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Review

# MMN in the visual modality: a review

P. Pazo-Alvarez *, F. Cadaveira, E. Amenedo

*Department of Clinical Psychology and Psychobiology, Faculty of Psychology, University of Santiago de Compostela, Campus Universitario Sur, S/N, 15782 Santiago de Compostela, Galicia, Spain*

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## Abstract

The mismatch negativity (MMN) component is an event-related potential (ERP) that can be elicited by any change in the acoustic environment, and it is related to memory-based, automatic processing mechanisms, and attentional capture processes. This component is well defined in the auditory modality. However, there is still a great controversy about its existence in the visual modality. This paper reviews the studies that are relevant with regard to memory-based, automatic deviance detection ERPs in the visual system. The paper discusses the main strengths and limitations of those studies and suggests what directions should be taken for future research.

*Keywords:* Event-related potential (ERP); Mismatch negativity (MMN); Vision; Preattentional processing

## 1. Introduction

Throughout the last decades, researchers with an interest in the psychophysiological correlates of automatic change detection processes have devoted considerable attention to the mismatch negativity (MMN) in the auditory modality. MMN is a frontocentrally distributed negative event-related potential (ERP) component that is obtained when a sound violates some preattentivelly detected regularity of the auditory stimulus sequence (Näätänen, 1990; Näätänen and Alho, 1997; Winkler et al., 2001). The acoustic regularities, determined from the memory trace representations of the auditory stimuli, form the basis for the MMN-generating change

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* Corresponding author. Tel.: +34-981-56-3100x13916; fax: +34-981-52-1581.
*E-mail address:* pcpazo@usc.es (P. Pazo-Alvarez).

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detection process (Näätänen, 1992; Näätänen and Winkler, 1999; Schröger, 1997). Although it may be obtained under attention conditions, MMN can be best observed when the subject's attention is directed away from the auditory stimuli. Otherwise, deviant stimuli also elicit another negative component that overlaps the MMN (N2b) (Näätänen, 1988; Näätänen et al., 2002). Basic conceptual and methodological issues related to auditory MMN may be found in Näätänen (2001), Näätänen and Winkler (1999), Näätänen et al. (2002) and Schröger (1997). Table 1 summarises some of the main characteristics of auditory MMN.

In ERP visual studies, the emergence of negative components in the N2 latency range (250–450 ms), elicited by infrequent task-relevant (Renault et al., 1980; Ritter et al., 1983; Simson et al., 1977) or omitted stimuli (Renault and Lesevre, 1978; Simson et al., 1976) is fairly common. The question is whether these N2-like waves contain automatic components that are elicited by stimuli that change in the visual

Table 1
Some central characteristics of auditory MMN

| |
|---|
| *Independence of attention* |
| MMN is best observed when the subject's attention is directed away from the auditory stimuli, as the overlap of other negative components at the same latency range, (e.g. N2b) is avoided |
| It reflects preattentive change detection because it is elicited even when participants perform a task that is not related to the auditory stimuli |
| It is not completely attention-independent in all conditions, but it is not abolished by the withdrawal of attention |
| *Endogeneity* |
| The latency of MMN is inversely related to, and its amplitude positively related to the magnitude of the difference between the standard and the deviant stimulus |
| There is a relationship between MMN latency and reaction time, since both diminish when the physical difference between standard and deviant stimulus is increased |
| *Sensory memory* |
| The MMN provides an index of experience-dependent memory traces in the human brain |
| It is a response to the relation between the present stimulus and the previous stimulus. It is elicited by infrequent violations of acoustic regularities |
| It has been recently suggested to reflect long-term memory traces for language sounds such as phonemes and syllables |
| *Sensory discrimination* |
| MMN provides an index of the perceptual discrimination accuracy for different simple and complex sound features |
| It is elicited by any discriminable change of a repetitive sound or regularity in sound sequences |
| It may be elicited by stimulus differences that approximate the behavioral discrimination threshold |
| *Cerebral sources* |
| The MMN has a bilateral auditory-cortex generator (auditory supratemporal cortex) and a right frontal cortex generator, among others |
| It has been observed that for deviancies in intensity, frequency and duration, the MMN is larger over the right hemisphere regardless of the stimulated ear |
| *Attentional reorienting* |
| It has been proposed that the cerebral discrimination process generating the MMN may play an important role in involuntary orienting, or attention switching to a change in the acoustic environment |

environment under unattention conditions, and whether they reflect a memory-based phenomenon as MMN. Recently, several studies have attempted to answer this question by controlling some, or almost all, sufficient conditions to consider the obtained visual ERPs as a genuine MMN counterpart. Other studies whose objectives did not concern obtaining a visual MMN-like wave have provided information about different visual components that shared some characteristics with the auditory MMN.

Up to now, it is still debated whether these components are really based on a memory comparison process and whether they reveal the same degree of automaticity as does the auditory MMN (see Näätänen et al., 2002). However, recent results that will be discussed below seem to provide convincing evidence for the existence of a visual MMN.

Because there are no published papers that have considered all these findings, we have reviewed the literature in our search for answers to the following questions: (1) What are the characteristics of the components related to stimulus change? (2) What are the similarities and differences between these components and the auditory MMN? (3) Which paradigms and experimental conditions have been used to obtain them? (4) What are the strengths and limitations of the studies reviewed? and (5) What directions should be taken for future research in this area?

## 2. Data that justify the search for a homologue of MMN in the visual modality

The MMN reflects the operation of a deviance detector in the acoustic environment. Authors such as Näätänen (1990, 1992) and Näätänen and Michie (1979), have proposed that the functional significance of the MMN generator is to initiate an attention switch (orienting response) to the eliciting stimulus change. However, as Michie et al. (1990) indicated, the main difference between the MMN and the orienting response is that the former has not been demonstrated in other modalities, whereas the latter may be triggered by any change in all sensory modalities. Therefore, the extrapolation of Näätänen's theory would imply the identification of an ERP component equivalent to the auditory MMN in other sensory modalities (Michie et al., 1990). Furthermore, as Verbaten (1990) commented, although the auditory and visual systems are based on different processing principles, subjects in both modalities normally perceive occasional deviant stimuli and, therefore, “it seems sensible to look for the presence of electrophysiological signs of precursors of attention.”

Another main characteristic of auditory MMN is that it is elicited when a memory-comparison process detects a discrepancy between the neural representation of the regularity inherent in recent stimulation and the representation of the current stimulus. This process does not depend on the active, wilful involvement of the participant (Jacobsen and Schröger, 2001; Winkler et al., 2001).

The visual system easily perceives, analyses and quickly categorises scenes. However, several lines of research have shown that there are important difficulties in detecting changes in the visual environment when they are not attended or cued (i.e. change blindness). For example, viewers often fail to detect changes in natural scenes when the change occurs during a visual disruption. It occurs across a range of conditions, including changes made across saccadic eye movements (Grimes, 1996), during blinks (O'Regan et al., 2000), and during cuts in motion pictures (Levin and Simons, 1997; Simons, 1996). Change blindness even occurs when observers expect changes and are explicitly instructed to search for them (Rensink et al., 1997). These failures led several researchers to conclude that memory for local visual objects is non-existent (O'Regan, 1992; O'Regan and Nöe, 2001), limited to the currently attended object (Rensink, 2000; Rensink et al., 1997; Wolfe, 1999) or limited to the currently attended object plus the two or three most recently attended objects (Irwin, 1992; Irwin and Andrews, 1996; Irwin and Zelinsky, 2002). In contrast to these proposals, Hollingworth and Henderson (2002), and Hollingworth et al. (2001) have provided evidence that representations from previously attended objects can be retained robustly in visual memory. Thus for these authors, change blindness derives from retrieval and comparison failures (see Hollingworth, in press).

In addition, as previously stated, without visual attention, significant changes can escape our awareness. The phenomena of "inattentional blindness" (Mack and Rock, 1998) and "attentional blink" (Luck et al., 1996; Raymond et al., 1992; Vogel et al., 1998) support the hypothesis that attention is a necessary prerequisite to detect change. However, some authors suggest that failure to detect an unattended change does not mean that our visual system cannot register it. For example, a number of recent studies have demonstrated that during trials where a change was not explicitly detected, effects of that change can be observed on more sensitive measures (e.g. forced guess, Fernandez-Duque and Thornton, 2000; fixation durations, Hayhoe et al., 1998; Hollingworth et al., 2001; and response latency, Williams and Simons, 2000). Priming measures in the inattentional blindness phenomenon have also indicated that the unseen stimulus was covertly processed (Mack and Rock, 1998). However, this topic is still being debated (Mitroff et al., 2002), as is whether these implicit mechanisms might or might not contribute to explicit change detection (see Smilek et al., 2000 for an alternative explanation).

Nonetheless, additional data indicate that considerable cognitive visual processing is possible without consciousness. Evidence comes from studies with brain-lesioned patients (e.g. blindsight; Poppel et al., 1973; Weiskrantz, 1997), neurophysiological impairments (see Köhler and Moscovitch, 1997 for a review), or priming studies in normal patients (e.g. Dehaene et al., 1998). The current data suggest that this type of processing is possible at a perceptual as well as semantic level (e.g. Bauer, 1984; Renault et al., 1989). Neuroimaging studies have also provided additional evidence in this direction (e.g. Morris et al., 1998; Sahraie et al., 1997; Whalen et al., 1998; see Dehaene and Naccache, 2001 for more detailed information).

Thus, there is some indication that visual processing can take place without awareness, but it seems that attention is necessary to explicitly detect a change. However, if attention is required for detecting a change, how do we ever become aware of unexpected information?

