

Running head: Two Distinct Components in the Distractor Effect

Surprise, surprise: Two distinct components in the visually evoked
distractor effect

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Abstract

The distractor effect is an inhibition of saccades shortly after a sudden visual event. It has been explained both as an oculomotor reflex and as a manifestation of the orienting response. In order to clarify which explanation is more appropriate, we investigated a possible habituation of this effect. Visual and auditory distractors were presented at gaze-contingent intervals during the perception of meaningful pictures. Both reflex-like and modifiable components were present in the visual distractor effect, with latencies of about 110 and 180 ms, respectively. The influence of visual and auditory distractors on saccades preceded the earliest changes in cortical ERPs. Only for long-term habituation in the visual modality was a correlation with ERPs (N1) found.

Descriptor terms:

EEG/ERP, Eye Movements, Visual and Auditory Distractors, Habituation, Novelty, Amygdala

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Introduction

An increase in saccadic reaction time is found when a target stimulus appears together with a visual distractor (Walker, Kentridge, & Findlay, 1995). Since the first report by Ariane Lévy-Schoen (1969), a large body of research has studied the phenomenon, demonstrating a robust saccadic inhibition in various conditions. In most of these studies, saccadic reaction time was measured within a "fixate-and-jump" paradigm: subjects had to fixate a designated point on the screen and then to execute a single saccade to a target. The gaze-contingent paradigm (McConkie & Rayner 1975) allows configuring similar experiments in a more natural manner. This approach was used by Reingold and Stampe (2000), who recorded eye movements in reading and in a visual search task while display changes occurred at various intervals following the onset of a fixation. In contrast to unaffected fixations, the frequency distribution of saccadic latencies exhibited a clear dip with the maximum at approximately 90-110 ms after the display change. The effect demonstrates an under-representation of saccades initiated during this interval, which can also be interpreted as a prolongation of fixations. Because the effect has such a short latency, Reingold and Stampe (2000, 2002) argued for a reflex-like nature of its mechanisms and suggested a locus related to inhibitory processes in the superior colliculus (SC). These inhibitory processes have been extensively studied by Munoz and colleagues (Munoz, Dorris, Pare, & Everling, 2000; Munoz & Wurtz, 1993a, 1993b).

A further study by Reingold and Stampe (2004) found no saccadic inhibition for auditory distractors. The opposite result was reported for tasks involving free exploration of naturalistic pictures. Pannasch, Dornhoefer, Unema, and Velichkovsky (2001) found a prolongation of visual fixations also for auditory distractors. Similar effects were recently reported for somatosensory

distractors (Amlot, Walker, Driver, & Spence, 2003; Marx, Pieper, Pannasch, & Velichkovsky, 2005). Although there is some conflicting evidence, the bulk of results seem to support the notion of multimodality of the distractor effect. Inhibition effects on saccades following non-visual distractors are not necessarily in conflict with the original reference to the SC (Reingold & Stampe, 2000). In fact, studies of multisensory integration have demonstrated that the SC receives information from different modalities (Colonius & Diederich, 2004; Kadunce, Vaughan, Wallace, & Stein, 2001; Peck, 1996; Perrault, Vaughan, Stein, & Wallace, 2005; Wallace, Meredith, & Stein, 1998).

A different explanation has been proposed by Pannasch et al. (2001) who argued that the distractor effect could be interpreted within the framework of novelty-based reactions such as the orienting response (OR) (Sokolov, 1963). The OR describes the behavioral and physiological responses to unexpected changes in parameters of stimulation, such as a deceleration of heart and breathing rates as well as an increase of the skin conductance (e.g. Barry, 1977; Graham & Clifton, 1966; Siddle, Stephenson, & Spinks, 1983; Stekelenburg & van Boxtel, 2002). A repeated presentation of the same stimulus, in particular, produces a habituation effect, where the behavioral and physiological manifestations of the OR decrease with the number of repetitions. The main feature of the OR, that is habituation, suggests a new approach for analyzing the distractor effect: if the latter has something to do with OR, it should habituate or, at least, react differently to the novelty of distractors. Previous research has not investigated such habituation processes in the distractor effect.

