive to manipulations of the direction of attention (Näätänen et al., 1978; Näätänen, Gaillard, & Mantysalo, 1980), difficulty of the task (Alho et al., 1992; Berti & Schröger, 2003; Dittmann-Balcar, Thienel, & Schall, 1999; Harmony et al., 2000; Kathmann, Frodl-Bauch, & Hegerl, 1999; Muller-Gass, Stelmack, & Campbell, 2005; Otten et al., 2000; Restuccia et al., 2005) and predictability of the deviance (Rinne et al., 2001; Sussman et al., 2003). However a few other studies manipulating visual task demands reported modulations of the MMN with task difficulty (e.g., Kramer, Trejo, & Humphrey, 1995; Yucel, Petty, McCarthy, & Belger, 2005a; Yucel, Petty, McCarthy, & Belger, 2005b).

For example, Yucel et al. (2005a; 2005b) found an attenuation of MMN when tracking difficulty was increased in a continuous perceptual-motor visual tracking task.

In an attempt to solve this controversy on the automaticity of MMN, Muller-Gass, Stelmack & Campbell (2006) optimized the experimental conditions for finding an effect of visual task difficulty on the MMN. This was accomplished by assuring a large separation in terms of difficulty between the easy and hard conditions and presenting stimuli at rapid and unpredictable rates. Under these conditions, they found no modulation of the passively elicited MMN component by visual task difficulty. The results also indicated that separate pools of resources are available for visual and auditory processing. Indeed, when participants were asked to simultaneously attend and discriminate changes in both the visual and the auditory stream, the auditory discrimination task was not affected by variations in difficulty in the visual task. Therefore separate pools of visual and auditory resources seem to exist. In consequence, the MMN elicited by auditory stimuli seems to be independent of visual task difficulty, as placing demand on the visual task does not deplete resources from auditory processing.

Nevertheless, the MMN is not completely independent of the direction of attention. In the same study by Muller-Gass et al. (2006), participants were more accurate detecting deviating stimuli when these stimuli were attended.

This attentional benefit however was only present in the case in which separation between deviants and standards was small, rendering the deviance difficult to detect. This pattern of behavioural results was accompanied by similar effects on MMN amplitude. MMN to small deviances was larger when the sounds were actively attended, but this effect was not present when deviances were large. This finding is in agreement with the results of previous studies (Alain & Woods, 1997; Arnott & Alain, 2002; Näätänen, Paavilainen, Tiitinen, Jiang, & Alho, 1993; Szymanski, Yund, & Woods, 1999; Trejo, Ryan-Jones, & Kramer, 1995; Woldorff & Hillyard, 1991; Woldorff, Hillyard, Gallen, Hampson, & Bloom, 1998).

Although in both studies I and III the modulation by WM load took place on the novelty-P3 component, this modulation was only found in the late phase on the NP3 in study I, where ERPs were measured, while in study III, the modulation occurred slightly earlier, at circa 230 ms, when the modulation was assessed on the magnitude of the dipoles fitted for the ERFs. Methodological differences between the studies might account for the latency differences, as EEG and MEG are each particularly sensitive to signals arising from neurons arranged in different orientations. It is thus possible that the modulation takes place at slightly different latencies in different areas of STG in which neurons are arranged in different orientations.

Although several ERP studies have found attentional modulations of the late phase of the NP3, only a few have found modulations of its early phase (e.g., Domínguez-Borràs, Garcia-Garcia, & Escera, 2008a). Therefore it seems that the late phase of the NP3 is more sensitive to attentional manipulations. Nevertheless, to date, a firm theoretical account for specific functional differences between the early and late phases of the NP3 does not exist, although the differentiation of these two phases is clearly supported by their different scalp distributions and sensitivity to attentional manipulations (Escera et al., 2001; Escera & Corral, 2007).

Altogether, the results support a model in which, although the initial mechanism of preattentive change detection might be enhanced by voluntary allocation of attention in certain conditions, it is largely unaffected by concomitant visual task performance. Involuntary orienting is therefore gated by visual task demands at a later stage. This stage of processing gated by task demand is associated to a more profound semantic analysis of the novel event and to the effective orienting of attention towards it. Indeed, although primary sensory responses are sensitive to attentional modulation, it is sensible to believe that the preattentive detection of novel events should take place regardless of the amount of focus that the visual task demands, as such events could be potentially relevant. Therefore involuntary orienting should only be gated after the relevance of the event has been assessed.

Moreover, the attentional modulation was found in STG in study III while in study II a modulation was only found on inferior frontal gyrus (IFG). Again, these differences might be due to fundamental methodological differences between the studies. Indeed, the MEG and fMRI techniques used in each of these studies respectively, measure different physiological phenomena that take place at different time scales. As fMRI measures integrate signals arising from the same area over several seconds, activity arising from STG related to the MMN and NP3 ERFs is summated. Therefore, as only part of this signal is modulated by WM load the contrast power at this region might have been reduced, leading to non-significant effects. On the other hand, discrete dipoles were fitted to the MMN and NP3 ERFs in study III, choosing to fit only one ECD for each hemisphere. As the ERFs could be explained by a single dipole fitted in STG, the contribution of other areas to the novelty response was not explored in this study, consequently missing any possible modulation over these additional areas.

Therefore, altogether the results indicate that WM load modulates novelty responses both in IFG and STG. These two areas have indeed been identified as novelty processing areas by several studies (Alho et al., 1998; Bledowski et al., 2004; Domínguez-Borràs et al., 2008; Downar et al., 2000; Kiehl et al., 2001). Moreover, it has been proposed that PFC would be engaged for the semantic analysis of novel events (Opitz et al., 1999; Tulving, Markowitsch, Craik, Habib, & Houle, 1996), therefore giving support to our hypothesis that involuntary orienting is modulated only at this stage and not before.

