

See discussions, stats, and author profiles for this publication at: <http://www.researchgate.net/publication/269728451>

# From pre-attentive processes to durable representation: An ERP index of visual distraction

ARTICLE *in* INTERNATIONAL JOURNAL OF PSYCHOPHYSIOLOGY · MARCH 2015

Impact Factor: 2.65 · DOI: 10.1016/j.ijpsycho.2014.12.007

## 4 AUTHORS, INCLUDING:



[Olga Sysoeva](#)

Moscow State University of Psychology and...

16 PUBLICATIONS 95 CITATIONS

[SEE PROFILE](#)



[Alexander Sorokin](#)

University of Helsinki

10 PUBLICATIONS 16 CITATIONS

[SEE PROFILE](#)



[Tom A Campbell](#)

University of Helsinki

21 PUBLICATIONS 145 CITATIONS

[SEE PROFILE](#)



ELSEVIER

Contents lists available at ScienceDirect

## International Journal of Psychophysiology

journal homepage: [www.elsevier.com/locate/ijpsycho](http://www.elsevier.com/locate/ijpsycho)

# From pre-attentive processes to durable representation: An ERP index of visual distraction ☆,☆☆

Olga V. Sysoeva <sup>a,i,\*</sup>, Elke B. Lange <sup>b</sup>, Alexander B. Sorokin <sup>c,d,e</sup>, Tom Campbell <sup>f,g,h</sup>

<sup>a</sup> MEG Center, Moscow State University of Psychology and Education, Russia

<sup>b</sup> Cognitive Brain Research Unit, Institute of Behavioral Sciences, University of Helsinki, Finland

<sup>c</sup> Mental Health Research Center, Russian Academy of Medical Sciences, Russia

<sup>d</sup> Center of Neurobiological Diagnostics, Moscow State University of Psychology and Education, Russia

<sup>e</sup> Scientific and Practical Center of Child Psychiatry and Neurology, Moscow, Russia

<sup>f</sup> Neuroscience Center, University of Helsinki, Finland

<sup>g</sup> Center for Mind and Brain, University of CA, Davis, USA

<sup>h</sup> Helsinki Collegium for Advanced Studies, University of Helsinki, Finland

<sup>i</sup> Autism Research Laboratory, Moscow State University of Psychology and Education, Russia

## ARTICLE INFO

## Article history:

Received 14 September 2014

Received in revised form 7 December 2014

Accepted 9 December 2014

Available online xxxx

## Keywords:

Visual search

Event-related potentials (ERP)

Distraction

Color change

Mismatch negativity (MMN)

Late fronto-central negativity (LFCN)

## ABSTRACT

Visual search and oddball paradigms were combined to investigate memory for to-be-ignored color changes in a group of 12 healthy participants. The onset of unexpected color change of an irrelevant stimulus evoked two reliable ERP effects: a component of the event-related potential (ERP), similar to the visual mismatch negativity response (vMMN), with a latency of 120–160 ms and a posterior distribution over the left hemisphere and Late Fronto-Central Negativity (LFCN) with a latency of 320–400 ms, apparent at fronto-central electrodes and some posterior sites. Color change of that irrelevant stimulus also slowed identification of a visual target, indicating distraction. The amplitude of this color-change vMMN, but not LFCN, indexed this distraction effect. That is, electrophysiological and behavioral measures were correlated. The interval between visual scenes approximated 1 s (611–1629 ms), indicating that the brain's sensory memory for the color of the preceding visual scenes must persist for at least 600 ms. Therefore, in the case of the neural code for color, durable memory representations are formed in an obligatory manner.

© 2014 Elsevier B.V. All rights reserved.

## 1. Introduction

A lurid and influential theoretical claim has been made that vision has no memory in excess of 100 milliseconds: “Vision has no memory, it exists in the present tense” (Wolfe, 2000). Evidence for this claim about sensory memory has stemmed from demonstrations that a large change in a visual scene, or the sudden onset of a visual object, can go

unnoticed – phenomena, such as change blindness (O'Regan et al., 1999), inattention blindness (Mack and Rock, 1998), and the attentional blink (Shapiro et al., 1997). Evidence from a flicker version of the change blindness paradigm (Rensink et al., 1997) suggests that sensory memory for the visual stimulation is thought to not even persist for 80 ms, unless stimulation receives some form of extensive attentional processing (Rensink, 2002). Accordingly, as in the inattention blindness and attentional blink paradigms, vision is shown to have no sensory memory.

On the other hand, the change detection process in vision is manifested as the visual mismatch negativity (vMMN) component of the event-related potential (ERP). This vMMN is typically elicited in a visual oddball paradigm when a repeated standard visual stimulus, such as a red square standard, is unpredictably and occasionally replaced by a deviant stimulus that differs from the standard stimulus by one feature, such as color, e.g., a green square deviant. Importantly, the inter-stimulus intervals between presentation of standard and deviant exceed 100 ms by far, suggesting that some representation of the standard persists. Such representation seems not to depend on attentional processing. The vMMN is also elicited when participants are ignoring the vMMN-eliciting features while attending to other aspects of the

☆ Elke Lange is now at the Max Planck Institute for Empirical Aesthetics, Frankfurt am Main. Tom Campbell was at the Center for Visual and Cognitive Neuroscience, North Dakota State University, the Medical Physics Section, Institute for Physics, University of Oldenburg, and at Theatre Academy, University of the Arts Helsinki.

☆☆ This work was supported by the Kone Foundation, the National Institute on Aging (grant number AG-16201), the Russian Scientific Fund (grant number 14-35-00060), the University of Helsinki, and the Academy of Finland (grant number 200522). The authors would like to thank Korena Onyper for collecting data in a separate behavioral pilot experiment, laboratory engineer Miika Leminen for advice on the apparatus, as well as Kimmo Alho and Lee M. Miller for comments and suggestions concerning earlier versions of this article.

\* Corresponding author at: The MEG center, Moscow State University of Psychology and Education, 127051 Sretenka 29, Moscow, Russia. Tel.: +7 499 256 45 13.

E-mail address: [olga.v.sysoeva@gmail.com](mailto:olga.v.sysoeva@gmail.com) (O.V. Sysoeva).

visual stimulation (Berti and Schröger, 2001, 2004, 2006; Kimura et al., 2008a,b).

The existence of vMMN, a scalp-elicited posterior bilateral negativity in response to visual deviance, has remained, until recently, a controversial topic (Näätänen, 1990, 1991; Cammann, 1990; Czigler, 1990; Pazo-Alvarez et al., 2003; Heslenfeld, 2003). However, throughout the past decade and into the current, a multitude of independent replications of the vMMN have placed vMMN upon a firm empirical footing (Astikainen and Hietanen, 2009; Astikainen et al., 2004, 2008; Berti, 2011; Clifford et al., 2010; Czigler, 2007; Czigler et al., 2004, 2007; Czigler and Pato, 2009; Czigler and Sulykos, 2010; Fisher et al., 2010; Flynn et al., 2009; Kimura et al., 2010a,c,d; Liu and Shi, 2008; Lyyra et al., 2012; Maekawa et al., 2009; Mao et al., 2004; Stefanics et al., 2011, 2012; Shtyrov et al., 2013; Sulykos and Czigler, 2011; Sušac et al., 2004, 2010a,b, 2011; for reviews, please see Kimura et al., 2011; Kimura, 2012; Winkler and Czigler, 2012). The vMMN is believed to be an analog of the more well-studied auditory MMN (Näätänen et al., 1978; Tiitinen et al., 1994), elicited at similar latencies and largely pre-attentively as well (Näätänen et al.; for a complementary perspective, see Erlbeck et al., 2015; Campbell, 2015). Yet functional differences could also exist between modalities – a key difference relating to the durability of the form of internal sensory memory representation indexed by vMMN. The orientation vMMN is elicited by an unexpected occasional change in orientation, occurring in response to visual stimuli separated by intervals of 200 ms, attenuating at intervals of 400 ms (Fu et al., 2003), and disappearing completely at intervals of 1100 milliseconds (Astikainen et al., 2008). Accordingly, the sensory memory responsible for the vMMN to orientation change is thought to only endure very brief intervals for vMMN. Thus the fleeting sensory memory for orientation in question is thought to have a duration of less than 1 s, as contrasts with estimates of 4–10 s for the pitch mismatch negativity in the auditory domain (Bottcher-Gandor and Ullsperger, 1992). However, the sensory memory for color may be considered more enduring: vMMN to color deviance can be elicited after intervals as long as 800 ms (Stefanics et al., 2011) albeit attenuated relative to a shorter interstimulus interval (ISI). The question of the duration of the to-be-ignored visual stimuli has remained open.

The value of an internal sensory memory representation for visual information has been subject to debate (Kimura et al., 2010b; O'Regan and Noë, 2001), the relatively static visual world typically being available as an external memory representation (Ballard et al., 1997). Indeed, the symbolic use of such external representations has been hailed as a major transition in human evolution (Donald, 1993), which compensates for the inherent limitations of working memory (see Miyake and Shah, 1999 for an overview).

Visual distraction paradigms have been shown to be promising in that they have revealed behavioral disruptions of performance produced by visual deviance, alongside a significant vMMN (Berti and Schröger, 2001, 2004, 2006; Kimura et al., 2008a,b). Further, it has been shown that when the to-be-ignored background exhibits deviance in the same dimension as the to-be-attended figure (color, orientation), the disruption of performance produced by the background is increased; alongside a concomitant vMMN augment (Czigler and Sulykos, 2010). However, vMMN to color change has not been shown to index distraction upon an individual level of performance (e.g., Czigler et al., 2002), whereas position deviance was effective in eliciting a vMMN as well as a behavioral distraction effect (Berti, 2009). To account for this difference, Berti (2009) suggested that peripheral presentation of color deviance might be necessary. In the present investigation, the amplitudes of significant differences between individual scalp-measured ERPs are thus evaluated as indices of behavioral distraction effects produced by to-be-ignored visual deviance, with the objective of assessing the functional relevance of vMMN to color change.

For this reason, a visual search task was adopted after Czigler et al. (2002); a paradigm which presented task-unrelated color deviance in the visual periphery, during which participants were required to look at a central fixation cross while searching for a unique target shape and ignoring a uniquely colored distractor within surrounding stimuli (Hickey et al., 2006). While the task of Czigler et al. (2002) did not prove sensitive to the distracting effects of color deviance, visual search distraction paradigms have been shown to be sensitive to color (Hickey et al., 2006). The present investigation aimed to evaluate the amplitudes of vMMN to color change of a distractor as indices of behavioral distraction, measured by the slowing of target processing. Crucially, the visual search task was extended by including a serial component: the distracting object differed in color from all other simultaneously presented objects, but that distractor occasionally changed in color within a sequence of trials. Hence, the effect of distraction was investigated in a series of visual search displays, where the distractor color was either a standard or a deviant color. Repetition of the uniquely colored “standard” distractor should facilitate the accumulation of a sensory memory trace for this color. To examine if the sensory memory mechanisms of the brain supported the detection of color change, an unexpected improbable “deviant” distractor (e.g., green) was employed. Note that this deviant differed in color from the preceding standard. Both the standard distractor and the deviant distractor differed in color from the remaining objects, which were blue. Visual Event-Related Potentials (ERPs) were derived from high-density EEG recordings to characterize the time-course of scalp-measured indications of the brain's responses to visual scenes containing deviant-colored distractors. A previously unexplored objective of the present investigation was thus to use these methods to build a new bridge between the discourses upon visual search and vMMN.