Many studies of habituation have used cortical event-related-potentials (ERPs). For example, a decrease of such ERP components as N1 and P3 was found when presenting visual and auditory stimuli repeatedly (Bruin, Kenemans, Verbaten, & Van der Heijden, 2000);

Kenemans, Verbaten, Roelofs, & Slangen, 1989; Ritter, Vaughan, & Costa, 1968; Romero & Polich, 1996; Rust, 1977; Verbaten, Roelofs, Sjouw, & Slangen, 1986; Wastell & Kleinman, 1980). A number of evidence has been obtained for short-term decrement of N1 within a train of rapidly presented stimuli (Budd, Barry, Gordon, Rennie, & Michie, 1998). Although such a decrease of N1 with stimulus repetition was often found, it has not been ascertained whether this reflects a unique habituation or a refractory process.

Recognizing this problem, Thompson and Spencer (1966) proposed stringent criteria for determining whether some decrement in response can be referred to as habituation or is best explained by other processes such as diminished arousal, sensory adaptation, receptor fatigue or changes in refractoriness. These discrimination criteria entail that, firstly, an increase of the behavioral correlates of the OR should occur in response to a changed stimulus after the repeated presentation of the original stimulus (response recovery) and that, secondly, the OR to the previously habituated stimulus should recover after a stimulus change (dishabituation). In the literature there is only little evidence for dishabituation (cf. Loveless, 1983) and results mostly concern response recovery (Barry, Cocker, Anderson, Gordon, & Rennie, 1992; Budd et al., 1998; Ritter et al., 1968; Woods & Elmasian, 1986).

Fewer studies have investigated long-term decrement of ERP components by comparing a number of accumulated responses to repeated stimuli. A decrease of N1 for auditory as well as for visual stimuli was reported in several studies (Kenemans et al., 1989; Laurian & Gaillard, 1976; Näätänen & Picton, 1987; Sambeth, Maes, Quian Quiroga, Van Rijn, & Coenen, 2004; Woods & Elmasian, 1986). As N1 amplitude is said to be related to general arousal, it is important to note that this decrease has been found to be independent of any decrement in arousal due to increasing fatigue from a monotonous task (Näätänen & Picton, 1987).

Concluding from this review, possible short- and long-term decrements in the distractor effect should be investigated to examine the novelty-based explanation. This required that similar distractors were repeatedly presented over longer periods of time. The insertion of a novel distractor stimulus within a series of equal distractors has, in addition, allowed the analysis of both response recovery and dishabituation effects. Furthermore, to elucidate the relationship between the distractor effect and the cortical components of the OR, we also decided to collect EEG data. On the one hand, this aided validation of the experimental manipulation: the distractor-related delay in saccade latencies could be analyzed with regard to the known indices of habituation from the ERP literature. On the other hand, this shed light on the relationship between event-related changes in eye-movements and in electrophysiological responses. Although eye tracking and EEG are commonly used, combining the two, so that stimuli are displayed temporally and spatially in a gaze-contingent way, has rarely been employed (Baccino & Manunta, 2005; Marx, Pannasch, & Velichkovsky, 2003). Through this form of eye-movement control, we expected to improve ERPs' signal quality and to open the way for their investigation in continuous visual behavior.

The general objective of this study was to improve our understanding of the mechanisms of the distractor effect. If this effect habituates it could be related to the broader class of novelty-based reactions of organism such as startle, surprise and orienting responses. Though these reactions have been intensively studied in different areas of psychophysiology, they have seldom been related to each other and, until now, have not been compared to the distractor influences on eye movements. The possible mechanisms of various novelty-based responses can be localized well beyond the SC extending from the amygdala (Holland & Gallagher, 2006; Panksepp, 1998, 2000) and the hippocampus (Habib, McIntosh, Wheeler, & Tulving, 2003) to the structures of

the temporal-parietal junction, right prefrontal and anterior cingulate cortex (Corbetta & Shulman, 2002; Dien, Spencer, & Donchin, 2003).

Method

Subjects

46 healthy volunteers (11 male and 35 female) with normal or corrected to normal vision participated in the experiment. Subjects ages ranged from 17 to 42 years ($M = 23.4$, $SD = 6.1$). All volunteers were naive with respect to the experimental task as well as to the purposes of the study. Informed consent was obtained according to local ethical guidelines. One half of the subjects were paid for their participation, the other half were undergraduate students (psychology) and received course credits.

Apparatus and Stimuli

Subjects were seated in a dimly-illuminated, sound attenuated room. Images were displayed using a 19-inch monitor with a screen resolution of 1152 by 864 pixels and a refresh rate of 100 Hz. Viewed from a distance of 80 cm, the screen subtended an angle of approximately 26° horizontally and 18° vertically. Auditory stimuli were produced by a standard PC-soundcard and presented binaurally via insert earphones (Eartone™ 3A).