5.3.5. Which structures or processes control the modulation?

The modulation of involuntary orienting by WM load could be due to a capacity limitation in the overlapping fronto-parietal systems of WM and attention (Linden, 2007). In an fMRI study, Mayer et al. (2007) combined a selective attention task with a WM task and independently manipulated the demands of selective attention or WM encoding. The brain areas recruited by these two tasks presented a high degree of overlap in distributed posterior and frontal regions, in agreement with previous studies (Corbetta, Kincade, & Shulman, 2002; LaBar, Gitelman, Parrish, & Mesulam, 1999; Pollmann & von Cramon, 2000). Some of the overlapping areas (e.g. in PFC) showed additive responses when either the demand of the selective attention task or the amount of WM load were increased, indicating that the demands on these regions were well within their processing limits. However, specific visual, parietal and premotor areas were severely reduced in their WM load response under conditions of high attentional demand, suggesting a limitation on neural processing resources in these areas when both WM and attentional demands are placed.

In relation to the studies of the present thesis, if involuntary orienting towards novel sounds and WM processes were to be carried out by overlapping and capacity limited neural substrates, reduced involuntary orienting might occur when WM demands are placed on the task. Novel sounds mainly activated bilateral STG in study II and the NP3 response could be explained by bilateral sources in STG in study III, therefore this explanation for the WM modulation seems unlikely for the present studies, as STG is not known to be involved in visual WM. However, this possibility was certainly not directly explored here.

On the other hand, several different proposals indicate that the attenuation of irrelevant information processing might be an active function of the WM system, and that modulatory signals could have their origin in PFC (Duncan, 2001; Fuster, 2001; Miller, 2000; Miller & Cohen, 2001; Postle, 2005; Postle, 2006; Sakai, Rowe, & Passingham, 2002). This assumption is also partly based on overlapping neural substrates of WM and attention control in PFC that send biasing signals to sensory and association areas. In study II, several areas of PFC related to attention control were indeed more active in trials immediately following a novel trial, in which a modulation of sensory processing areas occurred, biasing responses towards task-relevant stimuli and against irrelevant sounds. A frontally distributed sustained response was also found in study I during the period between trials in which information had to be maintained in WM. Although these results may provide partial support to the hypothesis that the modulation of involuntary orienting arises from PFC in the present studies, an unequivocal causal relationship cannot be ascertained from this data in the present tasks.

5.3.6. Distraction enhancement vs. distraction attenuation by cognitive load

In the present studies loading WM resulted in a reduction of distraction caused by irrelevant novel sounds. These results appear to contradict the findings of several studies that motivated the “load theory of selective attention and cognitive control” (Lavie et al., 2004; Lavie, 2005) in which when WM was loaded distraction increased. The apparent controversies regarding the effects of main task difficulty on the processing or interference of irrelevant aspects of stimulation might dissipate if several other factors that might influence these effects are taken into account.

The amount of physical separation between targets and distractors, may be an important factor influencing the effects of load on distraction. For example, Chen (2003) studied the effects of perceptual load when relevant and irrelevant information pertained to the same object in a stroop task, finding that different levels of perceptual load did not lead to differential distraction by the irrelevant information. The findings were interpreted in the frame of the “zoom-lens” model of Eriksen and James (1986), which states that processing efficiency is an inverse function of the spatial extent of attentional focus and that the spatial extent will narrow around the relevant aspects of stimulation when demands increase. Chen (2003) concluded that when relevant and irrelevant information pertain to the same object, narrowing the attentional focus increases distractor processing and perceptual load has a negligible effect on the extent of distractor processing.

Indeed, using an auditory-auditory oddball distraction paradigm similar to the tasks employed in studies I, II and III, Muller-Gass & Schröger (2007) found distraction enhancement rather than distraction reduction by WM load. In this task, however, distracting frequency deviations were embedded in the target stimuli on which participants had to make a duration discrimination. Muller-Gass & Schröger (2007) proposed that greater attention to the task-relevant stimulus enhanced the processing of all stimulus characteristics, including the irrelevant distracting frequency change. Conversely, in the studies I and III of the present thesis more resources were allocated to the visual task, possibly reducing auditory processing and distraction. Therefore, the physical separation between the target and distractor aspects of stimulation (i.e., “channels”) explains the discrepancy between studies.

Another important factor that might influence the effects of load on distraction is whether the information held in memory overlaps with distractor or target processing. Kim et al. (2005) used a stroop task and instructed participants to respond to the meaning of the coloured word. When participants were required to maintain verbal information in memory during the performance of the task, stroop interference increased. However, this modulation did not occur when spatial information had to be held in memory. Conversely, when participants had to hold verbal information in memory but respond to the colour of the stroop stimulus rather than the meaning, stroop interference was decreased. Therefore, target relevant WM load increased stroop interference whereas distractor relevant WM load decreased stroop interference in this study.

These results have been further replicated in another study in which either houses or faces had to be maintained in memory while performing a matching task on faces presented against a background of houses (Park, Kim, & Chun, 2007). The authors related the findings to the fact that several independent WM stores exist for different types of information (Mohr & Linden, 2005; Repovs & Baddeley, 2006; Sala, Rama, & Courtney, 2003), further suggesting that the same content-specific system subserves both WM and attentional selection (Kim et al., 2005). Therefore, they proposed a specialized-load account: increasing load in a task will reduce processing of individual items that share processing mechanisms with the specific type of load employed (Park et al., 2007).

This proposal however is difficult to extrapolate to the studies of the present dissertation, as here the WM task was the main task on which distraction was measured; therefore information held in WM did not compete in any way for processing resources with the task. That is, both the studies reviewed above leading to the specialized load account (Kim et al., 2005; Park et al., 2007) and the studies that have led to the perceptual vs. cognitive load account (Lavie et al., 2004; Lavie, 2005) employed dual tasks, in which a selective attention task had to be performed during the delay period of a delayed memory recognition task. Therefore, in those studies the memory task and the selective attention task competed for processing resources, while in all studies of the present thesis either a memory or a no-memory task had to be performed. Most likely, in the present studies increasing load on the task resulted in a greater focusing of attention, in turn leaving fewer resources for processing the distractors that were presented in a different channel to the memory task.

