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Research Report

Visual temporal window of integration as revealed by the visual mismatch negativity event-related potential to stimulus omissions

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ABSTRACT

We studied whether, similarly to the auditory modality, short-period temporal integration processes occur in vision. Event-related potentials (ERP) were recorded for occasional stimulus omissions from sequences of patterned visual stimuli. A posterior negative component emerged only when the constant stimulus onset asynchrony (SOA) was shorter than 150 ms. This upper limit is comparable with the duration of the temporal window of integration observed in the auditory modality (including experiments studying the effects of stimulus omissions). Parameters of the posterior negativity were highly similar irrespective of whether the stimuli were task-relevant or not (Experiment 1). Thus, we identified this potential as the visual mismatch negativity (vMMN) component, which reflects task-independent detection of violating regularities of the stimulation. vMMN was followed by an anterior positivity (the P3a), indicating attentional shifts induced by the stimulus omissions. In Experiment 2, a posterior negativity similar to that observed in Experiment 1 emerged after the termination of short trains of stimuli, again only when the SOA was shorter than 150 ms. These results support the notion of a temporal integration window in the visual modality, the duration of which is between 150 and 180 ms.

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1. Introduction

Although stimuli arrive continuously to our senses, extracting the features of external objects requires samples of some definite duration to ensure perceptual stability (temporal quantization). In audition, various analysis periods have been observed (Nelken et al., 2003; Poeppel, 2003), the most notable of which is the temporal window of integration (TWI) lasting for ca. 200 ms from the onset of isolated sounds. Basic sound analysis processes, such as establishing loudness or the temporal order between short sounds, appear to be bound to the TWI period, which is also regarded as the first form of auditory memory storage in the brain (for a review, see Cowan, 1984). Contrary to the auditory modality, some researchers

doubt the ecological validity of short-term stores in vision (Haber, 1983; see, however, Coltheart, 1983). Using a visual analogue of a well-established auditory event-related potential (ERP) phenomenon, the omission response (Yabe et al., 1997, 1998, 2001), the current study tested whether short-period temporal integration processes can be observed in the visual modality.

The question was studied using the mismatch negativity (MMN) component of ERPs, which is elicited when a sound violates some acoustic regularity of the preceding sound sequence. MMN is elicited by simple acoustic deviations in a repetitive sequence of sounds (e.g., by infrequently delivering a sound whose pitch differs from that of the repeating one; the auditory oddball paradigm; e.g., Schröger and Winkler, 1995) as well as by violations of more complex and even abstract regularities (e.g., occasional stimulus repetitions within a sequence of two alternating sounds; for reviews, see Näätänen and Winkler, 1999; Picton et al., 2000). However, MMN is not elicited by any acoustic change (e.g., by a sound following a long silent period, Cowan et al., 1993) but only when some regularity has been previously extracted from the sound sequence (Polich, 2003). On the other hand, MMN is elicited whether a deviant event is task-related or -irrelevant and it is largely insensitive to attentional manipulations (Näätänen, 1990; Sussman et al., 2003).

In the auditory modality, the omission response has been linked with the TWI because omissions elicit the mismatch negativity (MMN) component of the event-related brain potentials (ERP) when they are embedded in a sound sequence presented with a less than 200-ms stimulus onset asynchrony (SOA; onset-to-onset interval), but not when the SOA exceeds the duration of the TWI (Näätänen, 1990; Yabe et al., 1997, 1998, 2001). Comparable results were obtained using paired presentation of tones (Tervaniemi et al., 1994). Two explanations, both based on temporal integration phenomena, have been offered to explain the omission MMN. Yabe and his colleagues suggest that sounds arriving within the TWI period are treated a single chunk, which, however, retains the temporal structure of the acoustic events (Yabe et al., 1997, 1998, 2001). If the SOA of a sequence is shorter than the duration of TWI, two sounds appear regularly within the TWI. Omissions result in the formation of a "deviant temporal window", which contains only one sound. This deviation elicits the MMN. With longer SOAs, all integration windows contain only a single sound and, therefore, omissions do not cause deviation. It should be noted that the representations of the sounds encountered within a single TWI period can be decomposed at higher levels of perceptual processing (Czigler et al., 2003; Sussman et al., 2002). According to the alternative interpretation of omission MMN (Oceák et al., 2006), a sound following another sound within the TWI terminates the integration of the aftereffect of the first sound. As a consequence, the perceived loudness of sounds followed by another sound within the TWI is lower than that of the sounds preceding an omission (Cowan, 1987). Thus, infrequent omissions in a sound sequence presented with SOAs that are shorter than the TWI elicit a loudness-deviation MMN. Since loudness summation is limited to the TWI, no such effect occurs when the SOA exceeds the duration of the TWI.

In recent years, a visual analog of the MMN has been described. Visual mismatch negativities (vMMN) were elicited by deviations in spatial frequency (Heslenfeld, 2003), color (Czigler et al., 2002, 2004; Horimoto et al., 2002; Kimura et al., 2006), motion direction (Kremláèek et al., 2001, 2006; Pazo-Alvarez et al., 2004a, b), shape (Maekawa et al., 2005; Tales et al., 1999, 2002), line orientation (Astikainen et al., 2004; Fu et al., 2003), location (Berti and Schröger, 2004) and conjunction of color and spatial direction (Winkler et al., 2005) (for a review, see Pazo-Alvarez et al., 2003). The existence of vMMN provides the possibility to investigate whether omitting a visual stimulus from a sequence elicits event-related brain responses analogous to the auditory-omission-related response. The emergence of vMMN with short but not long SOAs would be taken to suggest that the implicit memory system underlying the detection of regularity violations in sequences of visual stimuli may show a critical period for unit formation, similarly to the assumed operation of TWI in audition.

In Experiment 1, we adapted the method developed by Yabe and his colleagues. Sequences of non-attended visual stimuli were presented with a constant SOA, and the event-related responses elicited by infrequent omissions were analyzed. By testing several SOAs, we aimed at assessing the critical duration of the assumed temporal integration period. In the *Detection task*, the participants performed a task unrelated to the sequence of non-attended stimuli. The task was the detection (in an RT situation) of the infrequent thickness change of a centrally presented cross. In order to assess the possibility of attentional effects, in the *Divided-attention* task, the stimulus omissions became task-relevant, that is, participants silently counted the number of stimulus omissions. In Experiment 2, we investigated whether the termination of a train of visual stimuli elicits similar brain responses.