If as evidence from attentional blink, inattention blindness, and change blindness paradigms have suggested, vision has no memory (Wolfe, 2000) of functional consequence, upon an individual level, then color deviance would not affect behavior in our serial distraction task. To examine whether vision has a sensory memory for color, the interval between presentations of visual arrays of objects was at least 600 ms. That is, if a sensory memory for the color of the preceding distractor existed, that memory must endure that interval for a color change to influence: (a) performance, and (b) the generation of brain processes.

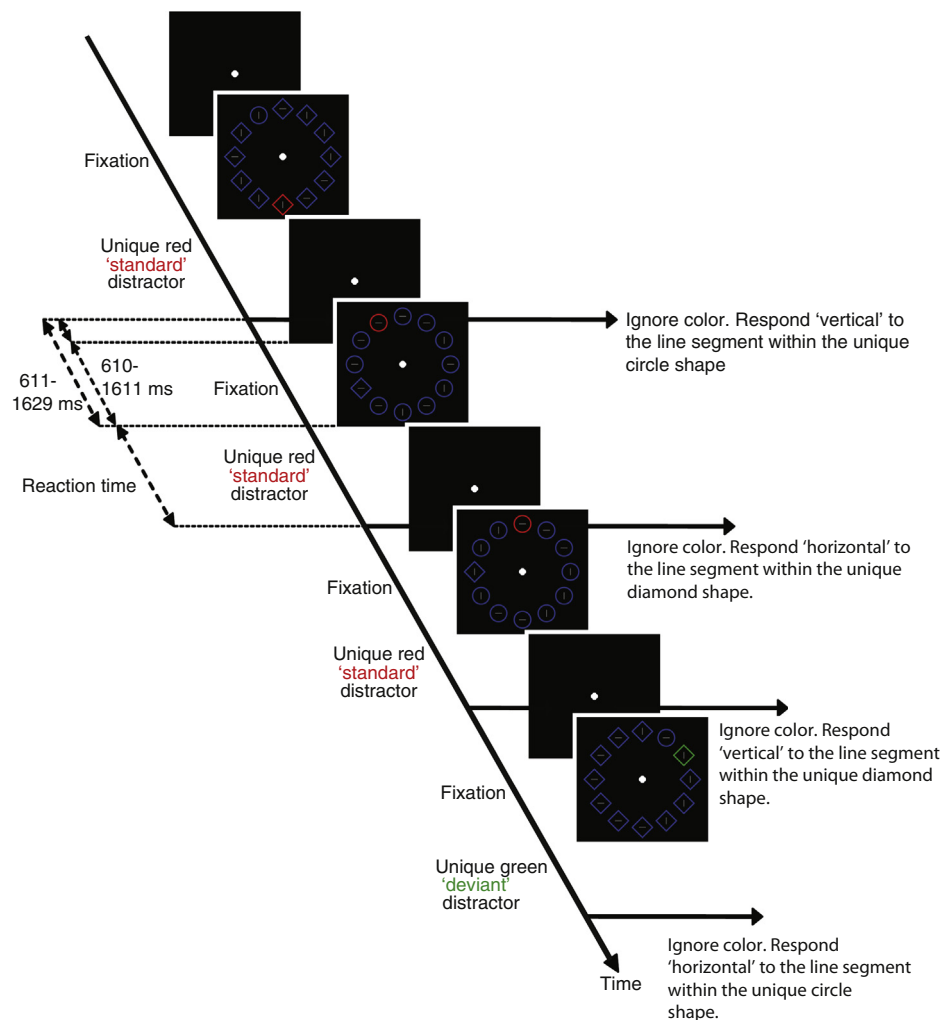
## 2. Method

### 2.1. Participants

Fourteen volunteers participated in this experiment in exchange for 4 cinema tickets. All participants gave their informed written consent voluntarily, with departmental ethical approval of the investigation, in accordance with the Declaration of Helsinki. Data from 2 participants had to be excluded from the analysis, because eye movements and blinking led to a loss of 65% of their data due to artifact rejection. The mean age of the remaining 12 participants (3 males) was  $23.3 \pm 2.5$  years. All were right-handed and reported normal ( $n = 4$ ) or corrected-to-normal ( $n = 8$ ) vision.

### 2.2. Materials

Stimuli were presented on an LCD monitor (G2G 2 msec) at a 0° screen orientation with black as the background color. Each visual scene consisted of a stimulus array of 12 objects with a color frame (blue, green, or red), shaped either as a circle ( $3.43^\circ$ ) or a diamond ( $4.23^\circ$ ), with a horizontal or vertical line segment ( $1.38^\circ$ ) at the center. As illustrated in Fig. 1, the objects were placed circularly (radius of  $9.3^\circ$ ) around a centrally presented fixation cross ( $1.38^\circ$ ). The luminance of the frame colors was adjusted to  $35 \text{ cd/m}^2$ , using a luminance meter (Konica Minolta, LS-110, with closing-up lens, correction factor



**Fig. 1.** Schematic of four successive trials. Screenshots are to scale. Participants searched for a uniquely shaped target amongst the objects arranged in a circular manner around a fixation cross. Each object consisted of a colored frame with a line segment at its center. The shape of the frame indicated the target stimulus. The uniformly shaped non-targets all had the same color, except for one that had a different color. Such a uniquely colored object is known to distract visual search (Hickey et al., 2006) leading to a slowing of reaction times. In the design of the present investigation, the distractor color remained the same in 90% of the trials (standard trials) but was exchanged with another distractor color upon the other 10% (deviant trials). Hence, it was possible to differentiate the effect of a deviant distractor from that of a standard distractor.

1.050, distance 20.4 cm, and pixel-based resolution). The distance between the participant's eye and the monitor was kept constant at 50 cm.

### 2.3. EEG equipment, recording and data treatment

EEG recordings were taken from a 64-channel electrode cap at a sampling rate of 512 Hz within a recording bandpass of DC to a half-power ( $-3$  dB) of 134 Hz using the Biosemi ActiveTwo data acquisition system, employing a third order sinc filter during decimation. Each scalp electrode within this system is described as "active" by virtue of containing a tiny amplifier that elevates the electrical signal before analog-to-digital conversion. The Biosemi ActiveTwo has replaced the classical "ground" electrode with two electrodes. The Common Mode Sense (CMS) active electrode detected the effects upon the participant of current return from the Analog-to-Digital converter via the Driven Right Leg (DRL) electrode containing no amplifier. A CMS/DRL feedback loop equated the potential of the participant to the reference voltage of the Analog-to-Digital Conversion apparatus. EEG was acquired at a scalp electrode in "raw" mode, that is, relative to this reference voltage. Thus the "reference" in "raw" recordings was the CMS electrode, which was situated at a right-posterior site between POz and PO4. However, this "raw" mode of recording did not permit the full Common Mode

Rejection (Fisch and Spehlmann, 1999) of artifactual signals that were present at both the active EEG electrode and the CMS (Campbell et al., 2012). Horizontal eye movements were monitored with a bipolar set-up of two electrodes attached laterally to the outer canthi of each eye. Vertical eye movements were monitored by bipolar channels using the pre-frontal electrodes (Fp1, Fp2, Fpz) on the cap amplified against an additional electrode upon the tip-of-the-nose. Additional electrodes were also attached to the left and right mastoids.

Measurements were digitally filtered offline using a 1536-point low-pass and then a 51-point high-pass Finite Impulse Response, with half-power cutoffs ( $-3$  dB) at 30 and 1 Hz respectively, with a low-pass transition width of 0.2 Hz and high-pass transition width of 5 Hz respectively. Filtered EEG was then re-referenced offline to the average of linked mastoids, so as to optimize Common Mode Rejection, and accordingly increase the signal-to-noise ratio of the measurements. ERPs to visual scenes were averaged from 600 ms epochs of EEG data inclusive of a 100 ms pre-visual scene baseline. ERPs time-locked to the onset of visual scenes were averaged from these epochs separately for those containing standards and deviants. Epochs were excluded from the analysis if they: (a) contained potentials in excess of  $\pm 75$   $\mu$ V (the individual rejection mean was 9.41%, ranging from 1.6% to 23.4%), (b) were from the first 2 blocks, (c) were from the first three trials within each block, (d) were from trials including a standard-

colored distractor that immediately followed a deviant distractor trial, (e) were from trials with incorrect responses (2% of trials), and (f) were from trials with outlier reaction times 3 SD longer than the individual mean reaction time (0.2% of trials). Overall, 20.0% of trials were excluded. Exclusion criteria for reaction time data were identical to those for EEG data.

#### 2.4. Procedure

During the experiment, participants were seated in an acoustically and electromagnetically shielded room of the Cognitive Brain Research Unit at the University of Helsinki. Written informed consent was obtained from all volunteers. Written instructions emphasized both speed and accuracy, while keeping blinking and eye movements to a minimum. Each trial started with the presentation of a fixation cross at the center of the LCD screen. After a variable interval, jittered randomly with a uniform distribution between 610 and 1611 ms, the 12 objects appeared surrounding the fixation cross. Participants were instructed to fixate upon the cross while searching for the unique target shape and ignoring the unique distractor color. Once the target was identified, participants responded to the orientation of the line segment in the center of the target by pressing one of two keys (left key: horizontal, right key: vertical) using the index and the middle fingers of the dominant right hand. The next trial was initiated by the response after a technical delay of 1 to 18 ms as determined by Presentation (Neurobehavioral Systems, Albany, California, USA). This short delay meant that the interval between visual scenes ranged from 611 to 1629 ms. The experiment consisted of 40 blocks with 80 trials each, resulting in 3200 trials per volunteer. Each block was initiated by the participants, who were free to take breaks between blocks, and the rate of the presentation of trials was also effectively self-paced by the speed of the participant's responses. Feedback regarding accuracy was given after each block upon the LCD monitor.

The standard color of the non-targets remained blue throughout, whereas the standard and deviant distractor colors varied blockwise between red and green, i.e., if red was the standard distractor color then green was the color of the deviant and vice-versa. The color of the "standard" distractor alternated every two blocks between red and green. The deviant probability during each such pair of blocks was 0.1, resulting in 320 trials per subject in the deviant condition. On the standard and deviant conditions separately, one quarter of trials included a lateral target with a distractor upon the vertical meridian; one quarter of trials encompassed a target on the vertical meridian with a lateral distractor; one quarter of trials comprised a lateral target with an ipsilateral distractor; one quarter contained a lateral target with a contralateral distractor. Serial order of deviant colors was counterbalanced across participants. Within each block the assignment of target and non-target shape varied randomly trial-by-trial. The target never matched the distractor.

The mean duration of a trial from the onset of the fixation cross to the response was  $2.329 \pm 0.267$  s (mean  $\pm$  s.d.), such that the mean net measurement time was 1 h 52  $\pm$  13 min. The mean interblock interval was  $87.756 \pm 16.960$  s, with a total of interblock intervals averaging  $51 \pm 9$  min, inclusive of feedback sessions and time spent reading the instructions. Participant took 2 to 4 breaks lasting in total for  $58 \pm 14$  min. The whole experiment including breaks and interblock intervals lasted for 3 h 42 min  $\pm$  26 min, with approximately 45 additional min for informed consent, capping-up, capping-off and debriefing.

#### 2.5. Data reduction and statistical analyses

For each individual, reaction times (RTs) for trials containing standards and deviants were averaged separately and compared with a pair-wise t-test. The effect of distraction on RT was computed for each

individual by subtracting the mean RT for standard trials from the mean RT for deviant trials.