There is evidence of a mechanism suggesting that automatic differentiation may occur (e.g. pop-out). So, in a simple visual search task where targets and distractors differ in a single dimension, it is said that the target “pops-out” over distractors. That is, targets automatically capture subjects’ attention (Julesz and Bergen, 1983; Treisman and Gelade, 1980). Johnston and Hawley (1990) proposed that the similarities between the phenomenon of pop-out in vision, and the detection of deviation in audition may indicate that these two phenomena have similar underlying mechanisms. Several studies of visual perception have observed that preattentive pop-out object clusters are grouped together on the basis of a common feature (e.g. Julesz, 1981; Nothdurft, 1990). Although the notion of preattentive grouping is not common in theories of auditory stimulus processing (Darwin, 1997), it has been shown that MMN depends, at least partly, upon contextual factors of tone grouping like “tone repetition, tone alternation, sound periodicity, etc.” (see Winkler et al., 2001).

The “pop-out” phenomenon may also exemplify the distraction process that takes place in vision. This effect, according to Berti and Schröger (2001), is produced by a pre-attentive deviant detection mechanism, which is an obligatory stage in the processing of the stimulus that may or may not be followed by a reorientation of attention to stimulus changes. The cited authors have also recently tried to prove whether the distraction process could be based on a pre-attentive sensory mechanism that operates also within the visual modality.

Another phenomenon related to visual search is visual texture segmentation, which characterises the ability to detect a deviation or discontinuity in a homogeneous field. Under some circumstances, the detection of an embedded irregularity occurs effortlessly and preattentivelly. Bach and Meigen (1992) found a segmentation-specific negativity in the VEP between 161 and 225 ms after stimulus onset. Saarinen et al. (1998) found activity in the right occipito-temporal area during a pop-out task that was also present in a passive viewing condition. Schubö et al. (2001) obtained two components sensitive to texture segmentation: a posterior N2 not affected by the complexity of a primary task, and a P3 that was more dependent on attentional resources (for more detailed information see Näätänen et al., 2002).

Apart from these studies in vision, additional evidence from psychophysiological research suggests the existence of ERPs similar to the auditory MMN in the somatosensory modality in humans (Kekoni et al., 1997; Shinozaki et al., 1998) and animals (Astikainen et al., 2001). This fact would confirm that it is possible to observe psychophysiological mismatch detection correlates in other sensory modalities.

Thus, it seems sensible to explore whether an MMN-like component could fall under this type of process in vision. However, another different possibility is whether we may detect its ERP correlate by using pericranial recordings or whether auditory and visual components share the same characteristics. Perhaps, as stated by Näätänen (1990), it will be possible to find a visual counterpart of the auditory MMN once experimental paradigms consider the specific properties of the visual system.

In the following paragraphs, we review the studies that are relevant to the visual analogue of the auditory MMN. It may be seen that, in most cases, the authors have only checked for the emergence of the characteristics of the auditory MMN without considering the peculiarities of the visual system, instead of searching for an electrophysiological correlate of change detection in the visual environment.

## 3. Studies of visual MMN

A description of studies carried out to evaluate the effect of task-irrelevant deviant stimuli on visual ERPs follows. Several authors, as previously mentioned, have focused their attention on confirming whether a visual counterpart of the auditory MMN exists (Astikainen et al., 2000; Cammann, 1990; Csibra and Czigler, 1991; Czigler et al., 2002; Czigler et al., submitted; Czigler and Csibra, 1990, 1992; Heslenfeld, 2002; Kenemans et al., 2001; Kremláĉek et al., 2001; Nordby et al., 1996; Nyman et al., 1990; Tales et al., 1999). In the remaining studies, the authors analysed the ERPs evoked by visual deviant stimuli within broader experimental objectives (Alho et al., 1992; Berti and Schröger, 2001; Iijima et al., 1996; Kenemans et al., 1992; Neville and Lawson, 1987; Tales et al., 2002; Wei et al., 2002; Woods et al., 1992). Most of the studies reported visual N2-like components elicited by deviances in several visual stimuli characteristics such as: direction of movement, form, orientation, location, contrast, size, spatial frequency and colour. These studies also used a variety of designs, ranging from visual discrimination studies to active, passive and delayed response oddball paradigms, as well as studies of intermodal selective attention.

We will first describe intermodal experiments, where two sensory modalities (visual and auditory) were used. We will then discuss intramodal studies, where only visual stimulation was used. Within these two broad categories, the reviewed papers are organised according to the type of change manipulated. Table 2 summarises the characteristics and main findings of the reviewed studies.

### 3.1. *Intermodal studies*

In the following sections, we will discuss studies in which the researchers tried to obtain an MMN-like component to visual stimuli presented outside the focus of attention while subjects attended to auditory stimulation. Other studies analysed mismatch detection correlates within broader objectives.

#### 3.1.1. *Changes in contrast*

One study conducted by Nyman et al. (1990), manipulated several conditions. Using an oddball paradigm, they presented auditory stimuli alone, visual stimuli alone and visual and auditory stimuli simultaneously. The visual deviant characteristic was the contrast in a sinusoidal grating, whereas in the auditory modality it was tonal intensity. The results revealed that the evoked responses were not significantly different, although the waves registered at Oz contained larger positive deflections to visual standards than to deviants in the latency range of 200–300 ms. According to the authors, these effects were related to the larger grating contrast used in the standard stimuli. As a result, they carried out a control experiment by interchanging

Table 2
Summary of studies about visual MMN

| Source | *N* | Task | Visual stimulation | Results |
|---|---|---|---|---|
| Neville and Lawson, 1987 | 12 | Focused attention to peripherally and centrally located visual stimuli | S = white squares of 0.6°, 33 ms; D = squares in apparent motion, 66 ms; ISI = 384 ms; S:D = 8:2 | A different response between standards and deviants can not be observed |
| Cammann, 1990 | 8 | Intermodal oddball paradigm for ignore conditions | S = mixed-light emitting diodes of orange colour; D = mixed-light emitting diodes of yellow colour; ISI = 500 ms; S:D = 9:1 | MMN-like change since: it is independent of attention. Scalp topography with a right hemispheric dominance unusual for an N2b |
| Czigler and Csibra, 1990 | 13 | Visual discrimination task | S = Two angles within a frame; D1 = Inverted angles; D2 = Thicker frame; Duration = 83 ms; ISI = 417 ms; S:D = 8:1:1 | The components are dependent on the salience of the deviant characteristics. The automatic early component is, therefore, only present for the more salient standard-deviant difference |
| Nyman et al., 1990 | 9 | Oddball task with only auditory stimuli, only visual stimuli and simultaneously presented auditory and visual stimuli | Sinusoidal gratings, 100 Hz; S = contrast 0.72; D = contrast 0.24; Duration = 100 ms; ISI = 490 ms; S:D = 9:1 | No MMN-like component can be observed |
| Csibra and Czigler, 1991 | 10 | Visual discrimination task independent of the deviant features, but connected to the stimuli of the task | S = Apparent motion (5.2 degrees of visual arc during 2260 ms); T = Specific shape in the center of the screen, 100 ms; D1 = Movement deviant. Opposite movement direction 2260 ms; D2 = Rotation deviant, 100 ms; D3 = Form deviant, 100 ms; ISI = 260 ms/1440 ms; Deviants probability = 0.5 each | Undetected deviant features do not elicit MMN-like components. When the deviance approaches spontaneous detection, an N2–P3a complex appears |
| Czigler and Csibra, 1992 | 12 | Visual discrimination task | S = Two angles within a frame; D1 = Inverted angles; D2 = Thicker frame, Duration = 80 ms; S:D = 8:1:1 | Like the MMN, the component diminishes when the ISI is increased, but unlike the MMN it is related to the salience of the deviant stimuli |
| Kenemans et al., 1992 | 22 | Visual oddball series while subjects had to perform an easy or hard task | Abstract visual patterns, Duration = 924 ms; ISI = 245 ms; S:D = 9:1 | P2–N2 complex larger for deviants that, as MMN is not affected by task load. Unlike the auditory MMN, has a maximum amplitude at Cz and Fz |
| Woods et al., 1992 | 11 | Intermodal selective attention task (auditory and visual) | White vertical gratings of high (2 cycle/deg) and low (0.7 cycle/deg) spatial fr.; lum. 7 fL; contrast 0.99; S = 3.9 × 4.4° (width × height); D = 2.9 × 3.9°; Duration = 50 ms; SOA = 200–400 ms; S:D = 9:1 | Visual MMN/N2b components, with an amplitude maximum over contralateral occipital and inferior temporal regions and a right hemisphere dominance. The component increased in amplitude with attention, but it is also evident during unattention |

Table 2 (*Continued*)