2. Experiment 1

2.1. Results

Reaction times (RT) recorded in the *Detection* and the *Divided-attention* conditions are shown in Table 1. A two-way dependent-measures ANOVA (Task × SOA) showed that RTs were longer in the *Divided-attention* than in the *Detection* condition [$F(1,9) = 132.05$, $P < .001$ Task main effect]. Neither Task nor SOA had significant effects on hit rates (they were between 0.85 and 0.96). In the *Divided-attention* condition, participants reported the number of omissions fairly accurately. SOA had a significant effect on the percentage of

Table 1 – Experiment 1: reaction times to the central target in the *Detection* and *Divided-attention* conditions (SEM in parenthesis)

SOA	75 ms	109 ms	144 ms	179 ms	211 ms
Detection	419 (26.7)	404 (25.2)	394 (18.5)	399 (18.6)	393 (17.1)
Divided-attention	565 (33.3)	515 (25.4)	540 (28.4)	519 (23.8)	526 (23.7)

omissions found (F(4,36) = 8.70, ε = 0.60, P < .01), which was caused by the relatively low number of omissions found with the shortest (75 ms) SOA (71%) as opposed to the higher performance with longer SOAs (85, 90, 91 and 92% at 109, 144, 179 and 211-ms SOA, respectively).

Fig. 1 shows the omission-related electric brain activity over the Cz, TP7 and Oz locations at the five different SOAs in both attention conditions. At the three shorter SOAs, the posterior omission-related negativity was more negative than the baseline derived from the pre-stimulus negative peak (see

Fig. 1, right column). As a comparison, Fig. 2 shows epochs without stimulus omission.

The ANOVA showed a significant main effect of SOA and a Task × Electrode-location interaction for the posterior SOA-related response [F(4,36) = 5.64, ε = 0.66, P < .01 and F(2,18) = 4.49, ε = 0.76, P < .05, respectively]. Table 2 shows that the SOA-related negativity disappeared at longer SOAs (179 and 211 ms). The interaction was caused by larger negativities appearing at O2 in the *Divided-attention* than in the *Detection* condition. A significant linear trend was found
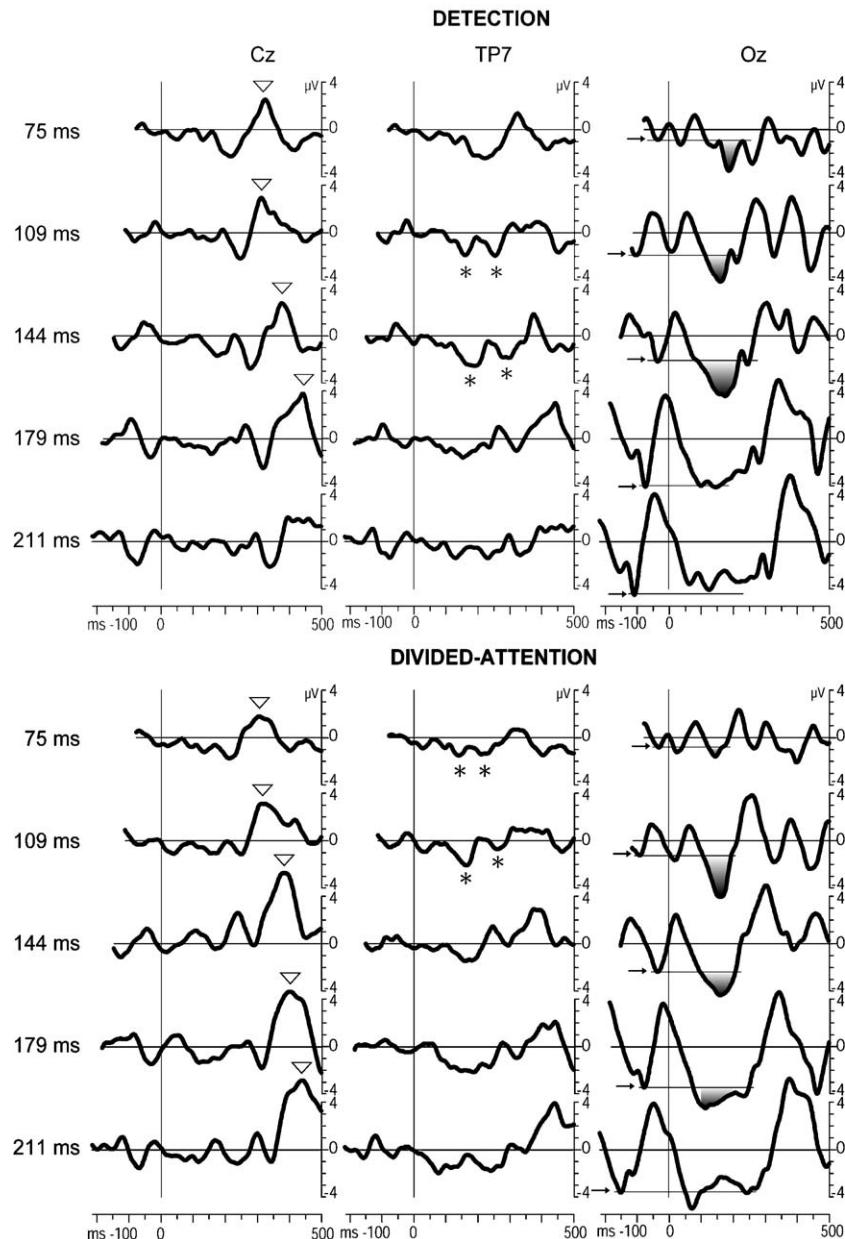