Pair-wise t-tests were used to examine the significance of the difference between standard and deviant ERPs, at each time-point, for each electrode (Fig. 2). Addressing the multiple comparison problem, clusters of significant differences were defined, consisting of at least 3 neighboring electrodes and 5 consecutive time points. With  $\alpha$  set to 0.05, the probability of a false alarm was  $4 * 10^{-11}$ . The application of such priors via these criteria precluded the erroneous misinterpretation of implausibly unclustered false alarm significant differences. The mean amplitude at the latency of significant clusters was calculated for channels with significant differences. For each electrode in a significant negativity cluster, a form of signal-to-noise ratio was calculated. This ratio was the maximal negativity of the deviant-standard difference wave in the post-stimulus time range, when the cluster was significant, divided by the maximal value of the deviant-standard difference wave in the pre-stimulus time range. The electrode selected for each negativity cluster was the one that demonstrated the maximal such ratio. Isopotential maps of the deviant-standard difference, integrated across the time range of significant negativity clusters, were plotted.

For each channel of a significant cluster, and for each cluster, the deviant minus standard amplitude differences were computed for cluster channels in each cluster's latency range. For each channel of a significant cluster, and for each cluster, Pearson product-moment coefficients were derived to test if slowing in RTs correlated significantly with the amplitude of this effect of deviance upon ERP amplitude. For significant correlations, the significance of the linear regression was assessed with an F-test and a t-test used to assay if the slope differed significantly from zero. Critical  $\alpha$  was set to 0.05 and testing was two-tailed throughout.

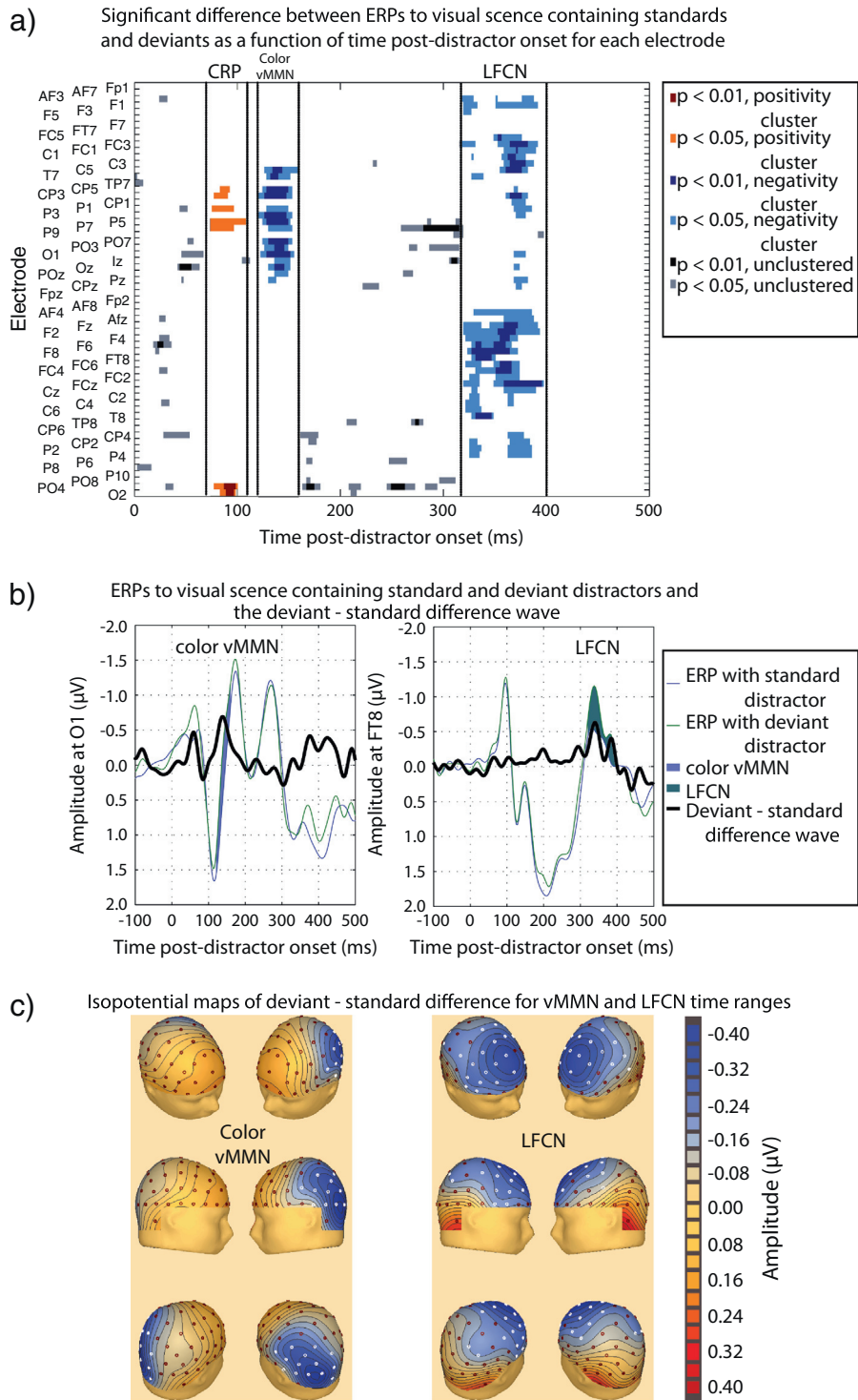
### 3. Results

#### 3.1. Color deviance causes a behavioral distraction effect

Performance upon the task demonstrated that accuracies approached ceiling ( $97.92 \pm 0.28\%$ ; mean  $\pm$  SEM) and drove the effects of distraction into the speed domain. Mean RTs for visual search were slowed by the presence of a deviant distractor ( $1178 \pm 85$  ms) relative to the presence of a standard distractor ( $1155 \pm 85$  ms). This color deviance-related slowing was revealed by inferential statistical analysis to be significant via a paired t-test,  $t(11) = 2.5$ ,  $p < 0.05$ ,  $\eta^2 = 0.354$ . To anticipate part of the results shown in Fig. 3, 10 out of 12 participants demonstrated a distraction effect, with the difference between mean RTs for standard minus deviant distractors being negative (pointing upwards in Fig. 3).

#### 3.2. Color deviance elicits two broadly distributed negativities

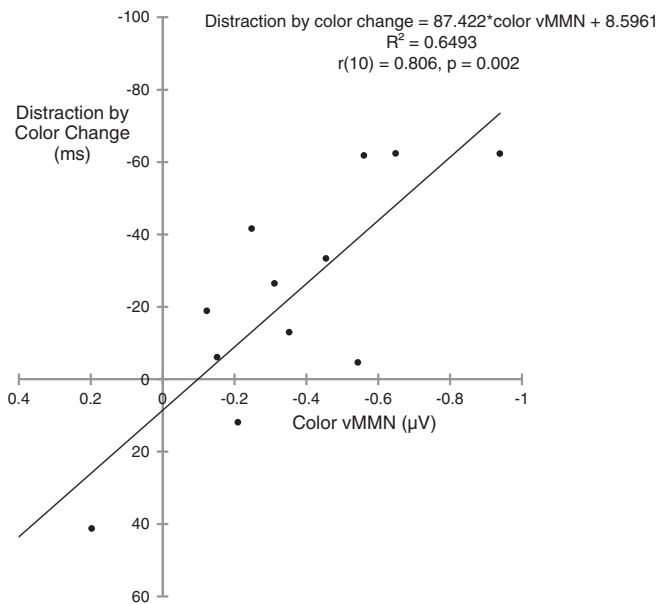
There were clusters of electrodes that exhibited significant differences due to color deviance. Moreover, different clusters of electrodes exhibited significant differences at different points in time, each of which is considered separately. Depicted in Fig. 2a is a data reduction of the time course of significant differences between responses to visual scenes containing standard and deviant distractors. As illustrated, there were well-defined spatiotemporal clusters of activation responsive to the color change of the deviant distractor. While the negativities were of key theoretical interest, all significant clusters are discussed in the order in which they occurred. The first cluster, upon which no theoretical weight is placed, was a positivity. This early Change-Related Positivity or CRP (Kimura et al., 2006a,b; Busch et al., 2010; Stefanics et al., 2011; for a kindred phenomenon see Berti, 2011) was apparent at left centro-parietal sites at the latency of 70–110 ms within the time-range of the P1 wave. However, the small size of the effect would suggest that the paradigm utilized in the present investigation was not optimal for CRP elicitation. The second and third clusters demonstrated two reliably measured negativities: (1) the early color



**Fig. 2.** (a) Overview of significant differences between ERPs after presentation of a deviant or standard distractor. The y-axis represents the electrodes and the x-axis time. Periods of significant differences are marked by light ( $p < 0.05$ ) or dark ( $p < 0.01$ ) shading. Three clusters of interest are outlined as CRP, color vMMN, and LFCN. Selected electrodes where ERPs and difference waves are plotted in Fig. 2b are highlighted upon the y-axis (b) ERPs and difference waves with the highest signal-to-noise ratio for color vMMN and LFCN (O1 and FT8, respectively) (c) Isopotential maps for spatiotemporal clusters of significance from the analysis depicted in Fig. 2a, respectively for color vMMN (left panel) and LFCN (right panel). Electrodes highlighted in white were those that exhibited significant differences between standard and deviant distractors within the time range depicted. The polarity of the effect is color-coded upon the scalp; red showing more positivity for the deviant than the standard condition and blue showing more negativity for the deviant than the standard condition. The clusters exhibit different distributions. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

vMMN at the latency of 120–160 ms, apparent at left posterior sites, and (2) a Late Fronto-Central Negativity (LFCN), at a latency of 320–400 ms, apparent at fronto-central electrodes and some posterior sites. ERPs to standards and deviants and the corresponding difference sites for

both negativities are illustrated in Fig. 2b, at selected electrodes; shaded areas between ERPs denoting time periods when the cluster was active. As depicted in Fig. 2b, the grand-averaged peak amplitude of color vMMN at O1 was at 141 ms, when the sample-based t-value of the



**Fig. 3.** A scatterplot of the behavioral distraction effect as a function of color vMMN amplitude collapsed across significant electrodes. The stronger the slowing of responses due to the distraction, the stronger was the ERP difference due to color change.

difference wave was maximal,  $t(11) = 8.33$ ,  $p < 0.001$ ,  $\eta^2 = 0.86$ , while that of LFCN at FT8 was at 339 ms,  $t(11) = 4.01$ ,  $p < 0.01$ ,  $\eta^2 = 0.59$ . The distinct topography of the difference waves during the time period of these negativities is illustrated by isopotential maps for each cluster in Fig. 2c.

### 3.3. Color vMMN predicts the extent of behavioral distraction

While significant clusters of activity were elicited by color change of the distractor, it remained to be determined whether neurophysiological activity could be related to the behavioral effect of the distraction. In fact, a correlational analysis of this distraction effect with the deviant-standard difference for each cluster revealed that the color vMMN (120–160 ms) showed a marked relation: behavioral slowing increased with the amplitude of the color vMMN, as was confirmed by significant correlations,  $r(10) = 0.81$ ,  $p = 0.002$ . Fig. 3 depicts this significant increase in distraction effect as a function of color vMMN amplitude averaged across the whole cluster. The linear regression predicting distraction from the color vMMN was also significant,  $F(1, 10) = 16.52$ ,  $p < 0.002$ , such that the slope differed significantly from zero,  $t(10) = 4.303$ ,  $p = 0.002$ . By contrast, the amplitudes of CRP and LFCN clusters did not correlate with the distraction effect,  $r(10) = -0.09$ ,  $p = 0.79$  and  $r(10) = 0.12$ ,  $p = 0.67$  respectively for CRP and LFCN. Accordingly, the amplitude of color vMMN indexed the extent of the distraction effect. As already pointed out, Fig. 3 depicts that 10 out of 12 participants demonstrated a distraction effect, in addition the Figure shows that 11 out of 12 volunteers demonstrated a color vMMN. Note that this ERP component, at a latency of around 120–160 ms, predicted a manual response that emerged several hundred milliseconds later.