An important finding in respect to the controversy between distraction enhancement and distraction attenuation by WM load was obtained in study IV. According to Lavie (2005), modulation by WM load occurs because load competes in resources with an executive control mechanism attempting to inhibit prepotent responses towards a distractor. However, in study IV, WM load modulated facilitation caused by novel sounds. Such a finding is difficult to accommodate in this explanation as, hypothetically, there would be no reason to inhibit a response that facilitates performance.

In summary, all the findings summarized above support the general proposal that distraction will be attenuated whenever fewer resources are available to process the distracting aspects of stimulation. Indeed, the finding that WM load modulated both distraction and facilitation supports the notion that it is the processing of the distractor per se what is modulated. The amount of physical separation between targets and distractors, the amount of overlap between information held in memory with either distractor or target processing resources and whether WM demands are placed on the main task or a secondary task are factors which will all influence the distribution of resources between distractors and targets. Whenever there is a larger conflict between distractors and target stimuli for processing resources distraction might be increased. In this sense, it is worth noting that novel sounds did not impose a specific conflict with target processing, while in stroop tasks such as those of Kim et al. (2005) and Lavie (2005), distraction is defined in terms of conflict between target and distracting features of stimulation.

5.4. Summary of findings

The present thesis investigated factors and brain mechanisms that can modulate involuntary orienting towards unexpected novel sounds and influence the impact that these sounds have on behaviour.

The results clearly showed that involuntary orienting towards novel sounds is not automatic and can be modulated by several factors. Moreover, the impact that involuntarily orienting towards a novel sound has on behaviour is also determined by the attentional or task set.

Novel sounds trigger a combined alerting and orienting response. The results suggested that the specific contribution of each of these effects can determine whether novel sounds result in distraction or facilitation in specific tasks. In this sense, distraction will occur whenever the relative contribution of orienting is larger than the relative contribution of alerting, and vice versa. In the present studies, the same sequence of electrophysiological indexes accompanied involuntary orienting to novel sounds irrespective of whether they resulted in facilitation or distraction. This result indicates that NP3 particularly, should not plainly be interpreted as an index of distractibility.

The findings indicate that the relative contribution of alerting and orienting processes can depend on the demands of the task that is being performed, particularly on the event rate. In the present studies, whenever the task being performed generated a high arousal state, the relative contribution of alerting generated by novel sounds was undermined.

The results showed that involuntary orienting towards unexpected novel sounds is reduced during the performance of visual WM tasks, at least when the specific task places significant demands on executive processing or the amount of load approaches capacity limits. The reduction of involuntary orienting by WM load in turn diminished any facilitation or distraction effects that these novel sounds had on behaviour.

The neurophysiological mechanism underlying the modulation of involuntary orienting to novel sounds by WM load in the present studies appeared to be the inhibition of specific cortical responses related to novelty processing. WM load inhibited responses to novel sounds in IFG and in STG. The inhibition of responses took place after the initial preattentive change detection response had taken place and resulted in a reduced NP3 recorded at scalp. These results indicate that involuntary orienting to novel sounds is prevented only after a certain semantic analysis of the event has taken place.

After distraction by a novel sound has occurred, subsequent adjustments in control were triggered. Although distraction apparently persists for at least up to 2 seconds, interference control processes were observed immediately after distraction. These adjustments in control were, in the present study, accomplished by enhancing sensory processing of task-relevant representations in visual areas while inhibiting auditory processing areas.

5.5. Future directions

In study IV a manipulation of event rate led to either distraction or facilitation by novel sounds. This result led us to conclude that the amount of task demands will determine the direction of novel sound effects. However, it remains unclear which factors specifically determine task demands. For example, manipulations of WM load clearly affected the demands of the task, and however did not lead to novel sound effects of opposite directions. The proposed model may serve as a general guide to test further assumptions. For example, a parametric manipulation of event rate should allow establishing the specific inflexion point in which the direction of novel sound effects reverses and novel sounds have virtually no effects.

Although this model provides a framework in which to interpret the nature of distraction and facilitation effects, it also remains unclear which specific processes are facilitated or impaired by novel sounds. Studies using the oddball paradigm have rarely investigated effects of novel sounds on brain responses to subsequent targets. In study V we found that when novel sounds resulted in facilitation, the P300 component elicited to visual targets was enhanced. A comprehensive investigation of modulations of brain responses elicited by target stimuli after the occurrence of novel sounds would shed some light into the nature of their effects and could also provide evidence to corroborate the proposed model.

The finding that NP3 is elicited both when facilitation and when distraction occur led us to attempt a reinterpretation of its functional significance, proposing that it is a complex response involving alerting, orienting and executive processing. This interpretation indeed encompasses all the different findings; however it renders the NP3 a very unspecific signal, therefore undermining its usefulness as an index of specific cognitive processes. Therefore, it appears that a decomposition of the different components of the NP3 signal is essential. For example, directly comparing NP3 deflections obtained under conditions of facilitation or distraction might allow differentiating specific subcomponents that are more directly involved in alerting or orienting. Another possibility would be to make a deep analysis of independent sub-networks of areas within the broadly extended activation pattern that is related to NP3 and then assess how the activity in these independent networks relates to different behavioural outcomes.

The present studies did not provide a clear account for the discrepancies that exist between studies obtaining either enhancement or attenuation of distraction by WM load. However, we have pointed out that the determining factor might be the amount of processing resources that are left to process the distractor. This general interpretation, however, can only be corroborated by an exhaustive evaluation of the different factors that might influence the amount of processing resources that are left to process the distractor. This can only be achieved by independently manipulating each of the possible factors that have been outlined in the present thesis and assessing the effects of each of these manipulations on the amount of interference by distractors.