Fig. 1 – Experiment 1. The effect of infrequent stimulus omission on grand-averaged ERPs in the *Detection* (upper panel) and *Divided-attention* (lower panel) conditions as a function of stimulus onset asynchrony (SOA). Omission-related activity over the Cz and TP7 locations was related to the mean value of the SOA period preceding omission (the zero lines on the figures), whereas at Oz the omission-related activity was related to the largest negative peak of the SOA period preceding the omission. This value is indicated by the arrows and the short horizontal lines. The two negativities, marked by asterisks at the TP7 traces, correspond to the posterior (earlier) and anterior (later) negative components, respectively. The triangles at the Cz traces show the P3a component.
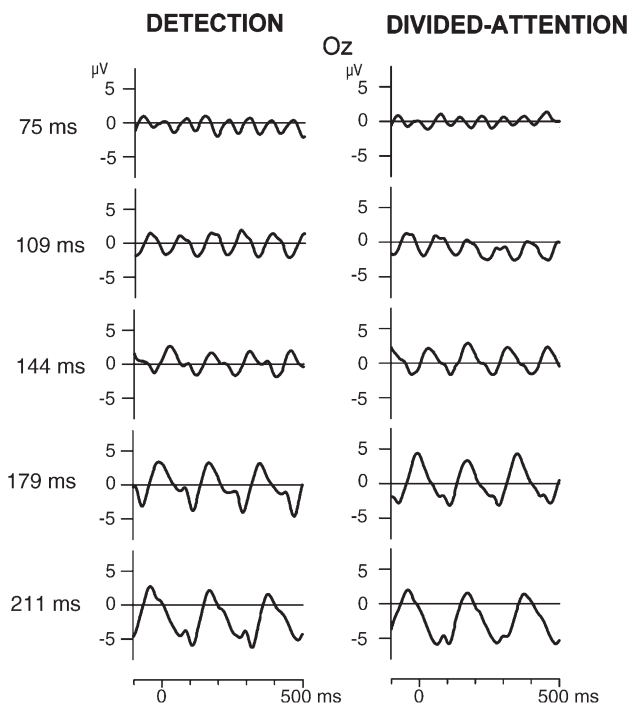
DETECTION   DIVIDED-ATTENTION

Oz

Fig. 2 – Experiment 1. Grand-averaged ERPs as function of stimulus onset asynchrony (SOA) in the *Detection* (upper panel) and *Divided-attention* (lower panel) condition.

for the amplitude of the omission-related response as a function of SOA [$F(1,9) = 9.71$, $P < .05$]. The quadratic and cubic trends were also significant [$F(1,9) = 8.27$, $P < .05$ and $F(1,9) = 6.25$, $P < .05$, respectively]. The non-linearity is an indication of the amplitude plateau at 109 and 142-ms SOA.

Elicitation of the omission-related negativity was separately assessed for each SOA with Student's t tests. MMN was elicited at 75, 109 and 144-ms SOAs [$t(10) = 2.28–3.03$, $P < .05$, each], whereas no significant MMN emerged at the two longer SOAs (179 and 211 ms). (The negativity appearing in the *Divided-attention* condition at 179-ms SOA, as shown on the bottom panel of Fig. 1, did not reach significance.)

Because the posterior omission-related negativity could only be detected reliably at the three shortest SOAs, analyses of the latency measure (latency of the largest negative value) were restricted to these SOAs. The peak latency of the omission-related negativity significantly increased with increasing SOAs [$F(2,18) = 7,57$ $\varepsilon = 0.73$, $P < .05$] (see Table 2).

Tukey HSD post hoc tests showed that the latency at 75-ms SOA was shorter than at 109 or 142 ms.

Over the anterior locations, omissions elicited a negative and a later positive response (see Fig. 1). The latency of the anterior negativity (Table 3) was longer than that of the occipital negativity as was shown by the significant Electrode-location main effect in a three-way dependent-measures ANOVA with factors of Task × SOA × Electrode-location (Oz and Cz) [$F(1,9) = 121.22$, $P < .001$]. There was also a significant SOA main effect [$F(4,36) = 37.99$, $\varepsilon = 0.69$, $P < .001$] and an Electrode-location × SOA interaction [$F(4,36) = 7.69$, $\varepsilon = 0.54$, $P < .01$]. The interaction was caused by the larger effect of SOA on the latency of the anterior than the posterior negativity. In Fig. 1, the anterior and posterior negativities are seen together as double negative peaks at the TP7 location (marked by asterisks on the middle column of Fig. 1).

In spite of the apparent difference in the amplitude of the anterior negativity between the *Detection* and the *Divided-attention* conditions, the ANOVA (Task × SOA) showed no significant effects.

Table 3 shows that the latency of the anterior positivity increased with increasing SOAs [$F(4,36) = 425.3$, $\varepsilon = 0.60$, $P < .001$]. Furthermore, there was a main effect of the Task [$F(1,9) = 8.46$, $P < .05$] and significant interaction between the two factors [$F(4,36) = 15,01$, $\varepsilon = 0.67$, $P < .001$]. The peak latency of the anterior positivity was longer in the *Detection* than in the *Divided-attention* condition, whereas no clear tendencies could be found that would explain the interaction.

The amplitude of the centrally maximal anterior positivity increased with increasing SOAs [$F(14,36) = 5.34$, $\varepsilon = 0.75$, $P < .01$] (see Fig. 1 and Table 3). The amplitude was also marginally larger in the *Divided-attention* than in the *Detection* condition [$F(1,9) = 4.16$, $P < .08$]. The interaction between the two factors was not significant, but Table 3 shows that the difference between the two conditions was larger at the longer SOAs.

2.2.   Discussion

Stimulus omissions embedded in a sequence of visual stimuli elicited a posterior negative ERP component in the 150–200 ms latency range. The elicitation of this component was confined to sequences with SOAs shorter than approximately 150 ms. The amplitude of this negativity was independent of the task relevance of the stimulus omissions. The auditory-omission-related negativity (Oceák et al., 2006; Yabe et al., 1997, 1998, 2001) has fairly similar characteristics. That is, it has a modality-specific distribution and SOA dependence with a

Table 2 – Experiment 1: latency (in ms) and amplitude (in microvolts, referred to the peak of the pre-omission negative peak)) of the posterior omission response (vMMN) at Oz (SEM in parenthesis)

SOA	75 ms	109 ms	144 ms	179 ms	211 ms
Latency (ms)					
Detection	153 (7.7)	175 (8.3)	190 (11.0)	–	–
Divided-attention	152 (7.3)	167 (5.9)	175 (11.1)	–	–
Amplitude (μV)					
Detection	−1.50 (0.62)	−1.85 (0.84)	−1.97 (0.96)	0.51 (0.90)	1.00 (0.86)
Divided-attention	−1.11 (0.54)	−2.56 (0.86)	−1.20 (1.17)	−0.22 (1.10)	0.46 (0.94)

170–200 ms upper limit. On the analogy of the MMN interpretation of the auditory-omission-related ERP response, we suggest that the posterior negativity found in the current experiment is a vMMN component (Czigler et al., 2002; 2004; Heslenfeld, 2003; Horimoto et al., 2002; Kremláèek et al., 2001, 2006; Lorenzo-López et al., 2004; Maekawa et al., 2005; Pazo-Alvarez et al., 2004a,b; Stagg et al., 2004; Tales et al., 1999, 2002). The current vMMN response was elicited by some TWI-related deviation, i.e., by breaking a regularity that stems from processing within a limited time window, such as the chunking process assumed by Yabe and his colleagues in the auditory modality.