| Source | *N* | Task | Visual stimulation | Results |
|---|---|---|---|---|
| Alho et al., 1992 | 14 | Intermodal selective attention task (auditory and visual) | White vertical gratings (spatial frequency 2 cycle/deg; luminance 7 fL; contrast 0.99), S = 3.9 × 4.4° (width × height); D1 = 3.9 × 3.9°; D2 = 3.9 × 2.4°; Duration = 50 ms; ISI = 200–400 ms; S:D = 8:1:1 | DRN components, restricted to occipito-temporal area (modality-specific sensory cortex), not affected by processing load during attention to the other modality. Unlike auditory MMN, deviant visual stimuli physically close to standards do not evoke the early DRN. No dependence on presence of standards |
| Nordby et al., 1996 | 12 | Stimuli were presented under three different task conditions; ignore events in the periphery, count feature deviants, and count spatial deviants | S = frequent circle moving around a fixation point; D1 = (feature deviant) substitution of circle by a cross; D2 = (spatial deviant) single-one step reversal of the moving circle; Duration = 50 ms; ISI = 650 ms; S:D = 9:1 | Spatial deviants elicited a negative wave peaking between 200 and 250 ms at occipital and posterior temporal leads. This negative wave was not significantly affected by attention |
| Iijima et al., 1996 | 20 | Subjects were instructed to listen to a radio while ignoring irrelevant visual stimuli | S = letter “X”; D = circle; Duration = 400 ms; Presentation rate = 1 Hz; S:D = 8:2 | Deviants elicited a more negative wave at latency from 70 to 250 ms |
| Tales et al., 1999 | 12 | Attention to central target while frequent and deviant stimuli were presented outside the focus of attention in the peripheral field | T = blue frame filled with red (10.5 × 10.5 cm); S = single white bars (3.9 × 1.2 cm); D = double white bars (3.9 × 0.6 × 2 cm); Duration = 200 ms; ISI = 612–642; S:D = 16:1 | Negative component that resembles the auditory MMN since: it is evoked by infrequent stimuli presented outside the focus of attention.<br>It is generated in the modality-specific cortex |
| Astikainen et al., 2000 | 7 | Visual oddball paradigm. (Animal subcortical recordings) | Vertical and horizontal bars applied as standards and deviants in two blocks in counterbalanced order; Duration = 50 ms; ISI = 500 ms; S:D = 19:1 | Component analogous to the auditory MMN because it shows dependency on the presence of standards and modality-specific cortical and subcortical contributions |
| Berti and Schröger, 2001 | 10 | Effects of task-irrelevant changes in a visual distraction paradigm. Task: button-press on long duration stimuli | S = Centered triangle; D1 = Rotated triangle (90°); D2 = Triangle in the lower half of the screen; T = Long duration stimuli; Duration = 400 or 600 ms; ISI = 1300 ms; S:D1:D2 = 15:1:1 | Occipital N200 effect similar to auditory MMN since: it is elicited by characteristics presented outside the focus of attention and presents a modality-specific distribution |
| Kremláčˇek et al., 2001 | | Attention and reaction to central targets, while standard and deviant stimuli are presented in the periphery | S = Upward peripheral motion (10°); D = Downward peripheral motion (10°); T = Central motion (5°); S:D = 88:6 | MMN-like response elicited without active attention |

Table 2 (*Continued*)

| Source | *N* | Task | Visual stimulation | Results |
|---|---|---|---|---|
| Kenemans et al., 2001 | | Sequences of two physically different irrelevant gratings while subjects had to perform a primary task | S = Grating; spatial frequency (0.6 cycle/deg); D = Grating, spatial frequency (2.4 cycle/deg) or v.v.; ISI = 400 ms; S:D = 8:2 | Deviance-dependent negativity is observed for both colour and spatial frequency. Unlike the MMN, the negativity is not dependent on the presence of standards |
| Heslenfeld, 2002 | 14 | Compensatory visuo-motor tracking task with three levels of difficulty, while task irrelevant gratings were presented in the upper and lower part of the visual field | Gratings (20% contrast, 16.7 ms); S = Low spatial frequency (0.58 cycle/deg); D = High spatial frequency (2.3 cycle/deg); Duration = 16.7 ms; ISI = 250–450 ms; S:D = 8:2 | Unattended deviant stimuli elicit more negative components with maximum amplitudes over occipital regions, independent of task load or spatial frequency |
| Wei et al., 2002 | 12 | Cross-modal delayed response oddball paradigm | S = colour scenery photograph; D = colour scenery photograph with a higher contrast; Duration = 30 ms; ISI = 652–700 ms; S:D = 85:15 | Early component (DRN1) elicited by unattended deviant stimuli with maximum amplitudes over primary sensory cortex or frontal regions |
| Czigler et al., (2002) | 8 | Passive oddball condition with irrelevant stimulus while subjects performed a detection task | Vertical square-wave gratings; (2.4 cycle/deg spatial frequency) varying in colour. Small deviance condition: S = red/, D = pink or v.v.; Large deviance condition: S = red/, D = green or v.v., Duration = 17 ms, ISI = 350–450 ms; S:D = 8.75:1.25 | Infrequent stimuli in the large deviant condition elicit an increased posterior negativity and an anterior positivity. The posterior negativity can be attributed to a memory-related mismatch process (possible genuine visual MMN) |
| Czigler et al. (submitted) | 20 | While ignoring the coloured gratings, subjects performed a detection task | Horizontal and vertical square-wave gratings. Two colour/direction conjunctions were presented frequently, whereas other two conjunctions were infrequent (deviant). Duration = 17 ms; ISI = 350–450 ms | Infrequent conjunction of two visual features (colour and direction) elicits a vMMN. Thus feature conjunctions are stored and deviant conjunctions are detected by the system underlying the vMMN |

D = deviant, S = standard, T = target, S:D = standard/deviant ratio, v.v. = vice versa.

the contrast values of standard and deviant stimuli. This gave the opposite results, confirming the exogenous effect caused by stimulus contrast on the observed differences. Because the authors could not obtain a clear visual MMN in the visual task, they concluded that the MMN was not a manifestation of a general attentional mechanism, but was probably specific to the auditory modality. These results, which suggest that no MMN may be observed in a purely visual task, should be interpreted with caution due to at least two important methodological limitations. Firstly, the visual and auditory stimuli were presented simultaneously, so it is probable that the components elicited by auditory stimuli masked those elicited by visual stimuli. Secondly, when the task included only visual stimuli, they were presented without a distracting task that could prevent attention from being directed away from the visual stimuli. Therefore, it is likely that N2b–P3 complexes, typical of active conditions, had overlapped the recorded components.

More recently, Wei et al. (2002) also manipulated this variable in order to observe the deviance effect on ERPs using a cross-modal delayed response oddball paradigm. The visual stimuli consisted of colour scenery photographs that varied in contrast, while auditory stimuli were tones of different frequency (800 and 1000 Hz). The results showed that the infrequent stimuli in both modalities, when unattended, elicited a deviance-related negativity at around 100–200 ms (deviance-related negativity 1 or DRN1) that was largest at frontal recording sites. When the subjects attended to the stimuli, this negativity was followed by a later negative wave (DRN2, 200–300 ms). The first component had a maximum amplitude at T4 when attention was in the auditory modality, but at O2 when attention was in the visual modality. The second component presented a frontal distribution. The authors concluded that the DRNs in the visual modality shared some characteristics with the auditory MMN. Like this component, the visual DRN was comprised of two components under attention, while the early deflection could be identified under unattention conditions. These components reached maximal amplitudes over their respective primary sensory cortices or frontal regions. One of the strengths of this experiment is the use of a delayed response paradigm, which makes it possible to control for possible contributions of target-detection-related components on the MMN. However, the possibility of exogenous effects of contrast on the ERPs was not examined in this study, because the authors did not reverse the standard and deviant characteristics.

### *3.1.2. Changes in shape*

With the purpose of studying the effects of age on visual MMN, Iijima et al. (1996) presented two types of visual stimuli (an “X” as standard stimuli and a circle as the deviant). They controlled the subjects’ attention by asking them to listen to a radio while irrelevant visual stimuli were presented. Visual MMN consisted of a negative wave with a peak latency of 166 ms and fronto-central distribution in the young group. This wave was followed by another negative wave (N2b) that peaked around 194 ms. Therefore, according to the authors, the occurrence of N2b indicated that some subjects paid attention to visual stimuli and it was not possible to conclude whether a true MMN component was recorded.

### 3.1.3. Changes in colour

In reply to the issue concerning the auditory specificity of MMN expounded by Näätänen (1990) and Cammann (1990) performed an experiment to gather more information about the existence of a visual MMN. In his experiment, Cammann presented a pattern of mixed-light emitting diodes (LED) of orange (standard) or yellow light (deviant), while the subjects heard pitches of 1000 Hz (standard) or 1500 Hz (deviants) through earphones. The subjects' task was to react to the deviant stimuli while ignoring the other stimuli. The subtraction curves in the ignore condition revealed a long MMN-like change to visual stimuli between 150 and 350 ms, with a maximum over the temporal region and right hemispheric dominance. The author did not interpret the MMN-like change as an N2b component because the primary task was particularly demanding, and no P3 waves were observed in the ignore condition. In addition, the negativity revealed right hemispheric dominance that would be unusual for an N2b component. The main limitation of this study is the incomplete description of the methodology. The author did not specify the timing of stimuli, electrodes, signal or data analyses employed, making it difficult to know whether significant differences occurred between deviant and standard stimuli waveforms. These deficiencies make it very difficult to replicate the experiment and, further, limit interpretation and comparison of the results with other studies.

### 3.1.4. Changes in size

Finally, we describe two studies carried out by Woods et al. (1992), in which they studied the effects of intermodal selective attention on ERPs. Woods et al. presented visual and auditory signals in a balanced intermodal sequence that required selective attention by the subjects. The visual stimuli consisted of gratings subtending 3.9° of visual angle that varied in height. The results revealed that when subjects paid attention to the visual deviant stimuli (targets), MMN/N2b waves were elicited with a latency onset of 155 ms, and with amplitudes of $-2.24$ μV at the contralateral occipital and posterior temporal sites. However, when these visual stimuli were unattended, the MMN/N2b amplitudes decreased up to $-0.69$ μV. These components were larger over the posterior temporal and occipital regions of the right hemisphere. These MMN/N2b deflections were elicited during both the attended visual and auditory conditions, and appeared to partially reflect automatic processes. As stated by the authors, these components, like the auditory MMN, may reflect the automatic detection of physical change in sequences of visual stimuli. Additionally, the visual MMN/N2b displayed a right hemisphere predominance, a characteristic reported for the auditory MMN (Paavilainen et al., 1991). In this study, a reduction of 70% in the MMN/N2 amplitude was observed when the stimuli were not attended. According to the authors, this effect was probably not due to the suppression of ERP components in the non-attended modality, but to an N2b contribution to the attended condition. It is also possible that the peripheral presentation of the stimuli caused a higher processing load, because the subjects had to divide their attention between two spatial locations within an attended modality. In this study, the authors manipulated the size of the deviant stimuli progressively during the experiment, depending upon the discrimination rate of the subjects.

Unfortunately, the authors did not analyse or compare the responses evoked by these gradual changes. It would have been informative to observe whether the differences between standard and deviant stimuli affected the deviance-related negativities.