In study II we found that after distraction by a novel sound, adjustments in the level of control take place, supposedly to prevent further distraction. This latter assumption, however, was not tested directly, as two distracting events were never presented in immediate succession. The question thus remains of whether the attention effects that were found would be indeed effective in avoiding distraction by a subsequent novel sound. Also, an intriguing question is what would happen in the case in which novel sounds result in facilitation. Hypothetically, no adjustments in control would be needed after a beneficial event. If adjustments were to occur also in this situation, this would indicate that they are not triggered in order to prevent distraction, but rather by novelty per se.

In different studies, we found that WM load modulates novelty responses in STG and in IFG. We have proposed that responses to novel sounds should not be modulated before an analysis of their relevance has been achieved. An analysis of the temporal pattern of modulation of these two areas could provide significant insights to understand the dynamics of the modulation of involuntary orienting. That is, does the evaluation of the relevance of the event take place first, and then involuntary orienting is triggered or not depending on this evaluation, or is orienting towards the novel event needed in order to be able to evaluate its relevance? Furthermore, the final trigger of involuntary orienting could be determined by recurrent loops of activation between these two areas, achieving a more profound evaluation of the event in each recurring loop.

Finally, studying the interaction of WM with attention can provide insights into the basis of significant individual differences that exist in distraction generated by unexpected events. Individual differences in WM capacity appear to correlate with the capacity to select relevant information and suppress irrelevant information and both WM capacity and the ability to suppress irrelevant information have been shown to diminish with ageing. An interesting extension of this work would therefore be to compare individuals that differ in their WM capacity and in their ability to suppress involuntary orienting in order to achieve a better understanding of how attention and WM interact.

6. Conclusions

The general aim of this thesis was to investigate how voluntary and involuntary mechanisms interact in the control of attention. The results clearly showed that involuntary orienting towards novel sounds is not purely stimulus-driven, but is modulated by top-down factors.

In study I, we investigated whether involuntary orienting towards novel sounds and the consequent distraction effects are modulated by WM load. The results showed that during the performance of a task requiring the maintenance of information in WM, distraction generated by novel sounds is attenuated. Moreover, this attenuation was reflected in a modulation of the NP3 component elicited by novel sounds, demonstrating that the modulation takes place after the preattentive detection of the change has occurred.

In study II, we investigated which specific brain areas show novelty responses that are modulated by WM load using fMRI, finding an attenuation in IFG. The precise spatio-temporal dynamics of WM modulation was investigated in study III using magnetic recordings. This study provided evidence that both MMN/N1-enhancement and NP3 can be explained by bilateral sources in STG and showed that the modulation of involuntary orienting is accomplished by attenuating the STG sources of NP3 at a latency of approximately 200 ms.

Study II also investigated possible adjustments in control taking place after distraction. The results showed that in trials immediately following a novel sound trial, auditory processing areas are inhibited while the activity of visual areas processing task-relevant information is enhanced.

Study IV aimed at clarifying the critical factors that determine whether the occurrence of novel sounds results in distraction or in facilitation. The results showed that when the event rate of the visual task is low, novel sounds result in facilitation while when the event rate is high, novel sounds result in distraction.

Finally, study V investigated whether the same sequence of electrophysiological responses is elicited by novel sounds when these sounds result in facilitation, as when they result in distraction. Novel sounds that facilitated task performance elicited the NP3 component, undermining its use as a general measure of distractibility. Moreover, the nature of the facilitation effect was investigated by comparing electrophysiological responses to visual targets following novel and standard sounds. Novel sounds resulted in an enhancement of the P300, a late cognitive component, to subsequent targets, suggesting that novel sounds do not facilitate the sensory processing of targets but rather postperceptual processes.

7. References

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ANNEX 1. Spanish summary

1. Introducción

Novedad y atención involuntaria

Nuestros sistemas sensoriales están específicamente diseñados para detectar cambios. Las neuronas responden preferencialmente a los inicios y los finales de la estimulación, mientras que las respuestas cerebrales se habitúan ante la estimulación continuada. Es decir, percibimos el mundo a través de sus discontinuidades. Los acontecimientos salientes o novedosos que destacan considerablemente del contexto en el que ocurren son preferentemente procesados en el cerebro. Estos estímulos generan una respuesta típica de orientación (Sokolov, 1963) que prepara al individuo para responder hacia el acontecimiento novedoso, dirigiendo por lo tanto el comportamiento.

La selección voluntaria e involuntaria deben estar en equilibrio

La selección de la información relevante se lleva a cabo por los mecanismos atencionales, que típicamente se clasifican como voluntarios e involuntarios (Corbetta & Shulman, 2002; Näätänen, 1992; Posner, Nissen, & Ogden, 1978; Posner, Snyder, & Davidson, 1980). La orientación involuntaria hacia un acontecimiento novedoso puede ir en perjuicio de los procesos cognitivos en curso, un fenómeno al que comúnmente nos referimos como distracción. La distracción ocurre cuando un acontecimiento novedoso captura la atención de manera involuntaria, y por tanto dejamos de atender a lo que previamente estaba en el foco atencional. Por tanto, es de importancia fundamental comprender como se consigue un equilibrio razonable entre mantener el foco de atención en las tareas en curso y detectar eventos en el contexto que pueden ser potencialmente relevantes.

Pero, ¿qué es la atención?

El concepto de atención es clave para entender el funcionamiento de la mente y adquiere relevancia a consecuencia de una limitación fundamental del sistema nervioso: no todo puede ser procesado al mismo tiempo. Tradicionalmente se han utilizado tareas de atención selectiva para su estudio (p.ej., Posner et al., 1980). En este tipo de tareas, los sujetos tienen que atender a un lugar indicado por una señal y posteriormente responder a un objetivo (el estímulo diana) que puede o no aparecer en ese lugar. Cuando el estímulo diana aparece en el lugar atendido, las respuestas a ese estímulo son más precisas y rápidas, mientras que si el estímulo diana aparece en un lugar no atendido, el rendimiento es peor. Además, si se presenta un estímulo inesperado que captura la atención involuntariamente en una localización no atendida, los estímulos diana que aparezcan posteriormente en esa localización también obtienen beneficios atencionales. Tradicionalmente se ha pensado que la atención involuntaria funciona de manera automática. Sin embargo, más recientemente se ha demostrado que la captura atencional exógena no depende únicamente de la estimulación externa, si no que también depende de si el estímulo distractor comparte alguna característica relevante para la tarea en curso (Folk, Remington, & Johnston, 1992).