Stimulus omissions also elicited an anterior negativity followed by a positivity. Both the peak latency and the amplitude distribution of the anterior negativity are clearly different from those of the posterior negativity. We identify the negativity as the N2b component and the positivity as the P3a. Both components are related to the involvement of attentional processing of stimulus change (e.g., Czigler and Csibra, 1992; Escera et al., 1998; Näätänen and Picton, 1986; Wijers et al., 1989). The strong latency dependence of the attention-related components on the SOA has been an incidental finding of the current study.

Finding a proper baseline for assessing the omission-related posterior negativity has been rather difficult due to the presence of the high-amplitude steady-state-like responses appearing with the short SOAs used in Experiment 1. This is because the time-course of the return to baseline after the termination of a steady-state response has not been systematically studied. We consider our choice of reference for the amplitude measurements in Experiment 1 reasonable, though, perhaps somewhat arbitrary. Therefore, in Experiment 2, we employed a procedure to by-pass this problem.

3. Experiment 2

We presented short isochronous trains of visual stimuli separated by longer inter-train intervals. The electric brain activity immediately following the termination of the trains should be initially similar to the response elicited by stimulus omissions. However, in Experiment 2, the interval between the last stimulus of a train and the first stimulus of the next train was much longer than the interval between the two stimuli surrounding the omitted one in Experiment 1. This way, the omission response (the initial part of activity triggered by the train offset) can be compared with a neutral baseline taken from a later time range of the inter-train period.

3.1. Results

Participants detected 95.7% of the targets (changes of the central cross). The mean RT was 421 (SEM = 20.3). These results are comparable with the corresponding results of Experiment 1.

Fig. 3 shows that the termination of the stimulus trains elicited two electric brain responses: a posterior negativity 150–250 ms from the time of expected continuation and an anterior positivity in the 250–350 ms latency range. The late posterior negative shift (compared with the artificial baseline) that is present at all SOAs after 400 ms from the time of expected continuation of the train represents the baseline following the offset of the steady-state response. Fig. 4 shows the scalp distribution of the two ERP responses.

The elicitation of the posterior negativity was tested at the O1, Oz and O2 electrode locations (referred to the average amplitude in the 400–500 ms interval). The effects of SOA on the amplitude of the posterior negativity were assessed with three different ANOVAs. In the first analysis, the negative peak amplitudes measured at O1 and O2 were referred to the mean value in the 400–500 ms epoch. This is a conservative assessment of the posterior negative wave, which is also insensitive to the steady-state activity of the preceding stimulus sequence. Both the SOA and the Electrode-location main effects were significant [$F(4,44) = 3.70$, $\varepsilon = 0.62$, $P < .05$ and $F(1,11) = 13.44$, $P < .01$ for SOA and Electrode-location, respectively]. Table 4 shows that the posterior negativity was only elicited at the three shortest SOAs. The linear trend of the amplitudes as a function of SOA was also significant [$F(1,11) = 6.24$, $P < .05$]. The Electrode-location main effect was due to the amplitudes being larger over the right than the left hemisphere (see Fig. 4).

In the second analysis, the peak of the posterior negativity was measured at T5 and T6, referred to the 100-ms baseline preceding the time of expected continuation, because at these posterior temporal electrode locations, the late negative shift was less pronounced. Both main effects and the interaction were significant [$F(4,44) = 7.32$, $\varepsilon = 0.57$, $P < .01$; $F(1,11) = 10.10$, $P < .01$, and $F(4,44) = 3.41$, $\varepsilon = 0.65$, $P < .05$ for the SOA and Electrode-location main effects and for the interaction, respectively]. Both the linear and the quadratic trend of the amplitude as a function of SOA showed significant effects [$F(1,11) = 15.60$, $P < .01$ and $F(1,11) = 4.88$, $P < .05$, respectively]. The quadratic trend was the consequence of the larger negativity obtained with 144-ms SOA. The interaction was caused by larger negativities appearing over the right hemisphere at short SOAs (see Fig. 4).

The third ANOVA assessed the anterior–posterior distribution of the posterior negativity. Amplitudes were measured as the average voltage in the 186–226 ms interval at the midline electrodes (Fz, FCz, Cz, Pz and Oz) and referred to the 100 ms baseline preceding the time of expected continuation. Both main effects were significant [$F(4,44) = 4.82$, $\varepsilon = 0.72$, $P < .01$ and $F(4,44) = 39.27$, $\varepsilon = 0.37$, $P < .01$, for SOA and Electrode-location, respectively]. The SOA main effect was due to the decreased negativity at the longer (179 and 211 ms) SOAs, whereas the Electrode-location main effect was caused by the gradual increase of the negativity in the anterior–posterior direction (see Fig. 4).

According to t tests, in the three shortest SOAs, all but one of the tests showed significant results ($t(11) = 4.48$–2.38; $P < .001$–0.05). (The exception was O1 at 109-ms SOA: $t(11) = 2.12$, $P < .06$.) At the longer SOAs, none of the t tests showed significant results.

The amplitude of the anterior positive component was largest over Cz (Fig. 3). The ANOVA with factors of SOA and Electrode-location (Fz, FCz, Cz, Pz and Oz) showed significant main effects and interaction [$F(4,44) = 7.29$, $\varepsilon = 0.57$, $P < .01$; $F(4,44) = 34.99$, $\varepsilon = 0.33$, $P < .001$ and $F(16,176) = 3.40$, $\varepsilon = 0.20$, $P < .05$ for the SOA and Electrode-location main effects and the

Table 3 – Experiment 1: latency (in ms) and amplitude (in microvolts) of the anterior negativity and positivity elicited by stimulus omission at Cz (SEM in parenthesis)

SOA	75 ms	109 ms	144 ms	179 ms	211 ms
Latency (ms)					
Negativity					
Detection	223 (4.2)	252 (3.4)	285 (3.2)	317 (3.4)	320 (5.0)
Divided-attention	215 (4.1)	250 (4.4)	292 (3.2)	315 (3.7)	343 (3.5)
Positivity					
Detection	322 (3.1)	318 (3.8)	388 (3.4)	435 (3.5)	428 (5.7)
Divided-attention	308 (4.3)	321 (5.0)	387 (4.5)	400 (4.5)	435 (3.9)
Amplitude (μV)					
Negativity					
Detection	−2.06 (0.85)	−2.10 (0.89)	−2.65 (0.58)	−2.32 (0.71)	−1.26 (0.49)
Divided-attention	−1.71 (0.72)	−1.08 (0.95)	−1.06 (0.99)	−1.63 (1.23)	−0.90 (1.23)
Positivity					
Detection	2.40 (1.07)	2.73 (0.76)	2.63 (0.53)	3.59 (0.27)	1.86 (0.84)
Divided-attention	1.73 (0.55)	3.09 (1.19)	5.91 (0.68)	4.57 (1.03)	5.75 (0.69)

interaction, respectively]. Larger positivities were elicited at the two shortest SOAs with small or no effect at 144-ms and longer SOAs (see, Table 5). The interaction was due to a larger amplitude decrease at the longest SOA at Oz location than at any other electrode. However, it should be noted that over posterior scalp locations the amplitude of the anterior positivity was influenced by the overlapping negative shift (see Fig. 3).