With the aim of extending the results of Woods et al. (1992) and Alho et al. (1992) used the same experimental design and again manipulated the size of the stimulus. Three types of stimuli were used: one standard consisting of white vertical gratings of 3.9 × 4.4° and two infrequent deviants that were either slightly shorter (3.9 × 3.9°) or markedly shorter (3.9 × 2.4°) than the standards. Using these three types of visual stimuli, they manipulated the difficulty of the task. The results revealed that the markedly shorter deviant stimuli elicited a larger negative wave at posterior sites (Oz) that was evident when the subtraction wave (deviant-standard) was calculated in the latency range of 90–290 ms. This visual negativity (DRN or deviance-related negativity) had two peaks at 120 and 200 ms, respectively. The earlier portion was restricted to Oz with equivalent amplitudes during attended and unattended conditions. The later visual DRN had a distribution that included T5, T6 and Oz. The authors suggested that an automatic discrimination process generated the first component of visual DRN, because it was not affected by visual attention or the difficulty of the auditory task. Therefore, according to the authors, this early component, shared some characteristics with the auditory MMN. Specifically, it was generated in modality-specific sensory cortex and the processing load did not affect it during attention to the auditory modality. However, the authors did not identify this component as a counterpart of the auditory MMN, because deviants that were more similar to the standard visual stimuli did not elicit it. Furthermore, a similar early visual deflection could be observed when the visual targets were presented alone. The authors, therefore, suggested that the "visual MMN" could have a higher threshold for elicitation than the auditory MMN or it may only be sensitive to changes in certain stimulus features but not others. Alho et al. (1992) did not conclude whether the DRNs observed were due to the detection of stimulus change or whether they reflected a less refractory sensory response to infrequent visual stimuli.

## *3.2. Intramodal studies*

### *3.2.1. Changes in motion direction*

Early evidence leading Näätänen (1990) to conclude that it was not possible to observe MMN in the visual modality came from a study by Neville and Lawson (1987). In this study, the authors investigated the effects of focused attention to peripherally and centrally located visual stimuli while subjects detected the direction of motion in a specified location. The stimuli were white squares presented in three positions on a monitor: centre and peripheral (to the left and right of the central fixation point). The standard stimuli were single presentations of squares for 33 ms and the deviant stimuli consisted of one 33 ms presentation of a square in the same position as the standards, followed by the illumination of one of eight adjacent squares for an additional 33 ms. The second square produced an illusory movement in the direction of the second stimulus. The subjects were asked to detect the direction of motion for targets at a predefined location (centre, periphery-right, and periphery-left). The results showed that correctly-detected targets were associated with a negative component at 289 ms (N2), followed by a large positive component at 493 ms (P3). The ERPs to unattended targets displayed a broad negative shift. One of the main limitations of this study, as previously mentioned by Verbaten (1990), is that no statistical analyses were conducted comparing the ERPs elicited by unattended standards with those elicited by deviant stimuli. Therefore, it is difficult to conclude whether a different ERP was elicited by both types of stimuli. The graphs also revealed that unattended deviants induced an N2 that was smaller than the N2s in the attended condition, probably due to the existence of an overlapping processing negativity (PN).

Csibra and Czigler (1991) investigated the effects of unattended deviant direction of movement. They also evaluated the effects of deviance in form and rotation. To create the apparent motion, the stimuli appeared at seven adjacent positions along a diagonal line, with a duration of 100 ms in each position, followed by an interval of 260 ms. Post-experimental subject interviews indicated that none of the subjects detected the form or rotation deviances. The ERPs showed that responses to form and rotation deviants did not differ from the responses to the standard shapes. Furthermore, half of the subjects detected the deviant movement direction. In these subjects, the deviant movement elicited a positive wave maximum at fronto-central locations in the 240–420 ms range that was preceded by a negative wave (N2b). This complex was absent in the subjects who did not detect the deviant movement. The authors concluded that undetected deviant features did not elicit ERP components similar to MMN, and that only an N2b–P3a complex could be observed in the sample of subjects who detected the movement spontaneously and consciously. However, in the “non-detection group”, they observed a positive deflection (P3) preceded by a negative wave (N2), though these components had a lower amplitude compared with the components recorded in the “detection-group.” A limitation of this study requiring mentioning is that some stimuli were presented simultaneously. The fifth stimulus that was part of the apparent motion sequence was presented at the same time as the first stimulus of the next sequence. Components elicited by central stimuli may have, therefore, overlapped those elicited by the deviant stimuli that changed in form and rotation (presented at the end of the sequence in the periphery). Another limitation found in additional studies conducted by the same authors, is that the target stimuli and the task-irrelevant stimuli shared some characteristics that may elicit specific negative components related to target selection.

Nordby et al. (1996) examined both automaticity and sensory specificity of stimulus processing in the visual system. The authors used a circle moving around a fixation point as a frequent stimulus. Additionally, two types of infrequent events were used: feature (the circle was substituted by a cross) and spatial deviants (one-step reversal of the moving circle). Stimuli were presented to subjects with one of three different sets of instructions: ignore events in the periphery, count feature deviants, or count spatial deviants. The results revealed that spatial deviants elicited a negative wave (maximum at about 230 ms at temporal and occipital locations) which was not significantly affected by attention. On the other hand, feature deviants elicited a negative wave that changed in distribution with attention. For the authors, the negative waves found in this study did not match the auditory MMN in terms of automaticity. Thus, according to Nordby et al., processing of deviant stimuli in the auditory and visual modalities seem to reflect fundamental differences between both sensory modalities. One of the major limitations of this study is that, in the "ignore" condition, the authors did not include a primary task to prevent the subjects from focusing their attention on the irrelevant stimuli presented in the periphery. As previously stated, the authors concluded that none of the deviance-related negative waves resembled the auditory MMN in terms of automaticity. In this experiment, this statement holds for the feature deviants. However, spatial deviants did elicit a negative component that like the auditory MMN was not significantly modulated by attention. We, therefore, think that the authors should have explored other MMN features using this type of spatial deviant (e.g. standard-dependency in motion-reversal irrelevant changes).

More recently, Kremláĉek et al. (2001) also evaluated the effects of direction-motion deviants. Specifically, they examined the ability of the magnocellular system to detect changes automatically through ERPs elicited by motion onset (motion-onset visual evoked potentials; MOP VEPs). This involved presenting horizontal low-contrast sinusoidal gratings of low spatial frequency (0.1 cycle/deg) outside the central visual area, and presenting high spatial frequency (1 cycle/deg) inside the central visual area. To elicit MMN, they presented standard (upward motion, 50 deg/s) and deviant stimuli (downward motion, 50 deg/s) in the periphery, while the subjects had to detect a target in the central area. The authors found that deviant stimuli elicited a negative peak with a latency around 160 ms (N160) and a later component (200–300 ms) that was larger for deviant than for standard stimuli. They concluded that, because the motion-onset VEP is insensitive to motion direction, the amplitude difference might be due to an MMN-like response that was elicited without the active attention of the subject. Since the characteristics described here are based on an abstract, we have no further information regarding the experimental design and the controls used to obtain the visual MMN. Therefore, it is not possible to conclude whether the recorded component is free of exogenous effects, motion adaptation, or if it is independent of attention.

### *3.2.2. Changes in form*

Using a discrimination task, Czigler and Csibra (1990) studied whether non-detected differences elicited negativities as in the case of auditory MMN. Three types of experimental stimuli were used: one standard consisting of two angles inside a dark frame, and two deviants. The first deviant was identical to the standard, but the angles faced towards each other. In the second deviant, the angles were in the same position as the standard but the frame was thicker. The results revealed that the ERPs were similar for deviants and standards when subjects did not detect the less deviant thickness of frame characteristic. However, when subjects were aware of the difference in frame thickness, the ERPs to the deviant were more negative than to the standards at posterior scalp sites in the range of 210–240 ms. When the task-irrelevant characteristic was the most salient (deviant orientation of two angles), these stimuli elicited two occipital negative waves with 145 and 210 ms peak latencies, respectively. Therefore, stimuli with a salient deviant feature elicited an early posterior negativity (range 120–180 ms) that was absent for less salient features. As a result, the authors interpreted this earlier component as a correlate of automatic detection that was only present for salient deviant characteristics.

The less salient deviant stimuli would remain undifferentiated and, therefore, would not elicit the early automatic MMN-like waves unless the subjects were aware of its presence. The authors concluded that it was not possible to obtain an MMN counterpart because it was not possible to obtain a component independent of detection. Czigler and Csibra suggested that the early negative deflection could be a correlate of processes similar to that underlying the elicitation of the NA waves described by Ritter et al. (1982). These waves are related to early processing of sensory input and stimuli classification and have a latency between 110 and 300 ms that varies according to the complexity of the stimulus (Ritter et al., 1983). However, unlike the NA, the early negativity obtained by Czigler and Csibra appeared in the difference wave between the ERPs elicited by the standard and the deviant stimuli of the same run, not as the difference between ERPs to stimuli of runs with repetitive stimulation and ERPs to identical frequent stimuli of runs with more than one type of stimuli. One limitation of this study is that the main conclusion, the requirement of attention to detect less salient deviances, was based on the comparison of two experimental conditions that differed not only in the type of attention required (focused vs. divided), but also in the salient value of the unattended stimuli. As the authors pointed out, the irrelevant deviants presented qualitatively different characteristics that impaired the comparison of the recorded ERPs.