### 3.4. Color vMMN: distribution, duration of sensory memory trace, and visual hemifield

The effect of distraction on ERP and behavioral response times indicated that the sensory memory representation for the preceding stimuli was still vivid when the distractor occurred. The ISI between search arrays varied from 610 to 1629 ms. An auxiliary question was thus whether this ERP index of the sensory memory trace for distractor

color attenuated as the ISI increases. To address this question, epochs time-locked to the visual search array were binned upon the basis of the duration of the preceding fixation interval (short: 610 to 1110 ms vs. long: 1110 to 1629 ms).

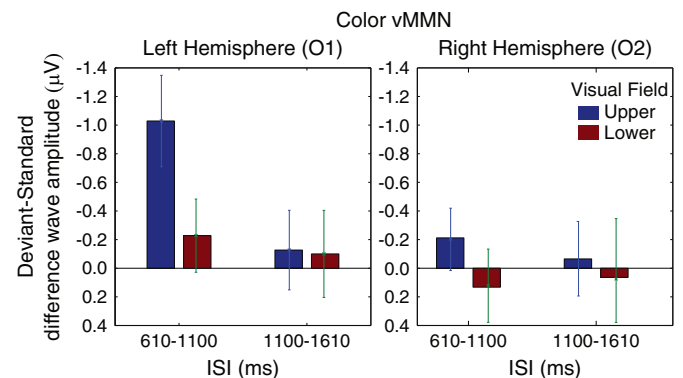
A further auxiliary question concerned the hemifield of presentation. Previous investigations of vMMN have addressed the influence of the visual hemifield in which the visual deviance is presented: some investigations have reported a vMMN that is confined to deviance presented in the lower hemifield and not the upper hemifield (Czigler et al., 2004; Müller et al., 2012), while other investigations revealed the converse (Berti, 2009). Accordingly, epochs binned upon the basis of ISI were further partitioned into subgroups according to whether deviants were presented in the upper or lower hemifield.

Of further interest was the distribution of the color vMMN that was examined by comparison of its amplitude in a window of integration 120–160 ms after the search array at the left and right occipital electrodes. These prior observations and questions of theoretical interest motivated the ensuing analyses of this section.

As depicted in Fig. 4, the difference of ERP amplitudes integrated across the color vMMN temporal window (120–160 ms), demonstrated a strong color vMMN with a short ISI, in a manner that was only apparent over the left hemisphere (O1) and upper hemifield. Such a strong color vMMN was neither present over the right hemisphere (O2) nor even at O1 with a long ISI. This pattern of mean differences suggested that the color vMMN depicted in Fig. 2 may have been caused by a left-distributed posterior response to color deviance in the upper hemifield with short ISIs. To foreshadow the results of the analysis, this observation was statistically supported.

A 4-way repeated-measures Analysis of Variance (ANOVA) with a 2 (Color deviance: standard, deviant)  $\times$  2 (ISI: short vs. long)  $\times$  2 (Visual Hemifield: upper, lower)  $\times$  2 (Hemisphere: left at O1, right at O2) performed on the ERP amplitude data from this window of integration confirmed these observations. The main effect of color deviance was marginal,  $F(1, 11) = 4.33$ ,  $p = 0.061$ ,  $\eta^2 = 0.283$ , although a significant Hemisphere  $\times$  Color Deviance interaction,  $F(1, 11) = 14.66$ ,  $p = 0.003$ ,  $\eta^2 = 0.571$ , corroborated cluster analysis results (Fig. 2a) of a left-distributed color vMMN. The significant ISI  $\times$  Hemisphere  $\times$  Color Deviance interaction,  $F(1, 11) = 6.10$ ,  $p = 0.031$ ,  $\eta^2 = 0.357$ , revealed that the left-lateralized color vMMN varied significantly as a function of hemifield and interstimulus interval. The other significant ISI  $\times$  Hemisphere  $\times$  Color Deviance interaction,  $F(1, 11) = 6.10$ ,  $p = 0.031$ ,  $\eta^2 = 0.357$ , suggested that brain response in the 120–160 ms time range is influenced by ISI, Hemisphere and Color Deviance, irrespective of Color Deviance, although these results should be regarded with caution due to significance of higher-order interactions. No other effects were significant,  $F_s < 1$ ,  $p_s > 0.107$ .

The predicted effect of Color Deviance was investigated separately for each ISI, separately for distractors in each Visual Hemifield,



**Fig. 4.** Mean amplitude of color vMMN as a function of ISI (x-axis), visual hemifield (upper – black, lower – white), and hemisphere (left vs right panels).

separately for each Hemisphere via 8 pairwise critical planned comparisons using Holm's adaptation of the Bonferroni test. These analysis revealed that the effect of color deviance was only significant for the "short" ISI at the "upper" level of visual hemifield for the "left at O1" level of hemisphere,  $t(11) = 3.87$ ,  $t_{\alpha/8} = t_{0.00625} = 3.30$ , all other  $t_s < 1$ . That is, as depicted in Fig. 4, the color vMMN was only significant over the left hemisphere when the color deviant was presented in the upper hemifield and with a short ISI ( $< 1100$  ms), as exhibited an effect size of 1.58 standard deviations.

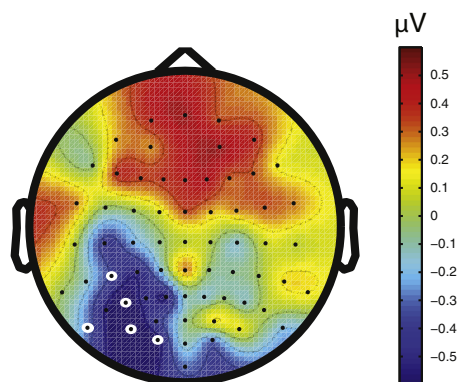
### 3.5. Color vMMN: ruling out the lateralized component hypothesis

A hypothesis considered was that a potential lateralization of the component of interest was due to 10 out of 12 of the color distractors being lateralized, even though distractors were equally often presented in the left visual field and right visual field. A corollary of this possibility was that there could have been an incidental rejection of more artifact epochs when color deviant distractor stimuli were presented in the left side of the search array than in the right side of the search array. To rule out this possibility, a subset of standard and deviant arrays – those scenes containing only vertical distractors – were included in an additional analysis. Vertical distractors were presented in a non-lateralized manner on the vertical meridian at a position above or below the fixation cross, i.e., a 6 or 12 o'clock position. Isopotential maps for the component of interest were compared visually and confirmed using paired Student's t-tests: the significant color vMMN was present only at sites over the left hemisphere (O1, PO7, P9, P5, CP5,  $p > 0.05$ , Fig. 5), as out-ruled this lateralized component hypothesis that the left distribution of color vMMN was a byproduct of the lateralization of distractors.

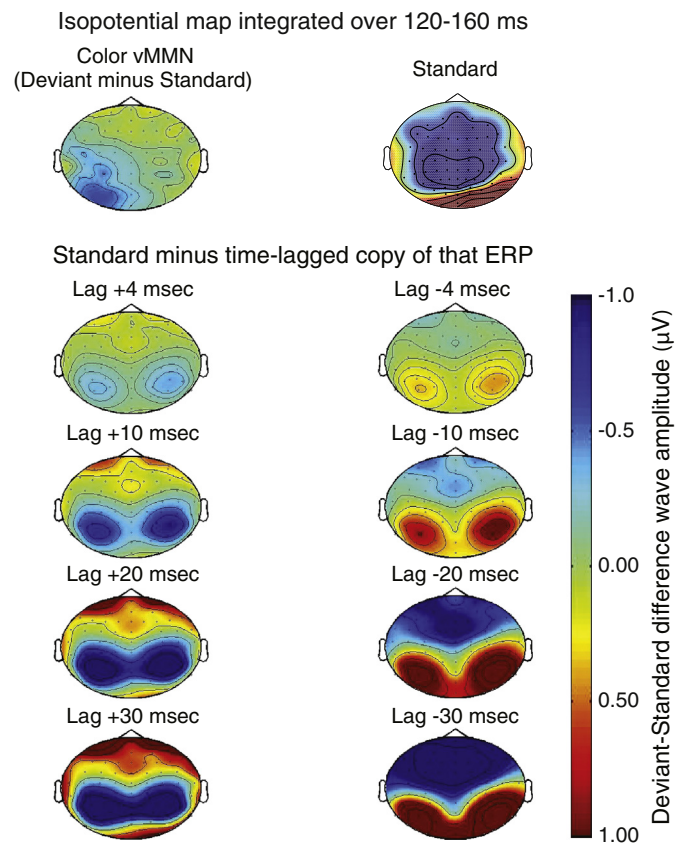
### 3.6. Color vMMN: ruling out N1 modulation and the latency shift hypotheses

The infrequent deviant stimuli might have elicited a higher amplitude of N1, compared to frequent standard stimuli, since the state of refractoriness of afferent neuronal populations that specifically respond to the feature values of deviant stimuli is lower than that of afferent neuronal populations that respond to the feature value of standard stimuli (see e.g., Kimura, 2012). To rule out this N1 modulation hypothesis a comparison of the color vMMN topography with those of standard ERP from the color vMMN time range (120–160 ms) was necessary. As depicted in the first row of Fig. 6 these topographies exhibited marked differences.

#### Color vMMN for vertical distractors



**Fig. 5.** Isopotential maps of color vMMN only for vertical distractors. The difference wave was derived from subtraction of measured ERPs to standard distractor from the ERP to those containing a deviant distractor and integrated across a 120–160 ms temporal window. Electrodes highlighted in white exhibited significant differences between standard and deviant ( $p < 0.05$ ). Note the left-distribution.



**Fig. 6.** Isopotential maps of the difference wave derived from subtraction of measured ERPs to visual scenes containing standard distractors from the ERP to those containing a deviant distractor, with a window of integration 120–160 ms, isopotential maps of ERP for standard distractors, again integrated over 120–160 ms, and isopotential maps of the artificial difference wave derived from the subtraction of the measured ERP to visual scenes containing a standard distractor from an artificially time-lagged copy of that ERP also with a window of integration 120–160 ms. Please note that the topography of color vMMN over the left hemisphere is not exhibited in the distribution of the difference waves produced by these artificial latency shifts.

Additional analyses tested if the color vMMN component was, rather, a latency shift of one of the neighboring ERP waves, namely the P1 and N1 waves. This "latency-shift hypothesis" assumed that color vMMN might be a byproduct of a P1 or an N1 latency shift. Here, O1 was the electrode of interest, as this site was where the color vMMN exhibited the optimal signal-to-noise ratio. In all but two of the included volunteers, the P1 peak was evident as a positive ERP deflection 90–140 ms post-stimulus onset, followed by a distinct N1 wave in the time range 127–194 ms, as was exhibited in all but one of the volunteers. Subtle numerical differences in the latencies of P1 peaks (standard:  $115.5 \pm 3.1$  ms, mean  $\pm$  SEM; deviant:  $115.8 \pm 3.4$  ms) and N1 peaks (standard:  $161.4 \pm 6.4$  ms; deviant:  $157.1 \pm 5.5$  ms) at the O1-electrode were found not to be reliable via paired two-tailed Student's t-tests,  $p > 0.05$ . It was also worth considering that the grand-averaged P1 (115 ms) and N1 (159 ms) peak latencies were either outside of, or bordering upon the temporal interval of significant amplitude differences, as was revealed by paired t-tests in the color vMMN time range (120–160 ms, see Fig. 2).