The latency of the anterior positive component decreased with increasing SOAs (see Table 5). Contrary to the apparently
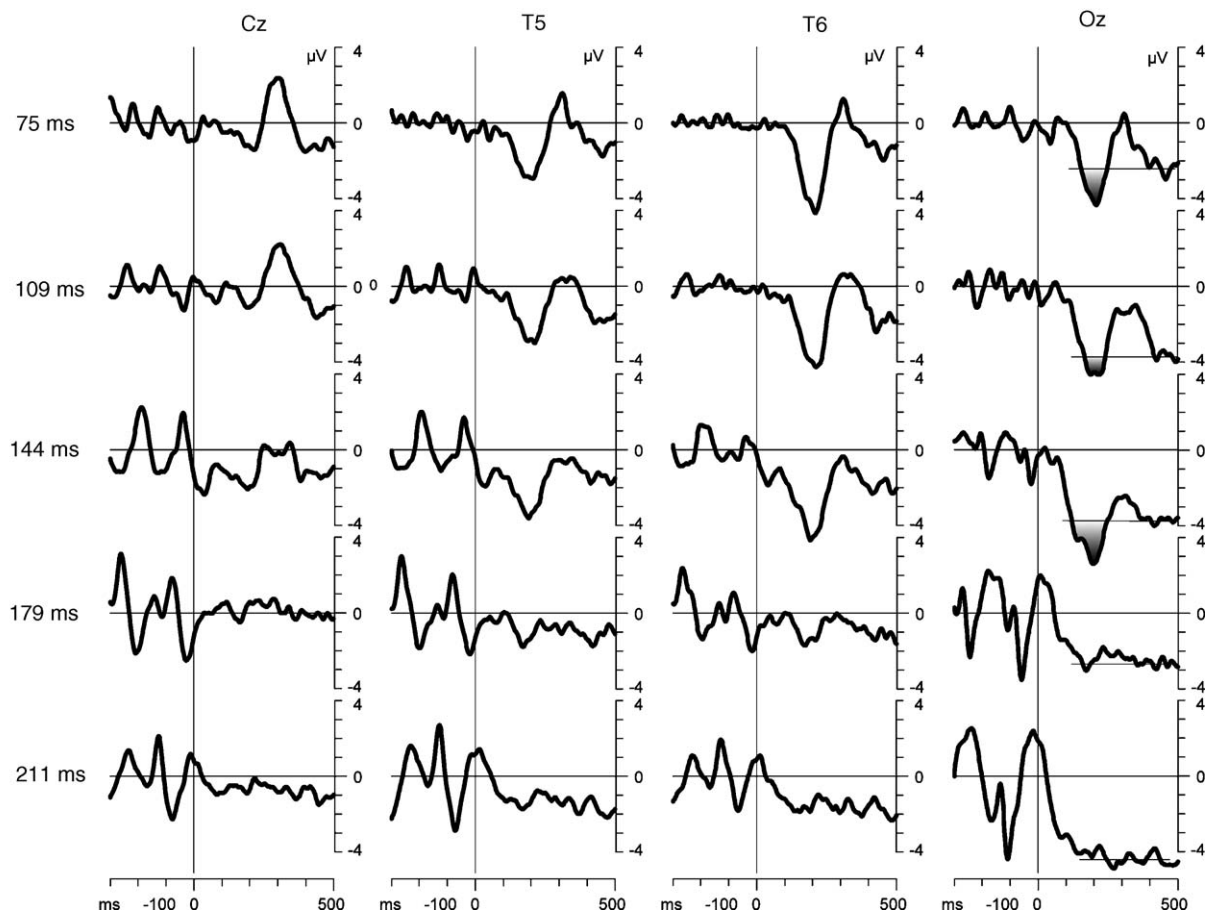

Fig. 3 – Experiment 2. Grand-averaged ERP responses elicited by the termination of short stimulus trains of variable duration as a function of the stimulus onset asynchrony. Timing is related to the moment of expected continuation of the train (0 ms). The mean voltage in the 100 ms period preceding the time of expected continuation was used as baseline in this figure. At the Oz location, the signal amplitudes have been referred the average voltage in the 400–500 ms period (the stable voltage level after the offset of the train), shown as short lines on the left (Oz) column.
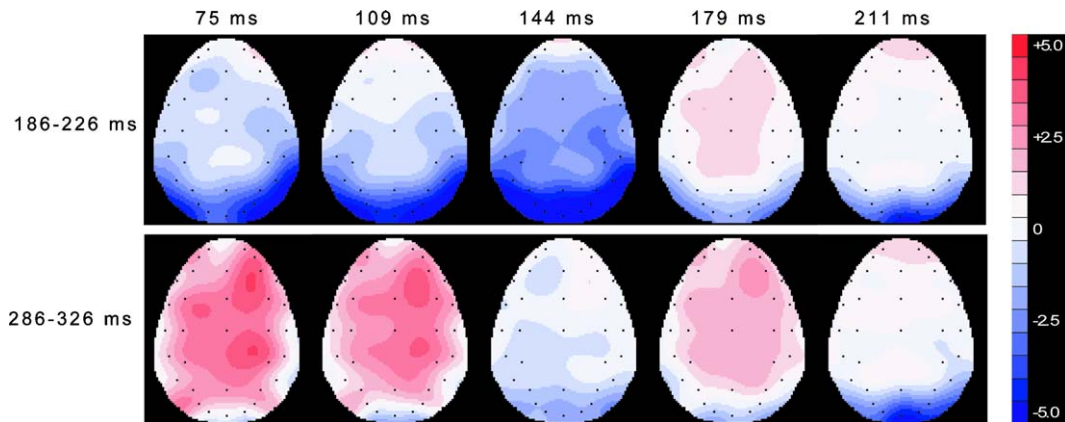
Fig. 4 – Experiment 2. Scalp distribution of the posterior negative (measured in the 188–226 ms interval) and anterior positive (286–326 ms) ERP responses elicited by the termination of short stimulus trains as a function of stimulus onset asynchrony.

shorter latency at Oz, the ANOVA with factors of SOA and Electrode-location (Fz, FCz, Cz, Pz, and Oz) showed only a significant effect of the SOA [$F(4,44) = 7.67$, $\varepsilon = 0.58$, $P < .01$].