In order to extend the results of their previous study, Czigler and Csibra (1992) investigated whether the ERP effects were related to particular types of deviance. They used the same stimulation, but included stimuli with two deviant features (angle orientation and deviant frame thickness). As in the previous study, only salient deviant features (deviant angle orientation) elicited the early negative component. They also compared the ERPs at two interstimulus intervals (340 and 1020 ms) to examine the possible effects of ISI manipulation on these components. The results revealed that when the short ISI was used, the irrelevant angle orientation elicited the early occipital negativity. However, with long ISIs, the unattended deviant orientation did not elicit ERP activity different from the ERPs to the standard. According to the authors, the pattern of ERPs in the latency range of 140–260 reflects two discriminative processes. The first is related to the salient deviant feature (a deviance that is detected even when it is task-irrelevant). This component (posterior negative wave in the 140–180 ms latency range) seems to be a correlate of automatic deviance detection. The second, posterior negativity and anterior negativity, are both related to attentional processes because they are absent when deviant features are task-irrelevant. Therefore, the second negativity belongs to the family of the selection negativities. These waves, observed by Harter and Aine (1984), are attention-related components that can be elicited by target stimuli and stimuli with features that share characteristics with the task-relevant stimuli. In conclusion, the authors stated that the early negativity was similar to the auditory MMN because its amplitude decreased as the interstimulus interval increased, although, unlike the auditory MMN, the appearance of this negative component was related to the salience of the deviant stimuli.

Kenemans et al. (1992) examined whether the frequently observed enhancement in P2–N2 amplitude by occasional visual deviant stimuli relative to standards could be observed in a condition designed to withdraw processing capacity from the eliciting stimuli (standards and deviants). According to the authors, such finding would suggest that a pre-attentive mechanism for change detection might also operate in the visual modality, because capacity limitations are assumed to only affect central attentive processing. In this experiment, they used two stimuli consisting of abstract visual patterns varying in shape. The processing capacity was manipulated by presenting the deviants and the standards while subjects had to perform either a difficult or a simple task. Results showed that occasional visual deviants that were task-irrelevant elicited enhanced P2–N2 and P3 amplitudes relative to standards. This P2–N2 enhancement was not affected by task difficulty. Thus, according to the authors, the P2–N2 complex may reflect the outcome of a comparison process that could be conceived as automatic because it was not affected by processing load. One of the main constraints of this study is that deviants elicited a P3. Therefore, in this study the authors failed to effectively control the allocation of attention.

One study that specifically tried to verify the existence of a visual counterpart of auditory MMN was carried out by Tales et al. (1999). They recorded evoked potentials to target stimuli (red squares filling a blue frame) presented at the centre of the visual field, and to frequent standard and infrequent deviant stimuli presented outside the focus of attention. The standards were comprised of single white bars presented at the same time above and below the central fixation point; deviants were double bars equal to the standards in total area, brightness, and location. The results showed that the deviants evoked a more negative potential than standards 245–400 ms after the stimulus. This negativity was maximal at electrodes O1, O2, T5 and T6. In order to control for possible exogenous effects, the authors reversed the stimuli used as standards and deviants in a second experiment. When the deviants consisted of double bars, the responses to standards and deviants began to diverge as early as 160 ms after the stimuli. However, this early effect was eliminated when the simpler single bars were used as deviants which led to differences in the 250–400 ms latency range. According to Tales et al. (1999), the negative potential associated with stimulus change in the visual modality shared some features with the auditory MMN. In particular, it was automatically evoked by infrequent stimuli presented outside the focus of attention, and it was generated in the sensory association cortex. However, there were differences associated with stimulus shape, since when single bars appeared as deviants, the deviance effect was reduced, revealing a less endogenous character than the MMN. Thus, in this study the authors controlled for exogenous effects, but unfortunately they found different responses to both types of stimuli. As the authors suggested, the effect could be due to the stimulus energy and not necessarily to the difference between them.

More recently, these authors (Tales et al., 2002), using the same experimental design, compared the responses elicited by visual stimuli in young (mean age 30.5 years) and older adults (mean age 77 years). As in their previous study, the deviant stimuli elicited a more pronounced negativity than the standards in the 200–400 ms latency range in the younger group. However, they did not counterbalance deviant and standard stimuli, therefore, limitations previously-mentioned concerning the earlier study may also be true in this case.

#### *3.2.3. Changes in orientation*

In a serial presentation of stimuli, Berti and Schröger (2001) studied the process involved in the involuntary reorienting of attention due to a distractor event. To do so, the authors designed an experiment consisting of two independent conditions, one auditory and another visual. The subjects had to discriminate equiprobably-presented short- from long-duration stimuli. The task-irrelevant deviances consisted of changes in orienting or in the spatial location of the stimuli. The results revealed that the visual deviants elicited a more negative deflection at around 200 ms at occipital sites. The authors referred to this negativity as an occipital N200 effect, which mirrored the MMN obtained with auditory stimulation as it was elicited by changes that were task-irrelevant and, therefore, outside the focus of attention. According to the authors, the N200 effect evoked by task-irrelevant deviances was a functional correlate of the MMN, which was followed by P3a indicating an involuntary attention switch. One interesting issue of this study is that they focused on the functional significance of a possible visual MMN as responsible for triggering automatic attentional capture and involuntary reorienting of attention. Their results are also similar to studies that assume the distraction effect is caused by a mismatch detection process (Tiitinen et al., 1994). However, because this study found that task-irrelevant deviant stimuli also elicited a P3a, revealing an involuntary switch of attention, it cannot be ruled out that other negative components may be overlapping the N200 effect observed by the authors. Another minor constraint in this experiment is that the authors did not compare the standards and the two types of deviants separately, and therefore, it is not possible to evaluate the possible differential responses to deviances in orientation and spatial localisation.

In addition to studies carried out with human subjects, Astikainen et al. (2000) attempted to clarify whether MMN-like ERPs to visual deviances were elicited in animals. A primary goal of the study was to demonstrate whether this component revealed a dependence on the presence of standards similar to findings with humans. To examine this, the authors recorded intracranial ERPs to changes in the visual environment in rabbits. Two light bars constructed of eight high bright LEDs were presented, aligned vertically and horizontally in a counterbalanced order. The results showed that the ERPs to oddball-deviants differed from those to standards in all recording sites (cerebellar cortex, visual cortex, and dentate gyrus). In the visual cortex of rabbits, the components were similar to the human auditory MMN because they were more negative to deviants relative to standards in the 75–100 ms latency range. As the authors stated, there were no differences between ERPs to oddball deviants and deviants-alone, but the finding that ERPs to deviants in the deviant-alone condition and those to standards in the oddball condition did not differ at the same latency range suggests that the MMN-like ERP process seemed to be conditional upon the presence of standards. Therefore, it represents a similar situation to MMN in humans. These results were similar to the MMN-like ERPs observed in subcortical hippocampal and cerebellar activities recorded in turtles (Prechtl and Bullock, 1993). One of the most interesting issues in this study is that the authors tried to overcome the lack of dependence on the presence of standards observed in visual deviances in humans (Alho et al., 1992) and animals (Prechtl and Bullock, 1993). According to the authors, these characteristics could be present, but not observable, when the oddball deviant ERPs were compared with the deviant presented alone. They, therefore, applied an alternative test developed by Ruusuvirta et al. (1998), where the ERPs to deviants before and after the removal of the standards are compared with the ERPs elicited by standards. This method has shown the dependence on the presence of standards in MMN-like components to acoustic deviances in animals (Ruusuvirta et al., 1998).

### *3.2.4. Changes in spatial frequency*

Kenemans et al. (2001) presented subjects with rapid oddball sequences including two gratings that varied in spatial frequency (0.6 and 2.4 cycle/deg). The irrelevant gratings were presented simultaneously with a “plus sign” that flashed to the left or right of the fixation point. Subjects were required to react to this stimulus while ignoring the gratings. The authors found a component in the 100–200 ms latency range that was sensitive to deviance independently of the spatial frequency. Apart from the oddball sequence, they also presented “lonely deviants” sequences from which standards were omitted. The isolated deviants elicited a similar negative wave to the deviant presented in the oddball sequence revealing that, unlike the auditory MMN, the negativity recorded in this study was not dependent on the presence of standards, precluding considering it as a true visual MMN.

Heslenfeld (2002) presented low contrast gratings to observe the effects of change in spatial frequency while the subjects performed a visuo-motor tracking task. In order to evaluate the automaticity of the evoked response, this task was presented with three levels of difficulty. The author also controlled for exogenous effects by interchanging the stimuli that acted as deviant and standard in the different experimental blocks. The results showed that the deviant stimuli evoked a more negative response at 120–200 ms compared with the standards, regardless of the spatial frequency and processing load. At first, this response was more pronounced at occipital midline (Oz, 120–160 ms) and later at occipito-temporal sites (T5/T6, 160–200 ms), suggesting the existence of two possible neural generators. As Heslenfeld indicated, these components could be considered as homologous of the auditory MMN, since they were independent of attention and the individual physical characteristics of the stimuli. In this study, an earlier effect of deviance (120–180 ms), maximal at frontal and central leads, was also observed. This component was larger for the easiest visuo-motor task and low spatial frequency deviants, and was related by the author to the frontal component of the auditory MMN.

### 3.2.5. Changes in colour

In the above reported study, Kenemans et al. (2001) also included a colour-oddball experiment. They used again gratings with a spatial frequency of 0.6 cycle/deg but varying in colour (red and blue). In this experiment, they obtained similar results to those observed in their previous spatial frequency experiment. The infrequent colour deviants elicited more negativity in the 100–200 latency range. However, when the deviants were presented in the absence of the standard-colour stimuli a clear deviance-dependent negativity (DDN) could still be observed. Based upon the results from both experiments, the authors concluded that the deviant-standard difference was not due to a memory trace for preceding standards but to a selective refractoriness effect.

Recently, evidence for a memory-dependent “visual MMN” was provided by Czigler et al. (2002). In this study, they used coloured vertical square-wave gratings in two different types of sequences. They presented an oddball stimulus block, where two different colours were used as standards and deviants in a counterbalanced order. They also included an equal-probability multicolour (eight colours) stimulus sequence, similar to the condition used by Jacobsen and Schröger (2001) in an auditory MMN study. Additionally, in order to test the degree of deviance effects observed in the auditory MMN, they presented separately a similar (small deviance) and a widely different (large deviance) pair of colours as standard and deviant stimulus. The large deviants elicited an increased posterior negativity in the 120–160 latency range, both when compared with the standards in the traditional oddball condition, and with the same stimulus in the multicolour stimulus blocks. The deviants in the oddball condition also showed a larger positivity, peaking in the 120–160 ms latency range when they were compared with the standards in the same oddball series. On the contrary, no significant vMMN was elicited by the small deviance condition, indicating that larger stimulus differences are needed to elicit the visual than the auditory MMN. The authors concluded that this result could be considered as a homologue of the auditory MMN since the posterior negativity in the difference waveforms can be attributed to a memory-related mismatch process.