El mecanismo neurofisiológico que subyace a la selección atencional, parece ser una facilitación de las respuestas neuronales relacionadas con las representaciones relevantes, y una inhibición paralela de las respuestas neuronales relacionadas con las representaciones irrelevantes (Desimone & Duncan, 1995). Posner y Petersen (1990) propusieron que el control de la atención se realiza por una red independiente de áreas cerebrales, y que este sistema de atención se puede dividir en varios subsistemas o redes de áreas. Revisiones recientes de este modelo han diferenciado tres componentes fundamentales de la atención implicados en la orientación, el control ejecutivo y la alerta respectivamente, y que son llevados a cabo por redes independientes de áreas cerebrales (Fan, McCandliss, Sommer, Raz, & Posner, 2002; Fan, McCandliss, Fossella, Flombaum, & Posner, 2005). Una propuesta diferente ha señalado dos redes principales; una red dorsal fronto-parietal implicada en la atención voluntaria o “desde-arriba”, y otra red fronto-parietal ventral lateralizada al hemisferio derecho responsable de la orientación "desde-abajo" (Corbetta & Shulman, 2002; Corbetta, Patel, & Shulman, 2008).

Memoria de trabajo, corteza prefrontal y control ejecutivo

Una línea de investigación que ha demostrado ser muy productiva en el estudio de las interacciones entre el control voluntario e involuntario de la atención, ha sido la que manipula la memoria de trabajo (MT). Estos estudios han aportado evidencias de modulación por parte de mecanismos endógenos sobre la orientación involuntaria y han señalado a la MT como un factor importante en el control de la atención.

La memoria a corto plazo se refiere a la capacidad de mantener activa una cierta cantidad de información durante un período corto de tiempo. La MT se refiere al hecho de que esta información pueda ser manipulada mientras está activa. La capacidad de la memoria de trabajo es más reducida que la de la memoria a corto plazo y se ha concluido que depende de la naturaleza de la manipulación que tiene que ser realizada sobre la información que se mantiene en memoria.

El sustrato cerebral de la MT parece ser fundamentalmente el córtex prefrontal. Resultados recientes han apuntado además hacia una especialización funcional dentro de la corteza prefrontal, diferenciando dos regiones principales – la ventrolateral y la dorsolateral PFC- con funciones diferentes dentro de la memoria de trabajo (Courtney, 2004; Levy &

Goldman-Rakic, 2000). El córtex prefrontal envía señales que modulan la actividad en áreas de procesamiento sensorial para mantener activas las representaciones de los estímulos que se han de mantener en memoria (Miller, Erickson, & Desimone, 1996).

Numerosas evidencias apuntan hacia una relación directa entre el control de la atención y el concepto de MT (Awh, Vogel, & Oh, 2005). Por ejemplo, la memoria de trabajo sirve para mantener la distinción entre estímulos relevantes e irrelevantes en las tareas de atención selectivas (Rainer, Asaad, & Miller, 1998) y el contenido de la memoria de trabajo influye en la dirección de la atención (Downing, 2000). A partir de esta evidencia, numerosos modelos han asignado funciones ejecutivas a las funciones de MT que tienen su sustrato en la corteza prefrontal. Estos modelos proponen que el control cognitivo surge del mantenimiento de patrones de actividad en la corteza prefrontal que representan objetivos y planes para conseguirlos, a la vez que proporcionan señales moduladoras a otras estructuras cerebrales para guiar la conducta (Duncan, 2001; Fuster, 2001; Miller & Cohen, 2001).

El impacto de los sonidos novedosos sobre el comportamiento

Los sonidos novedosos pueden facilitar el rendimiento de varias maneras, como por ejemplo si se utilizan como avisos en las tareas típicas de atención selectiva. Sin embargo, también pueden ser una fuente de distracción en muchas situaciones. La distracción causada por los sonidos novedosos se puede estudiar con el paradigma "oddball" (Escera, Alho, Winkler, & Näätänen, 1998), donde los sujetos deben clasificar estímulos visuales según una categoría particular (p. ej., números pares/ impares), sin atender a los sonidos irrelevantes que preceden brevemente a los estímulos visuales. Los sonidos irrelevantes consisten en trenes de tonos repetitivos entre los que ocasionalmente se presenta un sonido novedoso.

Mediante la técnica de los potenciales evocados se han investigado extensamente los correlatos cerebrales del procesamiento de los sonidos novedosos. Para aislar la actividad relacionada con el procesamiento de la novedad, a los potenciales evocados obtenidos por los tonos repetitivos se les substraen los potenciales evocados ante los tonos novedosos, obteniendo el potencial de distracción (Escera & Corral, 2003; Escera & Corral, 2007). El potencial de distracción se caracteriza por una forma de onda tri-fásica: un pico temprano negativo denominado el potencial de disparidad (MMN), un segundo pico positivo, denominado P3a o novelty-P3 (NP3), y un tercer pico negativo denominado negatividad de reorientación (RON). Se ha propuesto que estos picos proporcionan un índice de tres etapas principales en el control exógeno de la atención (Escera, Alho, Schröger, & Winkler, 2000; Escera & Corral, 2007): a) la detección del cambio y el mecanismo de captura de la atención que están asociados a MMN, b) el componente NP3 que está relacionado con la orientación de atención, y c) RON que está relacionado con el retorno de la atención hacia la tarea principal después de una distracción momentánea.