3.2. Discussion

Termination of stimulus sequences elicited a posterior negative component in the 150–250 ms latency range (measured from the time of expected continuation) with the three shortest, but not with longer SOAs. Unlike in Experiment 1, in this experiment, the negativity cannot be attributed to the absence of the positive deflection of the steady-state response. In analogy to the very similar (modality-specific, confined to short SOAs) component found in Experiment 1, this component is probably a vMMN. Unexpected termination of short trains may violate some TWI-related regularity, such as the regular temporal structure of the temporal integration window, as was suggested by Yabe and his colleagues (Yabe et al., 1997, 1998, 2001). It should be noted that, in sequences with shorter SOAs, on the average, there were more stimuli within the sequences. However, even in case of the shortest sequence and the longest SOA, the number of stimuli far exceeded the number of stimuli necessary for the emergence of MMN (Cowan et al., 1993). Furthermore, in some control sessions, we obtained similar ERPs after runs of 6000 ms with 211-ms SOA and runs of 750 ms with 75-ms SOA than the results of Experiment 2.

In Experiment 2, we found no component similar to the anterior negativity observed in Experiment 1. The posterior negative component was followed by a positive component with a central scalp distribution. We identify this component as a P3a, which can be interpreted as an index of involuntary attention shifting triggered by the unexpected termination of the stimulus trains.

4. General discussion

The main finding of the present study was the elicitation of a posterior negative ERP component when unexpectedly a stimulus was not delivered in an otherwise isochronous repetitive stimulus sequence. In Experiment 1, stimulus omissions were randomly embedded in longer sequences of stimuli, whereas in Experiment 2, short trains were terminated unpredictably. The posterior negativity was only elicited at SOAs shorter than 179 ms in both experiments. This pattern of results closely matches the one obtained for omissions in the auditory modality, in which the omission-related response has been identified as MMN (Oceák et al., 2006; Yabe et al., 1997, 1998, 2001). Due to the similar dependence of the current negativity on SOA as that known for MMN and because of its posterior distribution, we identify the current posterior negativity as a visual analogue of MMN (termed vMMN), which is elicited when the brain detects deviations from a

Location	SOA (ms)				
	75	109	144	179	211
O1 [a]	−1.69 (0.66)	−1.11 (0.66)	−2.01 (0.45)	0.33 (0.87)	0.53 (0.70)
O2 [a]	−2.83 (0.77)	−1.87 (0.81)	−2.58 (0.62)	−0.21 (0.94)	0.16 (0.55)
T5 [b]	−2.37 (0.42)	−2.68 (0.74)	−3.54 (0.56)	−0.72 (0.80)	−0.38 (0.52)
T6 [b]	−4.22 (0.69)	−3.95 (1.02)	−4.52 (0.78)	−0.83 (0.97)	−0.96 (0.50)
Cz [b]	−0.81 (0.51)	−0.60 (0.85)	−2.04 (0.57)	1.06 (0.66)	0.16 (0.59)

Table 4 – Experiment 2: amplitude (in microvolts) of the posterior negative component (SEM in parenthesis)

[a] Referred to the average voltage in the 400–500 ms interval from the time of expected continuation.
[b] Referred to the average voltage in the 100-ms long interval preceding the time of expected continuation.

Table 5 – Experiment 2: latency (in ms) and amplitude (in microvolts) of the anterior positive component (SEM in parenthesis)

Location	SOA (ms)				
	75	109	144	179	211
Latency					
Fz	304 (8.0)	275 (15.8)	281 (15.5)	265 (13.3)	232 (19.7)
FCz	291 (6.9)	273 (15.6)	281 (15.0)	259 (12.8)	235 (18.7)
Cz	282 (13.3)	280 (14.9)	299 (15.3)	255 (12.5)	237 (21.2)
Pz	299 (4.5)	297 (15.4)	298 (14.4)	273 (15.0)	228 (26.9)
Oz	292 (11.9)	308 (12.4)	310 (7.3)	283 (10.4)	209 (12.3)
Amplitude					
Fz	1.92 (0.69	2.20 (0.58)	−0.46 (0.32)	1.09 (0.49)	0.09 (0.42)
FCz	2.67 (0.79)	2.71 (0.68)	−0.09 (0.43)	1.04 (0.64)	−0.04 (0.51)
Cz	2.61 (0.77)	2.47 (0.70)	−0.41 (0.43)	0.77 (0.63)	−0.12 (0.51)
Pz	2.32 (0.84)	1.71 (0.88)	−1.14 (0.59)	0.19 (0.73)	−1.09 (0.59)
Oz	0.31 (0.62)	−1.26 (0.83)	−2. 06 (0.78)	−1.49 (0.94)	−4.76 (0.70)

previously established regularity (Näätänen and Winkler, 1999; Winkler et al., 1996). Yabe and his colleagues (Yabe et al., 1997, 1998) suggested that the regularity violated by omissions when the SOA is shorter than the 170 ms is based on the temporal structure of sounds within the TWI. An analogous interpretation of the current results would suggest that, similarly to the auditory modality, visual stimuli are also processed in temporal windows of approximately 150–170 ms duration. The alternative interpretation of the auditory omission MMN suggests that subsequent stimuli arriving within the TWI period influence perceptual characteristics of the preceding events by terminating the analysis of the features of the first event (Oceák et al., 2006). In the current case, this would mean the termination of the visual persistence of a stimulus by the subsequent one, which would not occur when a stimulus is omitted or when a train of stimuli ends. However, a comparison with the known duration of visual persistence (e.g., Loftus and Irwin, 1998) points out that the longest SOA at which vMMN was elicited in the current study exceed by far the interval in which perceptual effects of visual integration were obtained (subjective rating as well as performance measures). On the other hand, previous research showed that the formation of short-term conceptual representations for complex scenes requires less than 200 ms (for a review, see Intraub, 1999) and that categorical identification is achieved within ca. 150 ms (VanRullen and Thorpe, 2001). According to these results, the visual system processes information with sufficient speed to create chunks of information with a duration comparable to the TWI in the auditory modality. What is then the functional significance of the SOA-related omission effect in the visual modality? Temporal chunks of ca. 150 ms duration may form an implicit memory system enabling a more elaborate processing of the incoming information (see e.g., Chun and Potter, 1995). If this was the case, then similarly to other instances of vMMN elicitation, violating regularities based on this assumed implicit memory system should also lead to the emergence of vMMN. The detection of such irregularities is a necessary but not sufficient condition for initiating the processes of orienting.