In a forthcoming paper, Czigler et al. (submitted) (personal communication) provide an even stronger test of the existence of a vMMN dependent on a memory trace. In this study they investigated whether infrequent conjunctions of two visual features (colour and direction of gratings) elicit a vMMN within a series of frequent conjunctions of the same features. The results showed that infrequent conjunctions elicited a posterior negative wave in the 120–160 latency range, which was followed by a positivity. Since the values of the colour and direction of stimulus appeared in equal probability, emergence of the vMMN could not be attributed to processing at the feature level. The authors concluded that the contribution of low-level refractoriness is unnecessary for the emergence of vMMN and that the memory system is capable of storing feature conjunctions.

## 4. Summary of reviewed studies

In most of the studies reviewed in this paper involving electrophysiological experiments, results concerned components that were associated with changes in some physical attributes of visual stimulation. However, in three of the articles there are no components that can be considered as an automatic correlate of visual change detection.

This is the case in Neville and Lawson's (1987) study. Although a different response was elicited by presentation of infrequent, deviant directional-motion in unattended locations, it is difficult to determine if this response was significantly different from that elicited by standard stimuli. Csibra and Czigler (1991) as well, did not find a detection-independent ERP using deviances in the direction of movement, rotation or shape. In this study, they only observed an N2b–P3 complex when the subjects detected the deviant characteristic. Additionally, the study carried out by Nyman et al. (1990) did not reveal a clearly different response between standards and deviants.

The remaining studies revealed responses associated with deviation or visual stimulus change. Even though the distribution of the visual components is less precise than that of the auditory MMN, they also present maximum amplitudes at the specific-modality cortex, such as occipital cortex and inferotemporal cortex contralateral to the stimulated visual field (Woods et al., 1992), occipital sites (Berti and Schröger, 2001; Czigler et al., 2002; Czigler et al., submitted; Kenemans et al., 2001), and visual cortex in animals (Astikainen et al., 2000). These components have also been obtained at occipital and posterior temporal areas (Alho et al., 1992; Heslenfeld, 2002; Nordby et al., 1996; Tales et al., 1999) and at occipito-parietal regions with right hemispheric dominance (Cammann, 1990). Resembling the auditory MMN, Czigler et al. (2002), Czigler et al. (submitted), Heslenfeld (2002) and Wei et al. (2002) also observed deviance-related components at frontal regions. As an exception, mention should be made of research conducted by Iijima et al. (1996) and Kenemans et al. (1992), in which the observed negativities were maximal at Cz and Pz, and at Cz and Fz, respectively. However, in both studies only midline electrodes were employed for the ERP recordings. For a more detailed description of the different components related to visual change, see Table 3.

We have seen that data concerning topographic distribution is quite consistent with the modality-specific distribution of MMN. However, regarding other characteristics observed in the auditory MMN, the results are less conclusive. We will now explore these in greater detail.

### 4.1. Independence of attention and processing load effects

The auditory MMN indexes early, automatic processing of auditory input, independent of subjects' attention, and it shows a similar amplitude when subjects attend to stimuli and when they ignore them. Some visual deviance-related potentials found in the reviewed papers seem to be elicited without attention, revealing a pre-attentive automatic mechanism, as seen in the studies of Alho et al. (1992),

Table 3
Characteristics of components related to visual change

| Source | Stimulus change | Latency (ms) | Localisation | Characteristics |
|---|---|---|---|---|
| *Non MMN like components* | | | | |
| Neville and Lawson, 1987 | Motion direction | – | – | ERPs to unattended targets display a broad negative shift |
| Nyman et al., 1990 | Contrast | 100–200 | Oz | The deviants are more negative than standards at Oz, between 100 and 200 ms<br>This difference disappears when the deviant is the stimulus with the highest contrast |
| Csibra and Czigler, 1991 | Motion direction | Max 322 (240–420) | Positive front-central peak | Detected deviant stimuli elicit an N2b component followed by a positive P3a, that can not be observed for non-detected deviants |
| | Rotation, shape | | | Deviances in rotation and form do not evoke components different from standards |
| *Posterior negativity at 100–180 ms latency range* | | | | |
| Woods et al. 1992 | Size | 165 (230–330) | Right temporal and occipital | Unattended deviants elicit MMN/N2b components with similar latency (165 ms) and peak duration (230–220 ms) that when they are attended, but with lower amplitude (−0.69 μV)<br>Maximum amplitude over contralateral temporal cortex similar for attended and unattended conditions |
| Iijima et al., 1996 | Shape | 166 | Cz, Fz | Deviants elicit a negative deflection at around 166 ms that is maximal at frontal and central sites |
| Astikainen et al., 2000 | Orientation | 75–150, 175–500 | CerCx, DG | Increased positivity to visual deviants in dentate gyrus (DG) of right hippocampal formation and cerebellar cortex (CerCx) |
| | | 25–50, 75–100, 150–175 | VCx | Increased negativity to visual deviants in visual cortex (VCx) |
| Kenemans et al., 2001 | Spatial frequency/ colour | 100–200 | Occipital | A deviance-related negativity in occipital regions can be observed in the 100–200 latency range. This negativity does not depend on a memory trace for preceding standards |
| *Negativity at 100–180 ms and posterior negativity later than 200 ms* | | | | |
| Czigler and Csibra, 1990 | Angle orientation | Max 145 (120–180) | Oz | Infrequent salient deviant stimuli elicit two occipital negative waves with 145 and 210 ms peak latencies |

Table 3 (*Continued*)

| Source | Stimulus change | Latency (ms) | Localisation | Characteristics |
|---|---|---|---|---|
| | Thickness of frame | Max 210 (240–300) | – | Less salient deviant stimuli elicit only the second component |
| Czigler and Csibra, 1992 | Angle orientation | Max 148 (140–180) | Oz | Detected deviant salient stimuli elicit two components, including the early automatic component |
| | Thickness of frame | 180–260 | – | This effect diminishes when the ISI is increased |
| | | | | The less salient characteristic elicits the late occipital negative component only when it is task-relevant |
| Alho et al., 1992 | Size | DRN1: Max 120 | Oz | Deviance-related negativities (DNR) in posterior sites around 90–290 ms. Elicited only by more deviant stimuli |
| | | DRN2: Max 200 | Oz, T5 and T6 | Two components: DRN1 between 120 and 200 ms restricted to Oz, similar for auditory and visual attention and not affected by attentional load. DRN2 has a wider distribution that includes Oz, T5 and T6 |
| Tales et al., 1999 | Shape/spatial frequency | Max 180 | O2, O1, T5, T6 | The N2 is larger to deviants than to standards. The difference begins at 160 ms and remains until 400 ms |
| | | 250–400 | | This effect is reduced when the standards are the more complex stimuli and it can only be observed between 250 and 400 ms |
| Kremláĉek, et al., 2001 | Motion direction | 160 | – | Deviants elicit a larger N160. As this component is insensitive to motion direction, it represents an MMN-like response independent of attention |
| Wei et al., 2002 | Contrast | DRN1:100–200 | F4/O2 | Unattended deviants elicit an early deviance-related negativity (DRN1) (100–200 ms, max F4) |
| | | DRN2: 200–300 | Wide distribution | Attended deviants elicit the DRN1 (max O2) followed by a later deviance-related negativity (DRN2) |
| *Anterior negativity at > 200 latency range* | | | | |
| Cammann, 1990 | Colour | 150–350 | Maximum over the parietal region (P4) | Subtraction curves in the ignore condition show a long MMN-like change, maximum over the parietal region with a right hemispheric dominance |
| Kenemans et al., 1992 | Shape | 240–450 | Cz, Pz | Deviants elicit a P2–N2 of larger amplitude that was not affected by task load |
| Nordby et al., 1996 | Motion reversal | 200–250 | O1, O2, T5, T6 | The negative wave elicited by spatial deviants is similar during both ignore and target condition |
| Berti and Schröger, 2001 | Localisation, orientation | 200 | O1, O2 | Deviants elicited a more negative deflection at around 200 ms at occipital sites for both long and short-duration stimuli |

Table 3 (*Continued*)

| Source | Stimulus change | Latency (ms) | Localisation | Characteristics |
|---|---|---|---|---|
| | | 400 | Fz, Cz | There is a small difference between standard and deviant stimuli at around 400 ms at Fz and Cz which is more pronounced for short stimuli |
| *Posterior negativity and anterior/posterior positivity* | | | | |
| Heslenfeld, 2002 | Spatial frequency | 120–160<br>160–200 | Oz<br>T5/T6 | Posterior scalp deviance effect, independent of spatial frequency and processing load with two possible cortical generators, since the first component has a maximum at Oz (120–160 ms), and the later at T5/T6 (160–200 ms) |
| | | 120–180 | Frontal/central | Anterior scalp deviance effect with higher amplitudes for the easy task and low frequency deviants. Related to the frontal component of auditory MMN |
| Czigler et al., (2002) | Colour | (136) 120–160 | Posterior negativity | Large deviances displayed a more negative wave at posterior scalp locations with a mean latency of 136 ms when compared with oddball deviants and ERPs elicited by the same stimulus in the multicolour condition |
| | | (136) 120–160 | Anterior positivity | ERPs to deviants and standards in the traditional oddball condition also revealed an anterior positivity with the same peak latency to the posterior negativity (136 ms) |
| Czigler et al. (submitted) | Conjunctions (colour/direction) | (128) 120–160 | Oz | Infrequent conjunction of colour and direction elicited a posterior negative wave. This component can be considered a vMMN dependent on a memory trace |
| | | (168–268) | Occipital | At occipital locations the negative difference ERP was followed by a positivity |
| | | 100–140 | Anterior locations | Over the anterior locations a small positivity appeared in the 100–140 ms range |

Cammann (1990), Heslenfeld (2002), Kremláĉek et al. (2001) and Tales et al. (1999) and Woods et al. (1992). In other studies, however, the deviant task-irrelevant stimuli elicited a N200 effect, but they were followed by other components related to active attention mechanisms (such as N2b, P3a, or the so called re-orienting negativity (RON)) (Berti and Schröger, 2001; Iijima et al., 1996; Kenemans et al., 1992).