Evitando la distracción: dificultad de la tarea y control ejecutivo

Una situación particular en la cual la distracción al parecer puede ser anulada ejerciendo control ejecutivo es en el caso en que ésta surge por un conflicto entre información relevante e irrelevante (Gratton, Coles, & Donchin, 1992). El conflicto es una de las fuentes de distracción que han sido investigadas más intensamente a través de tareas stroop (MacLeod, 1991). En este tipo de tareas, los efectos de distracción se reducen dramáticamente cuando el conflicto ocurre inmediatamente después de otro ensayo conflictivo. Esta reducción de la distracción aparentemente no se consigue inhibiendo el procesamiento de la información irrelevante, si no aumentando el procesamiento de la información relevante (Egner & Hirsch, 2005).

El impacto de los distractores sobre el comportamiento también puede ser regulado dependiendo de la dificultad de la tarea que se está realizando, sin embargo, diferentes resultados apuntan a un aumento o una disminución de la distracción cuando se incrementa la dificultad de la tarea. Lavie y colaboradores (Lavie, Hirst, De Fockert, & Viding, 2004; Lavie, 2005) han propuesto que cuando la tarea agota los recursos necesarios para poder inhibir las respuestas a los distractores, la distracción aumenta. Sin embargo, cuando la dificultad de la tarea no es de cariz cognitivo si no perceptual, la tarea principal puede agotar todos los recursos perceptivos, de manera que el distractor no sería procesado, llevando a una disminución de la distracción en estos casos.

La propuesta de Lavie (Lavie, 2005) contrasta sin embargo con otros estudios en los que se ha encontrado una disminución de la distracción en condiciones de carga cognitiva. Específicamente, se ha encontrado que durante la realización de tareas que requieren la MT, la interferencia de los distractores se reduce (Gazzaley, Cooney, McEvoy, Knight, & D'Esposito, 2005; Sreenivasan & Jha, 2007). De hecho, se ha propuesto que una de las funciones de la MT es prevenir que la información irrelevante entre en el foco de atención para evitar que interfiera con la información que se ha de mantener en memoria (Postle, 2006).

Las modulaciones de la orientación involuntaria de la atención se ven reflejadas en el potencial de distracción, lo que permite estudiar los mecanismos cerebrales subyacentes a esta modulación. Mientras que el mecanismo pre-atencional de la detección del cambio que refleja MMN se cree que es sumamente automático y no está bajo la influencia de factores endógenos (Näätänen, 1990; Näätänen, 1992), varios estudios demuestran que NP3 se ve modulado por factores atencionales, siendo su fase tardía más sensible a estas modulaciones atencionales (Berti & Schröger, 2003; Domínguez-Borràs, Garcia-Garcia, & Escera, 2008; Harmony et al., 2000; Restuccia, Della Marca, Marra, Rubino, & Valeriani, 2005).

2. Objetivos e hipótesis

Objetivo general

El objetivo de esta tesis ha sido estudiar mecanismos de control cognitivo que actúan sobre el tratamiento de los sonidos novedosos en el cerebro humano. Aunque tradicionalmente se ha pensado que la orientación involuntaria refleja un proceso automático, durante las dos últimas décadas se ha hecho evidente que de hecho se puede modular por mecanismos endógenos. Por tanto, el objetivo de esta tesis ha sido investigar cómo mecanismos involuntarios y voluntarios interactúan en el control de atención. Específicamente, hemos explorado varios factores que podrían determinar el impacto que los sonidos novedosos tienen sobre los procesos cognitivos en curso, y los mecanismos cerebrales subyacentes.

Objetivos e hipótesis específicas

Estudio I

El objetivo de este estudio ha sido investigar la interacción entre mecanismos endógenos y exógenos en el control de atención y establecer el papel de la memoria de trabajo en esta interacción. La hipótesis de partida de este estudio es que la orientación involuntaria no es completamente automática, si no que depende de la influencia de factores endógenos y por lo tanto puede ser modulada. Específicamente, hipotetizamos que el sistema de memoria de trabajo inhibe la orientación involuntaria en situaciones en que la tarea en curso es muy demandante. Esta modulación ejercida por el sistema de memoria de trabajo se debería reflejar en la reducción de índices conductuales y cerebrales de la orientación involuntaria hacia sonidos novedosos cuando se realiza una tarea que implica una carga sobre la memoria de trabajo, en comparación con cuando no se requiere memoria de trabajo para realizar la tarea.

Estudio II

Este estudio investigó diferentes mecanismos de control cognitivo ante la distracción por sonidos novedosos. Primero, investigamos la inhibición de la distracción por la carga en memoria de trabajo e intentamos localizar esta inhibición a áreas cerebrales específicas relacionadas con el tratamiento de la novedad. Segundo, investigamos ajustes dinámicos en el control cognitivo después de la distracción. Supusimos que después de la distracción causada por un sonido novedoso, tendrían lugar ajustes en el nivel de control ejecutivo para evitar la distracción en el siguiente ensayo. Por lo tanto, examinamos una posible inhibición del procesamiento de los estímulos novedosos en áreas auditivas o un posible aumento del procesamiento de los estímulos relevantes de la tarea en áreas visuales inmediatamente después de la distracción por un sonido novedoso. Además, examinamos si estos hipotéticos ajustes secuenciales en el nivel de control cognitivo también son modulados por la carga de memoria de trabajo.

Estudio III

Este estudio tenía como objetivo proporcionar un marco espacio-temporal a la modulación de la distracción por la carga en memoria de trabajo. En el Estudio I investigamos con registros electrofisiológicos en qué fase son moduladas las respuestas a los sonidos novedosos por la carga en memoria de trabajo y en el Estudio II investigamos qué áreas cerebrales específicas son moduladas por la carga en memoria de trabajo mediante respuestas hemodinámicas. Sin embargo, estas dos técnicas miden respuestas fisiológicas diferentes que ocurren en escalas de tiempo distintas. Por lo tanto, aquí utilizamos una técnica (MEG) que proporciona tanto resolución temporal como espacial, para establecer en qué fase se modula la actividad en respuesta a estímulos novedosos en áreas cerebrales específicas.