As peak latencies did not necessarily reflect all aspects of P1 and N1 generation, a further test of the latency shift hypothesis was necessary. We assume that the observed peaks in the ERP correspond to the real peaks of the underlying ERP component, which is not always the case (Luck, 2005a,b). Here, the idea was that if color vMMN reflected a latency shift of the N1 or P1 wave, then the artificial subtraction wave representing the difference between the original standard ERP and the standard ERP time-lagged by the hypothetical latency shift would



have the scalp distribution of the color vMMN within the component's time range. Thus, an artificially time-lagged version of the ERP waveform to the visual scenes containing a standard distractor (lags:  $-30$ ,  $-20$ ,  $-10$ ,  $-4$ ,  $4$ ,  $10$ ,  $20$ ,  $30$  ms) was subtracted from the originally measured ERP waveform in response to that standard distractor. The isopotential maps of this difference wave were plotted. The results of this approach are illustrated in Fig. 6, where the scalp distribution maps for the color vMMN time window, 120–160 ms, are presented. If the latency-shift hypothesis was valid, and a P1 or N1 latency shift caused the color vMMN effect, the scalp topography would have a pronounced distribution over the left hemisphere. As is depicted in Fig. 6, such a hypothetical dominance of the distribution over the left hemisphere was unapparent. The artificial latency shift of the standard ERPs produced a rather symmetric distribution with even a subtle tendency towards a higher voltage over the right, rather than the left hemisphere, as can be seen in Fig. 6. As has already been mentioned, under the assumption that the time-course of the components mirrors the timing of the underlying ERP exactly, these auxiliary analyses ruled out the latency shift hypothesis that color vMMN simply represented a latency shift between responses to standard and deviant stimuli. Therefore these analyses tentatively support the hypothesis that the elicited color vMMN was a distinct component and not a byproduct of P1 or N1 latency shifts.

#### 4. Discussion

The results from a visual search distraction paradigm showed that (1) color deviance of a distractor is coded by the brain as elicits three scalp-measured ERP components: CRP, color vMMN, and LFCN, (2) processing of color deviance that is unrelated to the task slows the performance of that task, and (3) one of the ERP components that is sensitive to deviance, color vMMN, correlates with that behavioral slowing. Therefore, turning to the objectives mentioned in the Introduction section, this investigation demonstrated an effect of task-unrelated peripheral color deviance within a visual search distraction paradigm. A component contributing to this effect, the color vMMN, was shown to be generated by the brain during visual change detection, in a manner that is associated with behavioral consequences. This association thus also met the objective of offering relatively strong support for the functional relevance of the color vMMN. A further objective was building a new bridge between the discourses upon visual search and vMMN. According to this logic, firstly, the nature of the mental processes revealed by the behavioral data is considered, after which follows a discussion of the associated ERP components of the response to color deviance and their candidate generators.

The findings of the present investigation have implications for the role of sensory memory processes during visual search and, at first glance, might be considered controversial given the broadly demonstrated failure of visual memory in paradigms such as change detection and change blindness. Sensory memory is required to process deviance detecting a change in color between one visual display and the subsequent display. Given the interval of 611 to 1629 ms between visual displays, sensory memory for color must have persisted for at least 600 ms to cause ERP and behavioral effects. Several other studies are in line with our research, demonstrating ERP evidence of to-be-ignored changes with ISIs of up to more than 1000 ms, consistent with the notion of a durable sensory memory trace. Those studies differ from ours in several aspects. First, the visual feature of interest differed, e.g., Berti and Schröger (2001) investigated orientation or location, Kimura et al. (2008a,b) luminance or size. Second, ERP results showed sometimes a rather mixed pattern, e.g., Kimura et al. (2008a,b) demonstrating distance components coding increments and decrements in size or luminance: increments elicited a negativity, perhaps kindred to an early vMMN, termed the CRN (120–140 ms), while a size or luminance decrement elicited a CRP (140–160 ms). CRP was also elicited by luminance but not size increments. Though neither CRN nor CRP was elicited by all

changes in size or luminance, a sophisticated functional interpretation could tentatively include the generation of these components during the processing of facets of change. Third, whereas some investigations showed that to-be-ignored changes were reflected both within ERP and behavioral distraction (Berti and Schröger, 2001; Kimura et al., 2008a,b), others reported ERP effects only (Astikainen et al., 2008; Stefanics et al., 2011). Fourth and importantly, the distraction of task performance in previous studies (Kimura et al., 2008a,b; Berti and Schröger, 2001) was accompanied by a posterior N200/N2 at a latency of 240–260 ms, and a later component, P3a, interpretable as indexing a form of attentional capture. A novel departure of the current investigation's findings from the data of these previous investigations was that the form of color vMMN shown here was associated with a distraction effect that occurred in the absence of a clear P3a, indicating that attentional capture was not reliably involved in our paradigm.

However, it needs to be considered that attention might have been captured involuntarily in the current investigation. In the paradigm of visual search a color singleton has been demonstrated to capture attention automatically (e.g., Theeuwes, 1994; Theeuwes and Burger, 1998) arguably by virtue of a uniquely colored object causing a more compelling attentionally capturing visual pop-out than a uniquely shaped stimulus. However, the present paradigm and results differed from those of classical investigations of attentional capture again in a number of ways, to which the discussion now turns.

The first difference, a paradigm difference, is that a search array of 12 objects was employed, whereas in classical procedures the number of objects is 7 or less (e.g., Theeuwes, 1994; Theeuwes and Burger, 1998). The large number of objects meant that neighboring proximal parafoveal objects that are similar in shape promoted crowding (Bouma, 1970; Felisberti et al., 2005; Obeidat et al., 2013, submitted for publication) rather than pop-out, a crowding not only hindering the identification of the target shape singleton, but also hampering the processing of the identically shaped color singleton during any attentional capture. This crowding argument concerning this paradigm difference is supported by the results: rather long mean RTs exceeding more than 1100 ms in the current data, whereas target pop-out leads to RTs of typically far less than a second (Theeuwes, 1994), and even with set sizes of 10 pop-out, results in shorter RTs when keyboard is used as a response tool (e.g., Hickey et al., 2006, Exp.1; for an alternative perspective, see McDonald et al., 2013).

Turning to the second paradigm difference from such investigations of attentional capture, the effect of distractor color deviance, here, was based on comparison of deviant and standard stimuli. But every single trial, including standard stimuli, contained a color singleton. Allowing for the tenuous possibility that such a to-be-ignored color singleton distractor could cause pop-out, then such a hypothetical pop-out would occur on each trial. When calculating the deviant effect, any such effect of color pop-out on reaction times and ERPs would thus have been subtracted out. Accordingly, it is difficult to imagine how the effects of color deviance could have been caused by pop-out.

The third difference from classical investigations of attentional capture – now concerning the experimental results – is that the color vMMN effect shown here was dependent on the preceding ISI. This finding militated further against a pop-out interpretation, given pop-out has been shown to be relatively stable with stimulus onset asynchronies longer than 200 ms (Olds et al., 2000). In sum, the present paradigm and results differed from those of classical investigations of attentional capture, indicating that the demonstrated deviance effect did not index the construct of attentional capture, but rather indexed the pre-attentive accumulation of a sensory memory trace.

Further support for the pre-attentive nature of the effect of deviance shown here can be gleaned from the visual ERPs – neither of two components were elicited: the Visual Awareness Negativity (VAN), which would have been expected to peak at about 400 ms, as would have indexed awareness (Ojanen et al., 2003); nor P3a, as elsewhere has been shown to be apparent with visual distraction (Kimura et al.,

2008a,b; Berti and Schröger, 2001) and would have been interpreted as indexing a form of attentional capture.

Taking all these arguments together, pre-attentive rather than attentional processes contributed to the effects of deviance shown here; cautiously considered arguments which were consistent with our own perceptual impressions while performing the task. That is, whereas the location of the color distractor was just noticeable, the color change of that distractor went completely unnoticed.

For these reasons, the processing of deviance that slows reaction times, just like the encoding of the standard stimulation, is thought to have been pre-attentive. The interpretation offered, here, is that the mental processes that encode the color of the standard stimulation into sensory memory and those mental processes that register the violation of the prediction of that sensory memory by distracting color deviants are pre-attentive or “automatic” rather than active processes; pre-attentive processes that take place below the subjective threshold of conscious awareness (Berry and Dienes, 1993). That is, change in color was unrelated to the task, in a manner that would discourage the deliberative encoding of color by a conscious strategy or “active process”, such as articulatory rehearsal (Baddeley, 1986), or recoding into the visuo-spatial sketchpad via an inner scribe (Logie, 1995). However, color information may have had obligatory access to some passively decaying storage system (e.g., the visual cache as in Quinn and McConnell, 1996, 1999; McConnell and Quinn, 2000; Dean et al., 2008).

Most changes have been demonstrated to remain undetected in the change blindness paradigm (Simons and Levin, 1997). In contrast to the current investigation, traditional change detection paradigms have relied upon the conscious report of changes. However, evidence for the automatic processing of visual changes has previously been reported. Even in the absence of change detection, the guessing probability to identify the changed target has been shown to be higher than chance (Fernandez-Duque and Thornton, 2000). Evidence from the contextual cuing paradigm has shown that repeated presentation of the same distractor configuration improves visual search, even though participants performed at chance on an explicit memory test trying to discriminate old and new distractor configurations (Chun and Jiang, 1998; Chun, 2000). A reconciliatory assumption offered here is that pre-attentive memory processes indexed by the speed of visual search that support durable sensory memory representations, differ from the processes tapped in change blindness paradigms. Accordingly, the function postulated for the pre-attentive formation of the sensory memory for the color standard distractor in the current investigation's task has been that of predicting the color of the next distractor, an expectancy that supports the suppression of the distractor stimulus. In turn, this automatic expectancy is thought to promote a faster visual search for the target shape. It is argued that color deviance of the distractor violates this prediction.

Turning now from the nature of the mental processes involved to the componentry of the ERP differences in response to deviance, a novel aspect of the present research was the finding of the color vMMN component in the visual search task. The new form of color vMMN, as such, demonstrated was distributed primarily over the left rather than the right hemisphere. That color vMMN, shown here, was the only ERP reflection of deviance processing that reliably indexed distraction. Auxiliary analyses tentatively indicated the color vMMN to be neither an amplitude augment nor latency shift of either the P1 or N1 wave (Fig. 6), although with the current study design it is not possible to completely rule out the potential contribution to our vMMN response of some sub-components typically active during the P1 and N1 deflections modulated by factors such as refractoriness (Czigler et al., 2002).

In any case, the color vMMN was elicited in ERPs collapsed across distractor locations, so it would be difficult to interpret the color vMMN, shown here, as one of the lateralized components thought to be implicated in distraction and visual search such as the N2pc (Luck and Hillyard, 1994a,b; Hickey et al., 2006), PD (Hickey et al., 2009; Sawaki and Luck, 2011), or the Ptc (Hilimire et al., 2009, 2010, 2011).

While not a lateralized component at first blush, it may have seemed conceivable that the left distribution of the negativity, seen here in the 120–160 ms time range, yet not in most investigations of the ERPs elicited by color deviance (Czigler, 2007; Kimura et al., 2006a), could in some way be related to the fact that distractors were presented laterally on 10 out of 12 of trials: the so-called lateralized component hypothesis mentioned in the results section, a hypothesis that went unsupported. That is, a significant left-distributed color vMMN was apparent even in trials containing only vertical distractors. It can thus be identified that the left distribution of color vMMN shown here was neither due to color vMMN being a lateralized component, nor the lateralization of the distractors, though eccentricity rather than lateralization from the central fixation point might have accounted for the discrepancy from the preceding investigations where stimuli were presented in central fixation. Indeed, it has been postulated by Berti (2009) that the visual periphery is more capable in providing automatic change detection. Such change detection could have recruited dominant generators within the left hemisphere that led to the left-distributed color vMMN evident in Fig. 5.