In Woods et al.'s (1992) study, automatic components elicited under non-attention conditions emerged, but they were considerably smaller than those elicited under attention conditions. Nevertheless, under certain conditions (Csibra and Czigler, 1991; Czigler and Csibra, 1990, 1992) the earlier N2 deflections were only elicited to the more salient stimuli and when the subjects detected the deviance.

In other studies, it is difficult to conclude whether they successfully controlled for the subjects' attention being directed away from the irrelevant stimuli. In some cases, as in the Nordby et al.'s (1996) study, they did not include a primary task. In other cases, the irrelevant characteristics were part of the same sequence of events (Tales et al., 1999), were presented in the centre of the visual field (Wei et al., 2002), or the irrelevant features were part of the same stimulus to be attended (Berti and Schröger, 2001). As suggested by one of the referees, a more suitable experimental approach would involve maintaining subjects' attention in a continuous task (as in the Heslenfeld, 2002, study) in which task stimuli were independent of the irrelevant ones. Another control procedure would involve directing the eliciting stimuli to the visual periphery, because under normal circumstances attention is directed to the fixated location.

In the auditory modality, some studies showed that the MMN amplitude can be modulated by strongly focused attention (e.g. in pattern changes, Alain and Woods, 1997; intensity deviation, Näätänen et al., 1993; Woldorff et al., 1991). However, frequency-MMN is relatively insensitive to attentional manipulations and no data suggest that the withdrawal of attention can totally eliminate the MMN (Näätänen, 2001). In the visual modality, the studies that controlled this characteristic revealed no effects of the processing load on deviant-related components for attributes such as size, spatial frequency or shape (Alho et al., 1992; Heslenfeld, 2002; Kenemans et al., 1992).

### 4.2. *Dependence on the presence of standards. Memory-based mechanism*

The MMN is a response to the relationship between the present stimulus and the previous stimulus sequence, rather than to the present stimulus "per se." It has been shown that MMN is elicited if a memory-comparison process detects a difference between the neural representation of the regularity in recent stimulation and the representation of the current stimulus (see Jacobsen and Schröger, 2001). This account was demonstrated for auditory MMN both to single stimulus features such as intensity changes (Snyder and Hillyard, 1976; Woldorff et al., 1991), or duration increments and decrements (Näätänen et al., 1989), and to higher-order feature changes such as omission of tones (Nordby et al., 1994; Tervaniemi et al., 1994) or interstimulus interval variations (Ford and Hillyard, 1981). Moreover, Schröger and

Wolff (1996) and Jacobsen and Schröger (2001) have demonstrated that the MMN can be considered a true memory-comparison-based brain response both for stimulus location and pitch, respectively.

It is, therefore, necessary to control for dependence on the presence of standard regularities to affirm that a visual MMN is present. However, only five of the reviewed studies controlled this aspect. Three of them (Alho et al., 1992; Astikainen et al., 2000; Kenemans et al., 2001) compared the ERPs to deviants when embedded in standard/deviant sequences with those obtained from deviants-alone sequences. The results were inconsistent. Alho et al. (1992) found that activity to deviant-alone stimuli was more negative and occurred later at occipital sites relative to activity elicited by standards, although the differences were not statistically significant. Kenemans et al. (2001) found that the observed deviant-related negativities disappeared in deviant-alone sequences. Conversely, in the study by Astikainen et al. (2000), the data appeared to confirm standard-dependence for visual deviance detection in rabbits.

The two other studies that controlled the dependence of deviance-related visual ERPs on memory comparison processes employed more sophisticated controls. Czigler et al. (2002) employed a method similar to those of Schröger and Wolff (1996) and Jacobsen and Schröger (2001). Their results are the first to demonstrate that, at least for changes in colour, a memory-dependent visual MMN can be recorded. This finding was confirmed later (Czigler et al., submitted), providing the first evidence that a visual memory system is capable of storing feature conjunctions for automatic detection.

### 4.3. *Endogeneity versus refractoriness effects*

It has been demonstrated that auditory MMN cannot be simply explained by a refractoriness hypothesis, where some neural populations are sensitive to the features of the standard stimulus while others respond to features of the deviant stimulus (Schröger, 1997). As has been seen in the above section, the MMN is an endogenous component triggered by differences between stimuli. In this sense, the latency of MMN is inversely related and its amplitude is positively related to the magnitude of the difference between the standard and the deviant stimuli (Näätänen and Gaillard, 1983). It is, therefore, necessary to rule out all possible exogenous effects of stimulus change on any deviance-related components obtained in the visual modality. This was controlled in several studies by presenting the deviant and standard stimuli in counterbalanced order. Astikainen et al. (2000) and Kenemans et al. (1992) observed similar negativities when they counterbalanced the stimuli, although they did not compare the responses when the deviant and standard stimuli were reversed in the experimental conditions. Using the same procedure, Heslenfeld (2002) obtained waves that were independent of the physical characteristics of the stimuli. More controversially, Tales et al. (1999) obtained different responses when they used the most complex stimulus as standard. Therefore, the results regarding the endogenous nature of deviance related visual components are divergent, with the exception of Heslenfeld's report.

### 4.4. Elicitation by any discriminable change

A change in any stimulus feature (tonal frequency, intensity, duration, etc.) appears to elicit an MMN (Näätänen, 1990) even when differences merely approximate the behavioural discrimination threshold (Amenedo and Escera, 2000). However, as demonstrated by Czigler and Csibra (1990, 1992), the emergence of the early negative visual deflection seems to be related to the more salient infrequent stimulus. This finding is in line with that of Alho et al. (1992) in which the earlier automatic negative component was only present when the stimuli used as deviants were those that most differed from the standards. In Czigler et al.'s (2002) study, no significant visual MMN was elicited by the small deviant condition. Alho et al. (1992) and Czigler et al. (2002) interpreted their results by suggesting that a visual MMN might have a higher elicitation threshold than the auditory MMN.

Another possible explanation is that in the visual modality only certain stimuli changes can elicit this type of component (Woods et al., 1992). However, considering the results described here, it is not possible to infer what specific stimuli changes are required to do so. In the case of contrast deviation, when Nyman et al. (1990) used gratings, no deviant-related negativities were observed. However, Wei et al. (2002) found an early negative deflection when changes in the contrast of natural colour scenes were beyond attentional-focus. The direction of movement also did not elicit deviant-related components with stimulus in apparent motion (Csibra and Czigler, 1991; Neville and Lawson, 1987). However, these responses were present when high-speed moving gratings (Kremláĉek et al., 2001) and motion reversals (Nordby et al., 1996) were used as deviants. Changes in size evaluated by Alho et al. (1992) demonstrated that the early deviant-related components were only elicited by stimuli that were less similar to the standard visual stimuli. With regard to orienting changes, no automatic components were observed by Csibra and Czigler (1991). Finally, deviations in colour (Cammann, 1990; Czigler et al., 2002; Kenemans et al., 2001) and spatial frequency (Heslenfeld, 2002; Kenemans et al., 2001) elicited MMN-like automatic responses in all instances. However, they showed different characteristics regarding other features observed in the auditory MMN (e.g. dependence on presence of standards or memory-based components).

### 4.5. Interstimulus interval effect

Czigler and Csibra (1992) evaluated the effect of the ISI on the visual modality and observed a reduction of their early automatic deflection when the ISI increased from 340 to 1020 ms. From this result, the authors stated that the early negativity was similar to the auditory MMN because its amplitude decreased while the interstimulus interval increased. This statement was based on the early findings about the ISI effects on MMN (Mäntysalo and Näätänen, 1987; Näätänen, 1995). However, more recently Winkler et al. (2001) have shown between-subjects differences in ISI-MMN dependence. Thus, it is difficult to establish whether the observed ISI effect on the visual modality can be compared with the results on the auditory MMN.

### 4.6. General considerations

Regardless of the difficulties in drawing conclusions from the above review due to the methodological heterogeneity of these studies we can make the following generalisations.

Most of the studies transcended the main limitation of the lack of attention control. However, other studies presented some methodological limitations that should be taken into account for the interpretation of results (see Table 4), since the employed paradigms failed to direct the focus of attention away from the deviant stimulation.

Some of the researchers who specifically looked for a visual analogue of the auditory MMN did not search for an index of automatic, memory-based detection of deviances in the visual system. They basically focused on the classical features of auditory MMN and then attempted to transfer them directly to the visual system. However, there is no reason to believe that the underlying mismatch detection mechanisms should be identical in both sensory modalities, in view of the existing functional and anatomical differences. In fact, some results reviewed here may indicate that both mechanisms could show different properties (e.g. larger deviances seem necessary to elicit a visual MMN). Secondly, despite the efforts made to reproduce the auditory MMN features in the visual system, only the most recent papers controlled essential features such as the lack of exogenous effects and more importantly the demonstration of a visual MMN as a memory-based phenomenon (see Table 5).