Supusimos que el procesamiento de la novedad sería inhibido por la carga de memoria de trabajo en la corteza auditiva en una fase tardía de procesamiento. Por lo tanto, los procesos pre-atencionales iniciales de detección del cambio auditivo que tienen lugar en la corteza auditiva no deberían verse afectados por la carga en memoria de trabajo, mientras que las respuestas subsiguientes en este área, reflejadas por el componente P3a, serían inhibidas por la carga en memoria de trabajo.

Estudio IV

Los sonidos inesperados causan distracción o facilitación de las tareas en curso en diferentes circunstancias. Este estudio tenía como objetivo la clarificación de los factores críticos que determinan que los sonidos novedosos generen distracción o facilitación. Además, existe una controversia entre estudios que muestran modulaciones cuantitativas del efecto de distracción por la carga de memoria de trabajo. Mientras que algunos estudios muestran que la distracción se ve reducida en situaciones de carga, otros estudios muestran el resultado contrario, que la distracción se ve aumentada. Por lo tanto, este estudio tuvo como objetivo aportar datos para resolver esta controversia. Supusimos que el set cognitivo o atencional determina la dirección de los efectos de los estímulos novedosos inesperados sobre el comportamiento. Específicamente, manipulamos la estructura de la tarea visual y las contingencias entre los sonidos irrelevantes y los estímulos relevantes de la tarea. Las demandas de la tarea también fueron manipuladas modificando la duración del estímulo diana y la tasa de presentación de los estímulos visuales. Hipotetizamos que al menos uno de estos factores debería determinar la dirección de los efectos de los sonidos novedosos. Además, hipotetizamos que la carga en memoria de trabajo debería modular cuantitativamente los efectos de los sonidos novedosos.

Estudio V

Este estudio se centró en el efecto de facilitación que fue descrito en el Estudio IV. El objetivo de este estudio fue establecer la naturaleza y el locus de este efecto de facilitación mediante el registro de respuestas electrofisiológicas. Además, investigamos si el efecto de facilitación es modulado por la carga de memoria de trabajo mediante los mismos mecanismos que modulan el efecto de distracción. El resultado obtenido en el estudio anterior de que los sonidos novedosos presentados en una secuencia oddball causan facilitación conductual postula una pregunta importante sobre las respuestas electrofisiológicas que se obtienen ante estos sonidos. Si la misma secuencia de respuestas electrofisiológicas es generada por sonidos novedosos siempre que conduzcan a distracción o facilitación, el empleo extendido de estas respuestas electrofisiológicas como índices de distracción o distractibilidad quedaría desaconsejado. Por lo tanto, en este estudio exploramos las respuestas electrofisiológicas generadas por sonidos novedosos en el caso en el que estos sonidos facilitan el rendimiento en la tarea.

3. Método general

Los estudios que componen esta tesis han sido realizados en los siguientes laboratorios y centros de investigación:

Estudios I y IV: Grupo de Investigación en Neurociencia Cognitiva, Departamento de Psiquiatría y Psicobiología Clínica, Universidad de Barcelona, España.

Estudio II: Institute for Cognitive Neuroscience, Department of Neuropsychology and Behavioral Neurobiology and Center for Advanced Imaging, Universidad de Bremen, Alemania.

Estudio III: Department of Neuropsychiatry, Hirosaki University School of Medicine, Japón.

Estudios IV y V: Wolfson Centre of Clinical and Cognitive Neuroscience, School of Psychology, Bangor University and North Wales Clinical School, Reino Unido.

Los sujetos que participaron en todos los estudios de esta tesis eran individuos sanos sin historia de enfermedades psiquiátricas o neurológicas, y con agudeza auditiva y visual normal o corregida a niveles de normalidad. Todos los participantes dieron su consentimiento escrito para participar después de que se les explicase la naturaleza de los experimentos, que fueron aprobados por los comités éticos locales correspondientes.

En todos los estudios, los voluntarios realizaron tareas visuales presentadas por ordenador mientras escuchaban estímulos auditivos irrelevantes. Los sujetos tenían instrucciones de concentrarse en la tarea visual e ignorar los sonidos irrelevantes y responder a los estímulos de la tarea visual tan rápidamente y correctamente como fuera posible.

En general, se utilizaron modificaciones de una tarea de distracción auditivo-visual bien establecida (Escera et al., 1998) en la que se presentan tonos repetitivos ("estándar") que ocasionalmente se sustituyen por sonidos novedosos. Además se utilizaron dos tipos de tareas de memoria de trabajo, tareas n-back y tareas de reconocimiento a corto plazo.

En todos los estudios se tomaron medidas conductuales de rendimiento y en todos excepto esl estudio IV se tomaron medidas de actividad cerebral. En los estudios I y V se registraron potenciales evocados (PEs), mientras en el estudio II se tomaron medidas de resonancia magnética funcional (RMf), y en el estudio III se tomaron medidas de magnetoencefalografía (MEG). Todas estas técnicas permiten la observación no invasiva de la actividad cerebral en vivo; sin embargo, cada una de las técnicas usadas está basada en fenómenos fisiológicos diferentes y proporciona datos en escalas de resolución anatómica y temporal diferente. Debido a estas diferencias fundamentales, se puede esperar un cierto grado de discrepancia entre técnicas. Además, la combinación de técnicas diferentes permite una visión de conjunto de los fenómenos de estudio.

Los potenciales evocados son señales eléctricas generadas por las neuronas mientras que la magnetoencefalografía mide los campos magnéticos asociados a estas señales eléctricas. Estas dos técnicas proporcionan una alta resolución temporal, y la magnetoencefalografía también permite localizar el origen de las señales con cierto grado de precisión. La RMf, sin embargo, mide el aporte energético a diferentes regiones cerebrales y es por tanto una medida indirecta de la actividad cerebral. Sin embargo, esta técnica tiene una alta resolución espacial, pudiendo localizar la actividad con un error de menos de un mílimetro.