Eye movements were recorded at 250 Hz using an SR Research Ltd. EyeLink I eye tracker. A 9-point calibration routine was executed and repeated if the error in any fixation point exceeded 1° or if the average error for all points was above 0.5° . Saccades and fixations were defined using the saccade detection algorithm. Saccades were identified by deflections in eye position in excess of 0.1° , with a minimum velocity of 30°s^{-1} and a minimum acceleration of 8000°s^{-2} , maintained for at least 8 ms. Fixations were defined by the absence of a saccade.

Electroencephalographic (EEG) activity was recorded with a SynAmps Amplifier (Model 5083, Neuroscan Inc. El Paso, Texas, USA). Ag/AgCl sintered electrodes were placed in an elasticated 10/20 EEG-cap system (Easycap, Falk Minow Services, Munich, Germany). Data were acquired from Fp1, Fp2, F7, F3, F8, F4, T7, Cz, T8, P7, P3, Pz, P4, P8, O1, O2 (Electrode Position Nomenclature of the American Electroencephalographic Society) electrode sites and Electrooculographic (EOG) data were recorded supra- and infra-orbitally (vertical EOG) and from the left versus right orbital rim (horizontal EOG). Linked earlobes served as reference and an electrode at AFz was used as ground. Impedances were kept at 5 k Ω or below. EEG was recorded continuously, sampled at a rate of 1000 Hz and filtered by the amplifier using a band-pass 0.3-70 Hz.

Stimulus material for the picture viewing task consisted of 80 digitized copies of paintings by different 18th century artists illustrating scenes of daily routines with one or more people. The images were displayed in monochrome colors. Visual standard distractor stimuli were light blue circles (2.7° in diameter, 0.3° margin width) and deviant distractor stimuli were violet squares (2.7° edge length and 0.3° margin width) displayed with horizontal aligned edges or rotated by 45° as a diamond. Visual distractors were displayed for 75 ms. An example of an image with a standard visual distractor is presented in Figure 1.

< insert Figure 1 about here >

Auditory standard distractor stimuli were pure sinusoidal 1500 Hz tones and auditory deviants were pure triangle shaped tones of 1400 or 1600 Hz. All tones had duration of 75 ms including 5 ms rise and fall time and were presented at a sound pressure level of 70 dB. In the experimental procedure both visual and auditory standard and deviant distractors appeared while the pictures were shown. Three different presentation modes were applied: (i) in *standard and*

deviant distractor pictures, 1 deviant and 16 standard distractors appeared (henceforth SDD pictures), (ii) in *standard distractor pictures*, 17 standard distractors appeared (henceforth SD pictures), and (iii) in *no distractor pictures*, no distractors were presented (henceforth ND pictures).

Procedure

Eye movements and EEG were recorded throughout the experiment. Participants were required to perform a free viewing picture task and were aware of the distractor presentations, but instructed to ignore them. They were asked to study the images in order to answer five questions regarding scene content which were shown after the picture offset (e.g. “Is there a fence in the background?” is an example for Figure 1). Subjects had to complete a short questionnaire before, in between and after the experiment to assess motivation, relaxation, concentration and tiredness on a five point scale.

The experimental session was run in two consecutive blocks, one containing 40 pictures with visual distractors only, and the other containing the remaining 40 pictures with auditory distractors with a ten minute break in between. Order of blocks was counterbalanced across subjects. In total, the experimental session took 90 min to complete.

Within a block, the different presentation modes were randomly assigned according to the following proportions: 30 SDD pictures, 5 SD pictures and 5 ND pictures. The SDD and SD pictures were presented to test the effects of short and long term habituation. SDD pictures were additionally used to analyze response recovery and dishabituation. This was achieved by assigning the deviant distractor randomly to position 8-12 of the distractor sequence. SD pictures were presented to reduce the predictability of deviant distractors. During ND pictures, no

distractors were shown, but the same distractor-presentation algorithm was used in order to allow the generation of a fixation-locked baseline for the ERP data.