We believe that it is necessary not only to search for the existence of a visual component that fulfils all main features to be considered a counterpart to the auditory MMN. Psychophysiological and neurophysiological approaches to visual processing can complement and be compatible with each other. Neurophysiological

Table 4
Main methodological limitations of reviewed studies

| Limitations | Studies |
|---|---|
| Lack of control over (or failure to control for) exogenous stimuli effects | Alho et al. (1992), Berti and Schröger (2001), Cammann (1990), Csibra and Czigler (1991), Czigler and Csibra (1990, 1992), Iijima et al., (1996), Nordby et al., (1996), Nyman et al. (1990), Tales et al. (1999, 2002), Wei et al. (2002) and Woods et al. (1992) |
| Overlapping of other negative components | Berti and Schröger (2001) and Kenemans et al. (1992) |
| Simultaneous presentation of visual and auditory stimuli | Nyman et al. (1990) |
| Comparison of samples after subjects' verbal report | Csibra and Czigler (1991) |
| Lack of statistical contrast between deviant and standard ERPs | Neville and Lawson (1987) |
| Insufficient description of methodological procedure | Cammann (1990), Kenemans et al. (2001) and Kremláĉek et al. (2001) |

Table 5
Auditory MMN characteristics, method of control, and studies that assessed the presence of this feature in visual deviance-related negativities

| Auditory MMN feature | Method of control | Studies |
|---|---|---|
| Memory-trace hypothesis/ | Infrequent stimuli in traditional oddball sequences compared with the same stimuli in equal probability blocks | Czigler et al. (2002) |
| Dependence on the presence of standards | Comparing ERPs to oddball-deviants with those to deviants presented alone | Astikainen et al. (2000), Alho et al. (1992) and Kenemans et al. (2001) |
| Endogeneity. Independence of stimulus energy | Counterbalanced order of deviant and standard stimuli and/or comparison of ERPs to physically identical stimuli that work as standards or deviants in different blocks | Astikainen et al. (2000), Czigler et al. (2002), Czigler et al. (submitted), Heslenfeld (2002), Kenemans et al. (1992), Kenemans et al., (2001), Tales et al. (1999) and Nyman et al. (1990) |
| Independence of processing load | Different levels of difficulty of the main task | Alho et al. (1992), Heslenfeld (2002) and Kenemans et al. (1992) |
| Dependence on the magnitude of stimulus change | Use of gradual changes in the magnitude of the deviant stimulus parameter | Alho et al. (1992) |
| | Manipulation of salience | Czigler and Csibra (1990, 1992) |
| | Small or large difference between deviants and standards | Czigler et al. (2002) |

approaches do not only provide the basis for a better understanding of visual processing but can also be useful in explaining the differences that may exist between both (auditory and visual) psychophysiological correlates.

## 5. Conclusions and directions for future research

In summary, the emergence of visual deviant related components is common in the research on visual discrimination. These studies attempted to verify whether ERP negative components in the N2 latency range had pre-attentional automatic characteristics by controlling attention with distraction tasks, or presenting the stimuli outside the focus of attention. However, only some recent studies have controlled the essential features for the operational definition of an MMN.

According to the results reviewed in this work, the component that seems to be the best candidate for a possible MMN counterpart is an early negative one, which appears in the N2 latency range with a topographical distribution that is modality-specific. This component, as in the auditory modality, is followed by another negative deflection when the deviant stimulus is attended or detected. Some studies have revealed that these waves can also be followed by frontal components. It is also an automatic component that seems to be independent of the processing load because, in the cases examined here, it is insensitive to attentional manipulations. However, considering the results of the review, it appears that a higher difference between standards and deviants is necessary to elicit it compared with the auditory MMN. The data are somewhat contradictory with regard to its elicitation by any physical change of visual stimulation. However, we cannot assume that there is a particular characteristic that does not elicit this automatic response. Changes in spatial frequency, and especially in colour, are the irrelevant deviances that have been proven until now to elicit automatic endogenous memory-based components.

Heslenfeld (2002) obtained a good candidate for a visual counterpart of the auditory MMN, because he found an automatic component free of exogenous effects. More recently, the results obtained by Czigler et al. (2002) and Czigler et al. (submitted) provided the first evidence for a visual automatic detection process based on a memory system which is probably the best candidate for a visual MMN homologue.

Therefore, we believe that, as a first step, it is necessary to include methodological controls that help disentangle refractoriness effects from memory-comparison effects, using the method initially proposed by Jacobsen and Schröger (2001) and adapted by Czigler et al. (2002) for the visual modality. This experimental technique should be applied to other deviances in visual stimulus features, such as direction of motion, spatial frequency, and contrast. Moreover, another line of research could be started which examines the properties of this automatic process in the detection and storing of feature conjunctions.

However, there are some questions raised while reviewing these studies that require answers. Which deviations in visual stimuli elicit a reliable mismatch response? Does the visual MMN share the same features than its homologous in the auditory system? Are there differences between the responses elicited by peripheral and central deviances? Or do they depend on the type of deviance (e.g. motion in periphery vs. colour in central visual areas) as well? What is the necessary threshold to elicit the response? What are the optimal parameters to elicit an MMN? What are its neural origins? Is there more than one neural generator depending upon the type of deviance/experimental procedure? These and related questions need to be address before concluding that a true visual MMN does exist.

Some of the questions stated above could be explored by enlightening the separate contributions of the visual system divisions to the ERP responses. The relative functional division of the visual system into two streams, the dorsal stream specialising in the processing of spatial and motion information, and the ventral stream responsible for the processing of object features such as colour and shape, is currently the predominantly accepted model (e.g. Ungerleider et al., 1998). However, it is known that some areas composing one of these streams also process stimulation properties theoretically corresponding to the domain of the other stream.

The magnocellular stream can be characterised by sensitivity to spatial and motion information, and more specifically low contrast, achromaticity, moderate-to-high temporal frequency and low spatial frequency (due to its large receptive fields). The parvocellular stream, in general, responds to high contrast (low sensitivity to luminance), chromaticity, low temporal frequency, and high spatial frequency (due to its small receptive fields), and is specialised in analysis of colour, shape and surface properties of objects. It would be worth controlling for these parameters, to vary them according to the sensitivity of each pathway, and to observe, for example, whether a reliable MMN response is optimised when they are taken into account (e.g. motion in the periphery at low luminance levels).

Heslenfeld (2002) and Kremláĉek et al. (2001) considered the neurophysiological properties of the visual system, since they both differentially stimulated one of the two distinct channel pathways for visual analysis (e.g. magnocellular stream using spatial frequency and motion direction changes in gratings with low contrast, respectively, and presented in the periphery). Czigler et al. (2002) also used changes in colour and presented them in a wide area of the visual field that also covered the centre. Is it possible that the positive results are based on an optimal visual stimulation? We believe that it is important to continue with this line of investigation in order to study the possible differential contributions that both dorsal and ventral streams could play in the mechanism that underlies the MMN.

The MMN generation process has a central role in the orienting response to changes in the acoustic environment (Näätänen et al., 2002). The magnocellular pathway is also related to other secondary routes different from the geniculostriate, such as the tecto-pulvinar pathway, that may be involved in attention capture processes and the re-orienting of attention. The tecto-pulvinar pathway is a phylogenetically older route that mainly involves projections from the retina to the superior colliculus (SC) of the midbrain, pulvinar, striate and extrastriate cortex. The functions of the SC have been connected with the control of saccadic movements, attention and spatial orienting (Kustov and Robinson, 1996), multisensorial integration (Stein and Meredith, 1991), motor preparation (Dorris and

Munoz, 1998) and target selection (Horwitz and Newsome, 1999; also see Sparks, 1999 for an extensive review). Furthermore, the pulvinar is a thalamic relay of visual inputs from the midbrain to various extrastriate cortical areas, but also plays a role in signalling the occurrence of saccadic eye movements (Bender and Baizer, 1990; Robinson and McClurkin, 1988; Robinson et al., 1991; Schmidt et al., 2001; Sundkamp and Schmidt, 2000), visual attention (Bender and Youakim, 2001; Benvento and Port, 1995; Michael et al., 2001; Robinson and Petersen, 1985), visual salience (Morris et al., 1997; Robinson, 1993; Robinson and Petersen, 1992), motion processing (Casanova and Savard, 1996; Davidson et al., 1992; Dumbrava et al., 2001; Merabet et al., 1998; Minville and Casanova, 1998) and high integrative functions (Chalupa, 1991). See Bender (1988), Grieve et al. (2000), Chalupa (1991) and Robinson (1993) for more detailed information about pulvinar functions.

Studies with striate lesions have demonstrated important functional contributions by this pathway. When the striate cortex is absent, many cells in MT still receive inputs about stimulus motion (Gross, 1991), while the responsivity of IT cells is eliminated. These results demonstrate evidence that visual processing in the ventral pathway mainly depends on inputs from the geniculostriate pathway, whereas the dorsal stream is more capable of using information from the tecto-pulvinar system.

The contribution of this secondary pathway would, therefore, be added to that of the dorsal stream in localising and orienting towards objects in the visual field. There is also evidence that suggests the involvement of this pathway in attention orienting. This has already been suggested in the models proposed by Posner et al. (1988) and Wright and Ward (1998). In particular, the posterior parietal cortex appears to work along with the pulvinar to capture and maintain visual fixation and the focus of attention, as well as working together with the superior colliculus to control the start of attention switches and saccades to a different location (Posner et al., 1988).

However, it is important to remember that the mechanism by which attention is shifted across the visual fields is still a subject of controversy, and alternative models exist that are still being investigated (Desimone and Duncan, 1995; Grossberg et al., 1994; La Berge et al., 1997).

There is also converging evidence of a special role of the midbrain pathway in reflexive orienting in humans from studies involving temporal-nasal asymmetry (Rafal et al., 1991), progressive supranuclear palsy patients (Rafal et al., 1988; Rafal and Henik, 1994) and patients with hemianopia or blindsight. The role of the fast tectal channel in the processing of motion in humans has also been reported (Ffytche et al., 1995).

In conclusion, the study of a visual MMN should include the necessary experimental controls to affirm that it is a reliable visual homologue of the auditory component. But we also believe that it would be interesting to manipulate the parameters that magnify the different responses of the various visual pathways. It would be particularly intriguing to explore the contributions of those areas that are involved in attentional capture and re-orienting of attention.

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