4. Resultados y discusión

Esta tesis ha investigado los factores y los mecanismos cerebrales que modulan la orientación involuntaria ante sonidos inesperados novedosos, así como el impacto que estos sonidos tienen sobre el comportamiento. Los resultados han evidenciado claramente que la orientación involuntaria hacia los sonidos novedosos no es automática y que puede ser modulada por varios factores. Además, el impacto que tiene la orientación involuntaria hacia un sonido novedoso sobre el comportamiento, también está determinado por el set atencional.

Los sonidos novedosos provocan una respuesta combinada de alerta y de orientación. Los resultados obtenidos sugieren que el hecho de que un sonido novedoso cause distracción o facilitación depende de la contribución relativa de los componentes de alerta y de orientación en tareas específicas. En este sentido, la distracción ocurrirá cuando la contribución relativa de la orientación sea mayor que la contribución relativa de la alerta, y viceversa.

En los estudios realizados, la misma secuencia de indicadores electrofisiológicos se obtiene ante los sonidos novedosos independientemente de si causan facilitación o distracción, desaconsejando el uso de estos indicadores como índices de distractibilidad.

Los resultados indican que la contribución relativa de los componentes de alerta y de orientación puede depender de las demandas de la tarea que está siendo realizada, en particular de la tasa de presentación de los estímulos. En los estudios de esta tesis, siempre que la tarea en curso generó un alto estado de activación, la contribución relativa del componente de alerta generada por los sonidos novedosos fue menor.

Los resultados han mostrado que la orientación involuntaria de la atención hacia sonidos novedosos se reduce durante el desarrollo de tareas de MT, al menos cuando las tareas requieren significativamente de control ejecutivo o cuando la capacidad de la carga alcanza los límites de capacidad de la MT. La reducción de la orientación involuntaria de la atención por la carga de la MT, a su vez, disminuye los efectos de facilitación o de distracción de los sonidos novedosos sobre la conducta.

El mecanismo neurofisiológico que subyace a la modulación involuntaria de la atención ante sonidos novedosos por la MT parece ser la inhibición de respuestas corticales específicas relacionadas con el procesamiento de la novedad. La carga de la MT inhibe las respuestas de los sonidos novedosos en el giro frontal inferior y en el giro temporal superior. La inhibición de las respuestas tiene lugar después de que la primera detección pre-atencional del cambio ha tenido lugar, y resulta en una reducción de la NP3 registrada sobre el cuero cabelludo. Los resultados indican que la orientación involuntaria de la atención ante sonidos novedosos se previene solo después de que cierto análisis semántico del estímulo ha tenido lugar.

Después de la distracción ante un sonido novedoso, se producen ajustes en el nivel control. Aunque la distracción persiste aparentemente durante al menos 2 segundos, inmediatamente después de la distracción se observan procesos de control ejecutivo que van dirigidos a impedir la distracción. Estos ajustes en el nivel de control, en el presente estudio, se observaron en un aumento del procesamiento sensorial de las representaciones relevantes a la tarea, y de la inhibición del procesamiento en áreas auditivas.

5. Conclusiones

El objetivo general de esta tesis ha sido investigar cómo interaccionan los mecanismos voluntarios e involuntarios de la atención para seleccionar la información relevante. Los resultados han puesto de manifiesto que la orientación involuntaria hacia los sonidos novedosos no está solamente inducida por el estímulo (de abajo a arriba), sino que también está modulada por los procesos cognitivos (de arriba abajo).

En el estudio I, investigamos si la orientación involuntaria hacia sonidos novedosos y los consiguientes efectos de distracción se modulan por la carga de la MT. Los resultados han mostrado que durante el desarrollo de una tarea que requiere mantener información en la MT, la distracción generada ante sonidos novedosos se atenúa. Además, esta atenuación queda reflejada en la modulación del componente NP3 generado ante sonidos novedosos, demostrando que la modulación ocurre después de la detección pre-atencional del cambio.

En el estudio II, investigamos mediante RMf cuáles son las áreas cerebrales específicas moduladas por la carga de la MT. Los resultados han puesto de manifiesto una atenuación de la actividad en el giro frontal inferior ante sonidos novedosos. La dinámica espacio-temporal de la modulación de la

MT fue investigada en el estudio III a través de registros de magnetoencefalografía. Este estudio ha aportado evidencias de que tanto MMN como NP3 pueden ser explicados por la activación de fuentes bilaterales en el giro temporal superior. Así mismo, muestra que la modulación de la orientación involuntaria se logra a partir de la atenuación de las fuentes de NP3 en el giro temporal superior, a una latencia de aproximadamente 200 ms.

El estudio II investigó también los posibles ajustes en el control atencional que ocurren después de la distracción. Los resultados han demostrado que en los ensayos inmediatamente posteriores a un sonido novedoso las áreas del procesamiento auditivo se inhiben, mientras que la actividad de las áreas visuales que procesan la información relevante de la tarea aumenta.

El estudio IV pretendía aclarar los factores críticos que determinan si la presencia de un sonido novedoso causa distracción o facilitación. Los resultados mostraron que cuando la tasa de presentación de la tarea visual es baja los sonidos novedosos facilitan la tarea, mientras que cuando la tasa de presentación es alta causan distracción.

Finalmente, el estudio V investigó si la misma secuencia de respuestas electrofisiológicas es obtenida ante sonidos novedosos cuando causan facilitación y cuando causan distracción de la tarea en curso. Los sonidos novedosos que facilitan el rendimiento de la tarea generaron el componente NP3, desaconsejando su uso como una medida general de distracción. Además, la naturaleza del efecto de facilitación fue investigada comparando las respuestas electrofisiológicas obtenidas ante los estímulos diana que seguían a los sonidos novedosos, a las respuestas de los estímulos diana que seguían a los sonidos repetitivos. Los sonidos novedosos aumentaron la amplitud del componente P300 generado por los estímulos diana, sugiriendo que los sonidos novedosos no facilitan el procesamiento sensorial, sino más bien los procesos post-perceptivos.

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