In both experiments, the negativities were followed by a positive component. We identified this component as P3a. This component often follows MMN (Näätänen and Winkler, 1999) and has also been seen in some vMMN studies (Czigler et al., 2002; Winkler et al., 2005). P3a is assumed to be a sign of orientation to deviants or other outstanding events, which occurs more often with large amounts of deviation (Escera et al., 1998; Friedman et al., 2001; Polich, 2003). In Experiment 1, we obtained a marked P3a latency change as a function of the SOA, whereas in Experiment 2, there was hardly any P3a latency change. One speculation about this difference is that, in Experiment 1, deviance was strongly connected with the presentation rate of the stimuli, whereas in Experiment 2, it was the termination of the sequence rather than a temporal violation that elicited the P3a. Whereas the memory-representation-based account of the auditory MMN has been substantiated by a large pool of evidence (for a recent review, see Näätänen et al., 2005), the similar interpretation of vMMN has been questioned (Kenemans et al., 2003). These authors argued for an explanation based on selective refractoriness suggesting that a deviant stimulus within sequences of identical standard stimuli activates a "fresh neural population", whose vigorous response would thus surpass the refracted responses elicited by the frequently presented standard stimuli. However, similarly to the auditory modality, a deviant-related negativity ('genuine MMN') (Jacobsen and Schröger, 2001; Schröger and Wolff, 1996) was elicited when the ERP response to the infrequent stimulus of an oddball sequence was compared with the ERP elicited by the same stimulus presented with identical probability within a sequence of several equiprobable stimuli (Czigler et al., 2002; Pazo-Alvarez et al., 2004b). Thus, the refractory state of the neuronal populations reacting specifically to the deviant stimulus cannot explain the vMMN response (just as it cannot explain the auditory MMN (Jacobsen and Schröger, 2001; Schröger and Wolff, 1996). In the auditory modality, one of the most important arguments against the refractoriness-based interpretation of MMN refers to omission results (Näätänen et al., 2005) because the MMN response to omission emerges without actual stimulation. In a similar vein, the current results make it difficult to maintain the selective refractoriness explanation of vMMN, whereas, as was described above, the memory-representation-based account of vMMN is compatible with the current results.

One may, however, also consider the posterior negativity found in the current study as a rebound phenomenon (release from an inhibitors state), which is caused by the over-stimulation of some neural population by the rapid repetition of the standard stimulus. The rebound explanation would suggest a gradual decrease of the intensity of the rebound as a function of SOA. However, the results of Experiment 2 showed that the amplitude of the posterior negativity was fairly stable within the 74–144-ms SOA range, then it suddenly disappeared with longer SOAs. In the auditory modality, the amplitude change of the omission-related MMN was found to be similarly steep at the border of the TWI (Poeppel, 2003). Thus, it appears that the current results argue for an explanation based on a time window of finite duration. Although the possibility of a rebound effect uniformly operating within but not at all outside the TWI cannot be ruled out, based on the similarities between the visual and auditory omission responses, it is more parsimonious to assume that the posterior negativity found in the current study is vMMN.

Posterior negativities are also elicited by attended (target) stimuli in visual search (e.g., Luck and Hillyard, 1994; Woodman and Luck, 2003) and matching tasks (Eimer and Mazza, 2005). The negativity of the present study could be related to such N2pc (or N2p) component or its magnetic counterpart (Hopf et al., 2002). However, this posterior negativity is considered to be the correlate of an attentional shift towards a new location and is present only for detected changes (Eimer and Mazza, 2005). Three results of the present study argue against identifying the omission-related negativity as an attention-related posterior negativity. First, the latency of the present omission-related negativity is shorter (150–200 ms) than that of the attention-related negativities. Second, we found that the amplitude of the posterior negativity was similar when stimulus omissions were relevant or irrelevant to the participants' task (Experiment 1). In contrast, task-demand has been shown to have no or only a slight influence on the auditory MNN elicited by task-irrelevant deviant sounds (e.g., Yucel et al., 2005, for a recent study of the effects of attention on MMN, see Sussman et al., 2003). Similarly, in the visual modality, the difficulty of a tracking task had no considerable effect on the vMMN elicited by stimuli of deviant spatial frequency (Heslenfeld, 16). Third, in the *Divided-attention* condition, detection performance was unrelated to the emergence of the posterior negativity, suggesting that the current posterior negativity is independent of the task-related attention.

Although the pattern of results regarding the posterior negativity was similar across our two experiments, there were also considerable differences between the results of these experiments. First, the posterior negativity peaked earlier in Experiment 1 than in Experiment 2. This may be explained by differences between the two experimental designs. In Experiment 1, the long stimulus sequences could have established much stronger representation of the regularities than the short trains of Experiment 2, thus making the detection of deviancy faster in Experiment 1, as is the case for larger deviations in the auditory modality (Schröger and Winkler, 1995). A further difference between the results of our two experiments is that, in Experiment 1, we recorded an anterior

negativity (identified as N2b), whereas this component was absent in Experiment 2. N2b has been suggested to be closely linked with orienting to outstanding stimuli (Näätänen and Picton, 1986). In line with the vMMN latency differences between the two experiments, we suggest that the more salient deviations of Experiment 1 evoked a stronger tendency to elicit orienting activity than the less salient deviations of Experiment 2.

In conclusion, the results of the present study support the notion of an automatic deviance detection process in vision as shown by the similar results obtained for task-relevant and -irrelevant changes. This process was reflected by a posterior negative component, the vMMN, which was sensitive to stimulus omissions only when the interval between successive standard stimuli was shorter than 180 ms. The latter result suggests that, similarly to audition, there is a stage of visual processing in which stimuli are analyzed within a temporal window of ca. 150–170 ms. Further processing of omission-related deviancy, however, appears to be dependent on the relationship between the "missing" stimulus and characteristics of the regular stimulation as well as on the relevance of omissions for ongoing voluntary behavior.

5. Experimental procedures

5.1. Experiment 1

The participants were ten paid students (2 women and 8 man, mean age = 21.4 years, SD = 2.32). They had normal or corrected to normal vision. Participants signed an informed consent before the experimental session.