The color vMMN demonstrated here was also unlikely to be the positivity elicited by a change in the flicker paradigm when a change is searched for under conditions of change-blindness (Eimer and Mazza, 2005; Lyyra et al., 2010). Eimer and Mazza interpreted this positivity as a reduction in the late Contingent Negative Variation that occurs when two stimuli follow each other at short predictable intervals (Walter et al., 1964) and is thought to index the participant's preparedness to detect a change, a preparedness that was higher in blocks of trials with a change than in blocks of trials when there was no change. As in Lyyra et al.'s (2010) investigation, the occurrence of a deviant change occurred in an oddball manner unpredictably and was thus unlikely to elicit the CNV. Accordingly, it would have been difficult to interpret the color vMMN, shown here, as a modulation of the CNV. Color vMMN also occurred with a posterior distribution and polarity distinct from the more frontocentrally distributed positivity elicited by deviants under change blindness conditions in an oddball flicker paradigm (Lyyra et al., 2010). These compelling demonstrations of a positivity under conditions of change blindness (Eimer and Mazza, 2005; Lyyra et al., 2010) provided corroborative ERP evidence for the processing of visual change by the brain despite a lack of conscious awareness, albeit of a rather different sort from the color vMMN of the present investigation or the vMMN of Berti (2011).

A further question concerned the hemifield of presentation. It has been shown that, presumably for anatomical reasons, the vMMN differs with respect to the site of presentation. Berti (2009) demonstrated that for position deviants the vMMN is observable only for deviants presented in the upper half of visual space. Other investigations have reported a color vMMN that is confined to deviance presented in the lower rather than the upper hemifield (Czigler et al., 2004; Müller et al., 2012). The results of the present investigation have paralleled Berti's vMMN to position deviants more than the color vMMN of Czigler et al. (2004) and Müller et al. (2012).

Additionally, the color vMMN found here exhibited discerning features from the vMMN reported elsewhere that leave open the possibility that this color vMMN could ultimately be re-interpreted as a distinct component. First, color vMMN here exhibited a left parietal-occipital distribution (Fig. 2c, left panel), while a bilateral posterior distribution of vMMN has typically been reported (Czigler, 2007; Kimura et al., 2006a). Secondly, the color vMMN shown here correlated with behavioral distraction (Fig. 3), demonstrating a relation between behavior and electrophysiological coding, as is largely unprecedented for color vMMN (e.g., Stefanics et al., 2011; but see also Stefanics and Czigler, 2012). Visual distraction by task-unrelated change has been accompanied by ERP components kindred to vMMN (Berti and Schröger, 2001, 2004, 2006; Kimura et al., 2008a,b), but not with an association that was demonstrated by the correlation of vMMN with distraction shown here. The working hypothesis offered is thus that the color vMMN

shown here, in part, could index a subset of the generators of vMMN particularly responsive to the salient feature of color deviance in the current procedure, and could be more closely related to visual distraction than other generators of vMMN. The color vMMN shown here at 120–160 ms exhibited features that were not canonical of vMMN, and may instead be a new component that warrants further investigation.

Besides the color vMMN, the LFCN was observed, which is a distinct response to color deviance. The time range as well as the scalp distribution overlapped highly with the N2 deflection. Two subcomponents of N2 have been discussed in the literature (for a review, see [Folstein and Van Petten, 2008](#)): a posterior component related to a visual mismatch and an anterior component indexing cognitive control. In the present investigation, the central–parietal deviance-elicited negativity of the LFCN might be related to the posterior N2 component, while the strong frontal aspects corresponded to the anterior subcomponent. Alternatively, the frontally distributed aspects of the LFCN also resembled those of the auditory MMN. In the auditory domain, the activation of this frontal generator has been found to be later than that from the auditory cortex ([Doeller et al., 2003](#); [Opitz et al., 2002](#); [Rinne et al., 2000](#)). Frontal generators of the auditory MMN have been shown to be predominantly located in the right hemisphere ([Deouell et al., 1998](#); [Restuccia et al., 2005](#)), while the distribution of LFCN was also over the right hemisphere. Arguably, the initial processing of: (a) visual deviance, primarily in the occipital lobes, and (b) auditory deviance, primarily in the temporal lobes, both fed-forward to polymodal mechanisms ([Fuster, 1997](#)) situated within the right frontal lobe. [Rinne \(2001\)](#) interpreted right frontal generators of responses to auditory change as a “call for attention” as is assumed to be pre-attentive by definition ([Campbell et al., 2003](#); [Schröger, 1997](#)). Accordingly, visual color deviance processes could be understood to share common right-frontal localized mechanisms with that of auditory deviance processing.

Within this theoretical framework, the generation of color vMMN could be related to the pre-attentive processing of color deviance, while generation of LFCN is postulated to be a neural correlate of a call for attention. As distinct from color vMMN, LFCN did not correlate with the distraction effect. The explanation offered is that color vMMN led to this call for attention by color deviance – as indexed by LFCN – yet that call for attention went unnoticed, such that attention was not captured by color deviance. Color vMMN might be interpreted as a product of stimulus-specific adaptation analogous to that demonstrated in the auditory domain ([Ulanovsky et al., 2003](#)). An afferent tuned to a repeated acoustical frequency fires more vigorously to a rare unexpected change in the acoustical frequency of the sound. Effects of unexpected pitch change upon such afferents have been revealed in response to pitch deviance ([Ulanovsky et al., 2003](#); [Moore, 2003](#)). It has been claimed that each such an individual afferent is a “memory” neuron ([Ulanovsky et al., 2003](#); [Ulanovsky, 2004](#)). An analogous automatically processed memory representation in the current experiment is considered to predict the color of the standard stimulation, as can be used to pre-attentively suppress the visual search of standard yet not deviant color distractors, resulting in a distraction effect when the processing of color deviance is prioritized over that of uniqueness of shape. A neural response such as color vMMN to the violation of such a prediction by color deviance may have served to promote the detection of new entities in a dynamic visual environment. Such an internal memory representation might also guide visual search in a manner that permits the effective use of external representations typically available in static visual environments ([Ballard et al., 1997](#); [Kimura et al., 2010b, 2011](#)), which can be used to compensate for the inherent limitations of working memory during the performance of natural tasks.

To conclude the new adventure of employing the visual search paradigm adopted here has brought some novel findings: the support for a left posteriorly distributed deviance-elicited component generated by (a subset of) vMMN generators at long ISIs, indexing a pre-attentively coded visual memory for color; the correlation of distraction with that pre-attentively elicited component; this distraction effect in a visual

search task without eliciting the clear P3a typical to attentional capture caused by visual changes in other paradigms; and the subsequent LFCN distributed over the right hemisphere in response to that to-be-ignored visual deviance. These new findings have contributed to the core theoretical aim of this work offering a novel resolution to the debate about the existence of an internal sensory memory representation in the visual domain. In sum, vision has a pre-attentive sensory memory for color affecting not only visual search but also influencing crucially the generation of a functionally associated form of color vMMN.

## References

- Astikainen, P., Hietanen, J.K., 2009. Event-related potentials to task-irrelevant changes in facial expressions. *Behav. Brain Funct.* 5. <http://dx.doi.org/10.1186/1744-9081-5-30>.
- Astikainen, P., Ruusuvirta, T., Wikgren, J., Korhonen, T., 2004. The human brain processes visual changes that are not cued by attended auditory stimulation. *Neurosci. Lett.* 368, 231–234. <http://dx.doi.org/10.1016/j.neulet.2004.07.025>.
- Astikainen, P., Lillstrang, E., Ruusuvirta, T., 2008. Visual mismatch negativity for changes in orientation – a sensory memory-dependent response. *Eur. J. Neurosci.* 28, 2319–2324. <http://dx.doi.org/10.1111/j.1460-9568.2008.06510.x>.
- Baddeley, A.D., 1986. *Working Memory*. Clarendon Press, Oxford, UK.
- Ballard, D., Hayhoe, M., Pook, P., Rao, R., 1997. Deictic codes for the embodiment of cognition. *Behav. Brain Sci.* 20 (40), 723–767.
- Berry, D.C., Dienes, Z., 1993. *Implicit Learning: Theoretical and Empirical Issues*. Lawrence Erlbaum, Hove, England.
- Berti, S., 2009. Position but not color deviants result in visual mismatch negativity in an active oddball task. *NeuroReport* 20, 702–707. <http://dx.doi.org/10.1097/WNR.0b013e32832a6e8d>.
- Berti, S., 2011. The attentional blink demonstrates automatic deviance processing in vision. *NeuroReport* 22, 664–667. <http://dx.doi.org/10.1097/WNR.0b013e32834a8990>.
- Berti, S., Schröger, E., 2001. A comparison of auditory and visual distraction effects: behavioral and event-related indices. *Cogn. Brain Res.* 10, 265–273. [http://dx.doi.org/10.1016/S0926-6410\(00\)00044-6](http://dx.doi.org/10.1016/S0926-6410(00)00044-6).
- Berti, S., Schröger, E., 2004. Distraction effects in vision: behavioral and event-related potential indices. *NeuroReport* 15 (4), 665–669.
- Berti, S., Schröger, E., 2006. Visual distraction: a behavioral and event-related brain potential study in humans. *NeuroReport* 17, 151–155. <http://dx.doi.org/10.1097/01.wnr.0000195669.07467.e1>.
- Botcher-Gandor, C., Ullsperger, P., 1992. Mismatch negativity in event-related potentials to auditory stimuli as a function of varying interstimulus interval. *Psychophysiology* 29, 546–550. <http://dx.doi.org/10.1111/j.1469-8986.1992.tb02028.x>.
- Bouma, H., 1970. Interaction effects in parafoveal letter recognition. *Nature* 226, 177–178. <http://dx.doi.org/10.1038/226177a0>.
- Busch, N.A., Dürschmid, S., Herrmann, C.S., 2010. ERP effects of change localization, change identification, and change blindness. *NeuroReport* 21, 371–375. <http://dx.doi.org/10.1097/WNR.0b013e3283378379>.
- Cammann, R., 1990. Is there no MMN in the visual modality? *Behav. Brain Sci.* 13, 234–235. <http://dx.doi.org/10.1017/S0140525X00078420>.
- Campbell, T.A., 2015. A theory of attentional modulations of the supratemporal generation of the auditory mismatch negativity (MMN). *Front. Hum. Neurosci.* 8. <http://dx.doi.org/10.3389/fnhum.2014.01065>.
- Campbell, T., Winkler, I., Kujala, T., Näätänen, R., 2003. The N1 hypothesis and irrelevant sound: evidence from token set size effects. *Cogn. Brain Res.* 18, 39–47. <http://dx.doi.org/10.1016/j.cogbrainres.2003.09.001>.
- Campbell, T.A., Kerlin, J.K., Bishop, C.W., Miller, L.M., 2012. Methods to eliminate stimulus transduction artifact from insert earphones during electroencephalography. *Ear Hear.* 33, 44–50. <http://dx.doi.org/10.1097/AUD.0b013e3182280353>.
- Chun, M.M., 2000. Contextual cueing of visual attention. *Trends Cogn. Sci.* 4, 170–178. [http://dx.doi.org/10.1016/S1364-6613\(00\)01476-5](http://dx.doi.org/10.1016/S1364-6613(00)01476-5).
- Chun, M.M., Jiang, Y., 1998. Contextual cueing: implicit learning and memory of visual context guides spatial attention. *Cogn. Psychol.* 36, 28–71. <http://dx.doi.org/10.1006/cogp.1998.0681>.
- Clifford, A., Holmes, A., Davies, I.R.L., Franklin, A., 2010. Color categories affect pre-attentive color perception. *Biol. Psychol.* 85, 275–282. <http://dx.doi.org/10.1016/j.biopsycho.2010.07.014>.
- Czigler, I., 1990. Is the attentional trace theory modality specific? *Behav. Brain Sci.* 13, 238–239. <http://dx.doi.org/10.1017/S0140525X00078468>.
- Czigler, I., 2007. Visual mismatch negativity – violation of nonattended environmental regularities. *J. Psychophysiol.* 21, 224–230. <http://dx.doi.org/10.1027/0269-8803.21.34.224>.
- Czigler, I., Pato, L., 2009. Unnoticed regularity violation elicits change-related brain activity. *Biol. Psychol.* 80, 339–347. <http://dx.doi.org/10.1016/j.biopsycho.2008.12.001>.
- Czigler, I., Sulykos, I., 2010. Visual mismatch negativity to irrelevant changes is sensitive to task-relevant changes. *Neuropsychologia* 48, 1277–1282. <http://dx.doi.org/10.1016/j.neuropsychologia.2009.12.029>.
- Czigler, I., Balazs, L., Winkler, I., 2002. Memory-based detection of task-irrelevant visual changes. *Psychophysiology* 39 (6), 869–873.
- Czigler, I., Balazs, L., Pato, L.G., 2004. Visual change detection: event-related potentials are dependent on stimulus location in humans. *Neurosci. Lett.* 364, 149–153. <http://dx.doi.org/10.1016/j.neulet.2004.04.048>.
- Czigler, I., Weisz, J., Winkler, I., 2007. Backward masking and visual mismatch negativity: electrophysiological evidence for memory-based detection of deviant stimuli. *Psychophysiology* 44, 610–619. <http://dx.doi.org/10.1111/j.1469-8986.2007.00530.x>.

- Dean, G.M., Dewhurst, S.A., Whittaker, A., 2008. Dynamic visual noise interferes with storage in visual working memory. *Exp. Psychol.* 55, 283–289. <http://dx.doi.org/10.1027/1618-3169.55.4.283>.
- Deouell, L.Y., Bentin, S., Giard, M.H., 1998. Mismatch negativity in dichotic listening: evidence for interhemispheric differences and multiple generators. *Psychophysiology* 35, 355–365. <http://dx.doi.org/10.1017/S0048577298970287>.
- Doeller, C.F., Opitz, B., Mecklinger, A., Krick, C., Reith, W., Schröger, E., 2003. Prefrontal cortex involvement in preattentive auditory deviance detection: neuroimaging and electrophysiological evidence. *NeuroImage* 20, 1270–1282. [http://dx.doi.org/10.1016/S1053-8119\(03\)00389-6](http://dx.doi.org/10.1016/S1053-8119(03)00389-6).
- Donald, M., 1993. Précis of origins of the modern mind: three stages in the evolution of culture and cognition. *Behav. Brain Sci.* 16, 737–748. <http://dx.doi.org/10.1017/S0140525X00032647>.
- Eimer, M., Mazza, V., 2005. Electrophysiological correlates of change detection. *Psychophysiology* 42, 328–342. <http://dx.doi.org/10.1111/j.1469-8986.2005.00285.x>.
- Erlbeck, H., Kübler, A., Kotchoubey, B., Vesper, S., 2015. Task instructions modulate the attentional mode affecting the auditory MMN and the semantic N400. *Front. Hum. Neurosci.* 8. <http://dx.doi.org/10.3389/fnhum.2014.00654>.
- Felisberti, F.M., Solomon, J.A., Morgan, M.J., 2005. The role of target salience in crowding. *Perception* 34, 823–833. <http://dx.doi.org/10.1068/p5206>.
- Fernandez-Duque, D., Thornton, I.M., 2000. Change detection without awareness: Do explicit reports underestimate the representation of change in the visual system? *Vis. Cogn.* 7 (1–3), 323–344. <http://dx.doi.org/10.1080/135062800394838>.
- Fisch, B.J., Spehlmann, R., 1999. *EEG Primer: Basic Principles of Digital and Analog EEG*. Elsevier, New York.
- Fisher, D.J., Scott, T.L., Shah, D.K., Prise, S., Thompson, M., Knott, V.J., 2010. Light up and see: enhancement of the visual mismatch negativity (vMMN) by nicotine. *Brain Res.* 1313, 162–171. <http://dx.doi.org/10.1016/j.brainres.2009.12.002>.
- Flynn, M., Liasis, A., Gardner, M., Boyd, S., Towell, T., 2009. Can illusory deviant stimuli be used as attentional distractors to record vMMN in a passive three stimulus oddball paradigm? *Exp. Brain Res.* 197, 153–161. <http://dx.doi.org/10.1007/s00221-009-1901-7>.
- Folstein, J.R., Van Petten, C., 2008. Influence of cognitive control and mismatch on the N2 component of the ERP: a review. *Psychophysiology* 45, 152–170. <http://dx.doi.org/10.1111/j.1469-8986.2007.00602.x>.
- Fu, S., Fan, S., Chen, L., 2003. Event-related potentials reveal involuntary processing of orientation changes in the visual modality. *Psychophysiology* 40, 770–775. <http://dx.doi.org/10.1111/1469-8986.00077>.
- Fuster, J.M., 1997. *The Prefrontal Cortex: Anatomy, Physiology and Neuropsychology of the Frontal Lobe*. Lippincott-Raven, Philadelphia, Pennsylvania.
- Heslenfeld, D.J., 2003. Visual mismatch negativity. In: Polich, J. (Ed.), *Detection of Change: Event-Related Potential and fMRI Findings*. Kluwer Academic Publishers, Boston, Massachusetts, pp. 41–59.
- Hickey, C., McDonald, J.J., Theeuwes, J., 2006. Electrophysiological evidence of the capture of visual attention. *J. Cogn. Neurosci.* 18, 604–613. <http://dx.doi.org/10.1162/jocn.2006.18.4.604>.
- Hickey, C., DiLollo, V., McDonald, J.J., 2009. Electrophysiological indices of target and distractor processing in visual search. *J. Cogn. Neurosci.* 21, 760–775. <http://dx.doi.org/10.1162/jocn.2009.21039>.
- Hilimire, M.R., Mounts, J.R.W., Parks, N.A., Corballis, P.M., 2009. Competitive interaction degrades target selection: an ERP study. *Psychophysiology* 46, 1080–1089. <http://dx.doi.org/10.1111/j.1469-8986.2009.00846.x>.
- Hilimire, M.R., Mounts, J.R.W., Parks, N.A., Corballis, P.M., 2010. Event-related potentials dissociate effects of salience and space in biased competition for visual representation. *PLoS One* 5. <http://dx.doi.org/10.1371/journal.pone.0012677>.
- Hilimire, M.R., Mounts, J.R.W., Parks, N.A., Corballis, P.M., 2011. Dynamics of target and distractor processing in visual search: Evidence from event-related brain potentials. *Neurosci. Lett.* 495, 196–200. <http://dx.doi.org/10.1016/j.neulet.2011.03.064>.
- Kimura, M., 2012. Visual mismatch negativity and unintentional temporal-context-based prediction in vision. *Int. J. Psychophysiol.* 83, 144–155. <http://dx.doi.org/10.1016/j.ijpsycho.2011.11.010>.
- Kimura, M., Katayama, J., Murohashi, H., 2006a. An ERP study of visual change detection: effects of magnitude of spatial frequency changes on the change-related posterior positivity. *Int. J. Psychophysiol.* 62, 14–23. <http://dx.doi.org/10.1016/j.ijpsycho.2005.11.005>.
- Kimura, M., Katayama, J., Murohashi, H., 2006b. Probability-independent and -dependent ERPs reflecting visual change detection. *Psychophysiology* 43, 180–189. <http://dx.doi.org/10.1111/j.1469-8986.2006.00388.x>.
- Kimura, M., Katayama, J., Murohashi, H., 2008a. Involvement of memory-comparison-based change detection in visual distraction. *Psychophysiology* 45, 445–457. <http://dx.doi.org/10.1111/j.1469-8986.2007.00640.x>.
- Kimura, M., Katayama, J., Murohashi, H., 2008b. Attention switching function of memory-comparison-based change detection system in the visual modality. *Int. J. Psychophysiol.* 67, 101–113. <http://dx.doi.org/10.1016/j.ijpsycho.2007.10.009>.
- Kimura, M., Ohira, H., Schröger, E., 2010a. Localizing sensory and cognitive systems for pre-attentive visual deviance detection: an sLORETA analysis of the data of Kimura et al. (2009). *Neurosci. Lett.* 485, 198–203. <http://dx.doi.org/10.1016/j.neulet.2010.09.011>.
- Kimura, M., Schröger, E., Czigler, I., Ohira, H., 2010b. Human visual system automatically encodes sequential regularities of discrete events. *J. Cogn. Neurosci.* 22, 1124–1139. <http://dx.doi.org/10.1162/jocn.2009.21299>.
- Kimura, M., Widmann, A., Schröger, E., 2010c. Human visual system automatically represents large-scale sequential regularities. *Brain Res.* 1317, 165–179. <http://dx.doi.org/10.1016/j.brainres.2009.12.076>.
- Kimura, M., Widmann, A., Schröger, E., 2010d. Top-down attention affects sequential regularity representation in the human visual system. *Int. J. Psychophysiol.* 77, 126–134. <http://dx.doi.org/10.1016/j.ijpsycho.2010.05.003>.
- Kimura, M., Schröger, E., Czigler, I., 2011. Visual mismatch negativity and its importance in visual cognitive sciences. *NeuroReport* 22, 669–673. <http://dx.doi.org/10.1097/WNR.0b013e32834973ba>.
- Liu, T.R., Shi, J.N., 2008. Event-related potentials during preattentive processing of color stimuli. *NeuroReport* 19 (12), 1221–1225. <http://dx.doi.org/10.1097/WNR.0b013e32834973ba>.
- Logie, R.H., 1995. *Visuo-Spatial Working Memory*. Lawrence Erlbaum Associates, Hove, UK.
- Luck, S.J., 2005a. *An Introduction to the Event-Related Potential Technique*. MIT Press, Cambridge, MA.
- Luck, S.J., 2005b. Ten simple rules for designing ERP experiments. In: Handy, T.C. (Ed.), *Event-Related Potentials: A Methods Handbook*. MIT Press, Cambridge, MA, pp. 17–32.
- Luck, S.J., Hillyard, S.A., 1994a. Electrophysiological correlates of feature analysis during visual search. *Psychophysiology* 31, 291–308. <http://dx.doi.org/10.1111/j.1469-8986.1994.tb02218.x>.
- Luck, S.J., Hillyard, S.A., 1994b. Spatial filtering during visual search: evidence from human electrophysiology. *J. Exp. Psychol. Hum. Percept. Perform.* 20, 1000–1014. <http://dx.doi.org/10.1037/0096-1523.20.5.1000>.
- Lyyra, P., Wikgren, J., Astikainen, P., 2010. Event-related potentials reveal rapid registration of features of infrequent changes during change blindness. *Behav. Brain Funct.* 6, 12. <http://dx.doi.org/10.1186/1744-9081-6-12>.
- Lyyra, P., Wikgren, J., Ruusuvirta, T., Astikainen, P., 2012. Explicit behavioral detection of visual changes develops without their implicit neurophysiological detectability. *Front. Hum. Neurosci.* 6. <http://dx.doi.org/10.3389/fnhum.2012.00048>.
- Mack, A., Rock, I., 1998. *Inattention Blindness*. MIT Press, Cambridge, Massachusetts.
- Maekawa, T., Tobimatsu, S., Ogata, K., Onitsuka, T., Kanba, S., 2009. Preattentive visual change detection as reflected by the mismatch negativity (MMN) – evidence for a memory-based process. *Neurosci. Res.* 65, 107–112. <http://dx.doi.org/10.1016/j.neures.2009.06.005>.
- Mao, W., Wang, Y.P., Shi, L.X., Wang, D.Q., 2004. Event-related potentials elicited by visual stimulus-duration discrimination tasks. *Clin. EEG Neurosci.* 35 (2), 78–83.
- McConnell, J., Quinn, J.G., 2000. Interference in visual working memory. *Q. J. Exp. Psychol.* 53A (1), 53–67. <http://dx.doi.org/10.1080/1713755873>.
- McDonald, J.J., Green, J.J., Jannati, A., Di Lollo, V., 2013. On the electrophysiological evidence for the capture of visual attention. *J. Exp. Psychol. Hum. Percept. Perform.* 39, 849–860. <http://dx.doi.org/10.1037/a0030510>.
- Miyake, A., Shah, P., 1999. *Models of Working Memory*. Cambridge University Press, New York, NY.
- Moore, D.R., 2003. Cortical neurons signal sound novelty. *Nat. Neurosci.* 6, 330–332. <http://dx.doi.org/10.1038/nn0403-330>.
- Müller, D., Roeber, U., Winkler, I., Trujillo-Barreto, N., Czigler, I., Schröger, E., 2012. Impact of lower- vs. upper-hemifield presentation on automatic colour-deviance detection: a visual mismatch negativity study. *Brain Res.* 1472, 89–98. <http://dx.doi.org/10.1016/j.brainres.2012.07.016>.
- Näätänen, R., 1990. The role of attention in auditory information processing as revealed by event-related potentials and other brain measures of cognitive function. *Behav. Brain Sci.* 13, 201–288. <http://dx.doi.org/10.1017/S0140525X00078407>.
- Näätänen, R., 1991. Mismatch and processing negativities in auditory stimulus processing and selection. *Behav. Brain Sci.* 14, 761–768. <http://dx.doi.org/10.1017/S0140525X00072459>.
- Näätänen, R., Gaillard, A.W., Mäntysalo, S., 1978. Early selective-attention effect on evoked potential reinterpreted. *Acta Psychol.* 42, 313–329. [http://dx.doi.org/10.1016/0001-6918\(78\)90006-9](http://dx.doi.org/10.1016/0001-6918(78)90006-9).
- O'Regan, J.K., Noë, A., 2001. A sensorimotor account of vision and visual consciousness. *Behav. Brain Sci.* 24, 939–1031. <http://dx.doi.org/10.1017/S0140525X01000115>.
- O'Regan, J.K., Rensink, R.A., Clark, J.J., 1999. Change-blindness as a result of 'mudsplashes'. *Nature* 398, 34. <http://dx.doi.org/10.1038/17953>.
- Obeidat, Q., Campbell, T., Kong, J., 2013. The zigzag paradigm: A new P300-based brain computer interface. Paper Presented at the *Proceedings of the 15th ACM on International Conference on Multimodal Interaction*, pp. 205–212. <http://dx.doi.org/10.1145/2522848.2522880>.
- Obeidat, Q., Campbell, T., Kong, J., 2015. Introducing the Edges Paradigm: A P300 Brain-Computer Interface for Spelling Written words (submitted for publication).
- Ojanen, V., Revonsuo, A., Sams, M., 2003. Visual awareness of low-contrast stimuli is reflected in event-related brain potentials. *Psychophysiology* 40, 192–197. <http://dx.doi.org/10.1111/1469-8986.00021>.
- Olds, E.S., Cowan, W.B., Jolicoeur, P., 2000. Tracking visual search over space and time. *Psychon. Bull. Rev.* 7, 292–300. <http://dx.doi.org/10.3758/BF03212984>.
- Opitz, B., Rinne, T., Mecklinger, A., von Cramon, D.Y., Schröger, E., 2002. Differential contribution of frontal and temporal cortices to auditory change detection: fMRI and ERP results. *NeuroImage* 15, 167–174. <http://dx.doi.org/10.1006/nimg.2001.0970>.
- Pazo-Alvarez, P., Cadaveira, F., Amenedo, E., 2003. MMN in the visual modality: a review. *Biol. Psychol.* 63, 199–236. [http://dx.doi.org/10.1016/S0301-0511\(03\)00049-8](http://dx.doi.org/10.1016/S0301-0511(03)00049-8).
- Quinn, J.G., McConnell, J., 1996. Irrelevant pictures in visual working memory. *Q. J. Exp. Psychol.* 49A, 200–215. <http://dx.doi.org/10.1080/1713755613>.
- Quinn, J.G., McConnell, J., 1999. Manipulation of interference in the passive visual store. *Eur. J. Cogn. Psychol.* 11, 373–390. <http://dx.doi.org/10.1080/713752322>.
- Rensink, R.A., 2002. Change detection. *Annu. Rev. Psychol.* 53, 245–277. <http://dx.doi.org/10.1146/annurev.psych.53.100901.135125>.
- Rensink, R.A., O'Regan, J.K., Clark, J.J., 1997. To see or not to see: the need for attention to perceive changes in scenes. *Psychol. Sci.* 8 (5), 368–373.
- Restuccia, D., Della Marca, G., Marra, C., Rubino, M., Valeriani, M., 2005. Attentional load of the primary task influences the frontal but not the temporal generators of mismatch negativity. *Brain Res. Cogn. Brain Res.* 25, 891–899. <http://dx.doi.org/10.1016/j.cogbrainres.2005.09.023>.