The stimulus display consisted of a 14 × 17 matrix of hollow squares with one-pixel wide outlines against a dark gray background appearing on the lower half-field of a monitor with 1024 × 762 pixel resolution. Results of previous research (Czigler et al., 2004) suggested that the lower visual half-field stimulation is more appropriate for eliciting the vMMN than the upper half-field. The size of an individual square was 0.5° viewed from 100 cm. The whole pattern subtended 5.24° horizontally and 4.29° vertically. Stimulus duration was 17 ms, and the SOAs used in the different blocks were 75, 109, 144, 179 and 211 ms, with 370–400 stimuli presented in a stimulus block. 9–10% of the stimuli were randomly omitted with the restriction that omissions were preceded by at least 4 stimulus presentations. Each SOA was presented in two stimulus blocks, separately for each condition (altogether 70–80 omissions per condition per SOA). The order of the stimulus blocks with different SOAs was separately randomized for each participant.

The participants' task in the first part of Experiment 1 (*Detection condition*) was to detect changes of a white cross (target events), which was continuously present in the center of the display. The cross subtended 0.5° both horizontally and vertically. Participants were required to respond whenever the cross became thicker for 17 ms, changing from one to two pixels width. The timing of the targets was independent of the onsets of the square pattern stimuli. Five to ten target events occurred in each stimulus block. Participants were told that the role of the square pattern was "to help maintain alertness" for the primary task. Instructions emphasized both accuracy

and response speed. In the second part of Experiment 1 (*Divided-attention condition*), in addition to detecting change in the cross, participants were instructed to silently count the number of pattern omissions and to report the number at the end of each sequence.

EEG was recorded (DC-70 Hz, sampling rate 500 Hz, NuAmps amplifiers, NeuroScan EEG recording system) with Ag/AgCl electrodes placed on Fp1, Fp2, AF3, AF4, F3, F4, F7, F8, FT7, FC3, FCz, FC4, FT8, T3, C3, Cz, C4, T4, TP7, CP3, CP4, TP8, P3, Pz, P4, A1, T5, PO3, PO4, T6, A2, O1, Oz and O2 locations, using an elastic cap (EasyCap). The reference electrode was placed on the tip of the nose and the ground electrode on the forehead. The horizontal EOG was recorded with a bipolar configuration between electrodes positioned lateral to the outer canthi of the two eyes. The vertical EOG was recorded with a bipolar configuration between electrodes placed above and below the right eye.

EEG signals were filtered offline (0.1–30 Hz), and epochs of 900 ms duration, starting 100 ms before a stimulus omission, were extracted from the continuous traces. Epochs with an amplitude change exceeding 70 μV on any channels (except 100 μV change on the occipital channels) were rejected from further analysis. This way, less than 15% of the epochs were rejected. There was no difference in the number of rejected epochs between the conditions. Epochs following the delivery of a cross-change target were also rejected. Stimulus omissions elicited different ERP responses at posterior and anterior scalp locations. Therefore, these responses were separately analyzed. For posterior locations, we analyzed the maximal negativity between 100 and 200 ms after the omission onset. Epochs recorded from posterior scalp locations showed high-amplitude steady-state responses. Therefore, the posterior omission-related negativity was referred to the maximal negativity of the previous SOA period (see the level marked by arrows at Oz traces of Fig. 1), and its emergence was verified with Student's *t* tests comparing the difference between this baseline and the maximal post-omission negativity. Deviance-related ERP responses (such as MMN and vMMN) are delineated by comparing the response to the deviant with the response elicited by a control stimulus that shares as many features as possible with the deviant, but which is not deviant within its own sequential context. (In the simplest case, the standard stimulus can be used as a control—for a discussion of the correct control, see Jacobsen and Schröger, 2001.) Since omission means "no stimulus", therefore, if it elicits a response, this response is *per se* due to the context, not to the acoustic input. Therefore, the best control for omission responses is 0, which is also the procedure used in auditory omission studies (Yabe et al., 1997, 1998, 2001). This is because in the omission procedure the null hypothesis is lack of the difference from the baseline.

SOA effects on the posterior omission-related negativity were tested with three-way dependent-measures ANOVA (Task × SOA × Electrode-location [O1, Oz and O2]). Where appropriate, Greenhouse–Geisser correction was applied and ε values and corrected *P* values are given. ANOVA results were further specified by Tukey HSD post hoc tests. The anterior omission-related responses (a negative wave followed by a positive one) were analyzed at Cz. Unlike at posterior locations, the steady-state activity was of low amplitude at anterior locations. Therefore, in the analyses of anterior omission-related effects, amplitude measurements were referred to the average signal in the whole SOA period preceding the omission (pre-omission baseline). The amplitude of the anterior negativity was measured at Cz as the mean voltage in a ±12 ms interval centered at the largest negative peak of the group-averaged ERP response in the 200–380 ms interval. The amplitude of the anterior positivity was measured at Cz as the mean voltage in a ±12 ms interval centered at the largest positive peak of the group-averaged ERP response in the 280–480 ms interval. Condition and SOA effects were analyzed with two-way dependent-measures ANOVAs (Task × SOA).

5.2. Experiment 2

The participants were twelve paid students (6 women and 6 man, mean age = 21.9 years, SD = 2.31) selected from the same population as the participants of Experiment 1. None of them participated in Experiment 1.

The stimuli were identical to those of Experiment 1. Stimuli were presented in trains of 1400–2200 ms (homogenous distribution) followed by breaks of 660–1000 ms (homogeneous distribution). The within-train SOAs were 75, 109, 144, 179 and 211 ms (just as in Experiment 1). Each SOA received 100 trains, and the order of the trains of different SOAs was separately randomized for each participant. Participants performed the *Detection* task described for Experiment 1.

EEG recording, filtering and artifact rejection were identical to Experiment 1. Epochs of 800 ms duration starting 300 ms before the time point at which the "one-after-the-last" stimulus would have arrived (the time of expected continuation) were extracted for each train and averaged separately for the different SOAs. Occipital measurements were referred to the main voltage in the 400–500 ms from the time of expected continuation (marked by horizontal lines at right side of the Oz traces in Fig. 3) because this period appeared to show the stabilized signal amplitude after the offset of the train.

The amplitude of the posterior negative and the anterior positive response was measured as the mean voltage in 186–226 ms and 286–326 ms intervals from the time of expected continuation, respectively. Peak latencies were measured separately for each participant at the amplitude minimum/maximum, in the 150–250 ms and 250–350 ms latency ranges, respectively. Elicitation of the ERP responses was tested with Student's *t* tests against the voltage at the baseline (400–500 ms after the time of expected continuation for Oz) and the effects of SOA with 2-way dependent-measures ANOVAs (SOA × Electrode-location).

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