- Rinne, T., 2001. Human Cortical Functions in Auditory Change Detection evaluated with Multiple Brain Research Methods. (Doctoral thesis), University of Helsinki, Helsinki, Finland (Retrieved from: <http://ethesis.helsinki.fi/julkaisut/hum/psyko/vk/rinne/>).
- Rinne, T., Alho, K., Ilmoniemi, R.J., Virtanen, J., Näätänen, R., 2000. Separate time behaviors of the temporal and frontal mismatch negativity sources. *NeuroImage* 12, 14–19. <http://dx.doi.org/10.1006/nimg.2000.0591>.
- Sawaki, R., Luck, S.J., 2011. Active suppression of distractors that match the contents of visual working memory. *Vis. Cogn.* 19, 956–972. <http://dx.doi.org/10.1080/13506285.2011.603709>.
- Schröger, E., 1997. On the detection of auditory deviations: a pre-attentive activation model. *Psychophysiology* 34, 245–257. <http://dx.doi.org/10.1111/j.1469-8986.1997.tb02395.x>.
- Shapiro, K.L., Raymond, J.E., Arnell, K.M., 1997. The attentional blink. *Trends Cogn. Sci.* 1, 291–296. [http://dx.doi.org/10.1016/S1364-6613\(97\)01094-2](http://dx.doi.org/10.1016/S1364-6613(97)01094-2).
- Shtyrov, Y., Goryainova, G., Tugin, S., Ossadtchi, A., Shestakova, A., 2013. Automatic processing of unattended lexical information in visual oddball presentation: neurophysiological evidence. *Front. Hum. Neurosci.* 7, 421. <http://dx.doi.org/10.3389/fnhum.2013.00421>.
- Simons, D.J., Levin, D.T., 1997. Change blindness. *Trends Cogn. Sci.* 1, 261–267. [http://dx.doi.org/10.1016/S1364-6613\(97\)01080-2](http://dx.doi.org/10.1016/S1364-6613(97)01080-2).
- Stefanics, G., Czigler, I., 2012. Automatic prediction error responses to hands with unexpected laterality: an electrophysiological study. *NeuroImage* 63, 253–261. <http://dx.doi.org/10.1016/j.neuroimage.2012.06.068>.
- Stefanics, G., Kimura, M., Czigler, I., 2011. Visual mismatch negativity reveals automatic detection of sequential regularity violation. *Front. Hum. Neurosci.* 5. <http://dx.doi.org/10.3389/fnhum.2011.00046>.
- Stefanics, G., Csukly, G., Komlosi, S., Czobor, P., Czigler, I., 2012. Processing of unattended facial emotions: a visual mismatch negativity study. *NeuroImage* 59, 3042–3049. <http://dx.doi.org/10.1016/j.neuroimage.2011.10.041>.
- Sulykos, I., Czigler, I., 2011. One plus one is less than two: visual features elicit non-additive mismatch-related brain activity. *Brain Res.* 1398, 64–71. <http://dx.doi.org/10.1016/j.brainres.2011.05.009>.
- Sušac, A., Ilmoniemi, R.J., Pihko, E., Supek, S., 2004. Neurodynamic studies on emotional and inverted faces in an oddball paradigm. *Brain Topogr.* 16, 265–268. <http://dx.doi.org/10.1023/B:BRAT.0000032863.39907.cb>.
- Sušac, A., Ilmoniemi, R.J., Supek, S., 2010a. Sensory-memory-based change detection in face stimuli. *Transl. Neurosci.* 1, 286–291. <http://dx.doi.org/10.2478/v10134-010-0042-7>.
- Sušac, A., Ilmoniemi, R.J., Pihko, E., Ranken, D., Supek, S., 2010b. Early cortical responses are sensitive to changes in face stimuli. *Brain Res.* 1346, 155–164. <http://dx.doi.org/10.1016/j.brainres.2010.05.049>.
- Sušac, A., Ilmoniemi, R.J., Ranken, D., Supek, S., 2011. Face activated neurodynamic cortical networks. *Med. Biol. Eng. Comput.* 49, 531–543. <http://dx.doi.org/10.1007/s11517-011-0740-4>.
- Theeuwes, J., 1994. Stimulus-driven capture and attentional set: selective search for color and visual abrupt onsets. *J. Exp. Psychol. Hum. Percept. Perform.* 20 (4), 799–806. <http://dx.doi.org/10.1037/0096-1523.20.4.799>.
- Theeuwes, J., Burger, R., 1998. Attentional control during visual search: the effect of irrelevant singletons. *J. Exp. Psychol. Hum. Percept. Perform.* 24 (5), 1342–1353. <http://dx.doi.org/10.1037/0096-1523.24.5.1342>.
- Tiitinen, H., May, P., Reinikainen, K., Näätänen, R., 1994. Attentive novelty detection in humans is governed by pre-attentive sensory memory. *Nature* 372 (6501), 90–92. <http://dx.doi.org/10.1038/372090a0>.
- Ulanovsky, N., 2004. Neuronal Adaptation in Cat Auditory Cortex. (Doctoral thesis). Hebrew University, Jerusalem, Israel (Retrieved from: <http://icnc.huji.ac.il/phd/theses/files/NachumUlanovsky.pdf>).
- Ulanovsky, N., Las, L., Nelken, I., 2003. Processing of low-probability sounds by cortical neurons. *Nat. Neurosci.* 6, 391–398. <http://dx.doi.org/10.1038/nn1032>.
- Walter, W.G., Cooper, R., Aldridge, V.J., McCallum, W.C., Winter, A.L., 1964. Contingent negative variation: an electrical sign of sensorimotor association and expectancy in the human brain. *Nature* 203, 380–384. <http://dx.doi.org/10.1038/203380a0>.
- Winkler, I., Czigler, I., 2012. Evidence from auditory and visual event-related potential (ERP) studies of deviance detection (MMN and vMMN) linking predictive coding theories and perceptual object representations. *Int. J. Psychophysiol.* 83, 132–143. <http://dx.doi.org/10.1016/j.ijpsycho.2011.10.001>.
- Wolfe, J.M., 2000. Inattentional amnesia. In: Coltheart, V. (Ed.), *Fleeting Memories*. MIT Press, Cambridge, MA.