Picture presentation began with an initial 5 s period without distractors, followed by the relevant experimental presentation. After an intervening delay of two seconds, questions regarding the picture content were shown. Within the experimental period distractor stimuli were presented at every 5th fixation using the gaze contingent paradigm (McConkie & Rayner, 1975). Distractors were triggered by the fixation onset and appeared with a stimulus onset asynchrony (SOA) of 100 ms. Visual distractors appeared on screen at the spatial location of the selected fixation; auditory distractors were presented without any spatial orientation. If fixations were terminated before reaching the SOA the program waited for the next suitable fixation resulting in more than five fixations between the distractors. The length of the experimental period varied due to different fixation durations. In average, the presentation of an image lasted for about 34 seconds.

Data analysis

SPSS 12.0 software package was used for data analyses. EEG data preparation was performed with BrainVision Analyzer software. For the auditory modality, data of two subjects were rejected due to technical problems with the recording device. Furthermore, data of other three subjects did not meet the quantitative requirements for ERP analysis and were also removed from further processing.

The general analysis was similar for eye movements and ERPs. Distractors of 10 consecutive pictures were subsumed into four groups to evaluate long-term habituation effects. The number of SD and SDD pictures per group varied due to the randomized presentation order of the ND pictures. Results referring to these analyses are termed *slow habituation*. Processes of

short-term habituation were investigated by analyzing only the first seven distractors within each picture: later distractors were omitted due to the possible appearance of the deviant distractor. Henceforth, results referring to these analyses are termed *fast habituation*. In addition, response recovery and dishabituation were evaluated by comparing the effect of a *deviant distractor* to its preceding and following distractors.

All fixations preceded by a blink, outside the screen area or with durations less than 100 ms were excluded from further analysis. Experimentally manipulated fixations were removed if the distractor presentation exceeded the $SOA \pm 10$ ms. Due to the right-skewed distribution of fixation durations, all analyses were performed using the median score for each subject and condition.

Only valid data remaining after the eye movement filtering procedure were used for EEG analysis. Segmenting of data was done off-line: an epoch was defined as starting at 500 ms before the onset of a distractor fixation and lasting 1500 ms. A manual inspection was then carried out to remove segments containing strong muscle activity, blinks or other artifacts. EEG data was subsequently treated in the following order: digital band pass filtering (1-40 Hz, zero-phase-shift) before segmentation and ocular correction (Gratton, Coles, & Donchin, 1983), local DC trend correction and baseline correction after segmentation. EEG segments were then averaged to obtain fixation-contingent ERPs which corresponded to condition-specific distractor fixations. For further analysis subjects' data had to consist of 60 uncontaminated segments for slow habituation and of 20 segments for fast habituation as well as for deviant distractor. In order to analyze the significance of the ERP changes, we firstly applied the randomization technique for testing waveform difference potentials suggested by Blair and Karniski (1993). With this procedure we identified and selected the interval of earliest significant difference throughout all

electrode locations. In the next step, mean values of ERP activity within these intervals were calculated and used for statistical testing.

One-way repeated measures ANOVAs were performed separately for both modalities and all analyses, and Bonferroni-corrected t-tests for paired samples were calculated to specify the temporal loci of the effect.

Results

Responses to the questionnaire were pooled into one measure, in order to estimate subjects' fatigue. The analysis revealed a significant increase of fatigue over time, $F(2, 90) = 54.4, p < .001, \eta^2 = .55$. Post hoc comparisons indicated a steady increase of fatigue from the beginning to the break and from the break to the end of the session. The change in fatigue was used as covariate in the statistical analysis of slow habituation.

Eye Movement Data

The general influence of the distractor presentation on fixation duration was first analyzed. Table 1 provides mean values and standard deviations of fixation durations for the fixation affected by the distractor and the two preceding and following fixations of both modalities. The presentation of visual distractors resulted in a prolongation of fixations of about 70 ms whereas a smaller increase of about 7 ms was found for auditory distractors. The appearance of distractors led to significant effects in both modalities: visual, $F(4, 180) = 531, p < .001, \eta^2 = .92$, and auditory, $F(4, 172) = 13.2, p < .001, \eta^2 = .24$.

< insert Table 1 about here >

In order to investigate habituation effects, we subtracted the fixation duration of the baseline condition from that of the distractor condition. The baseline value was defined as the median score of the two fixations preceding and following the distractor. Since variability within

the baseline counteracted the use of difference values, baseline variation was always analyzed before statistical testing. Results for slow habituation are shown in Figure 2A. A decrease in the difference values for the fixation duration was found for visual distractors, $F(3, 132) = 14.4$, $p < .001$, $\eta^2 = .25$ but not for auditory distractors, $F \leq 1$. For the visual condition, post hoc comparisons indicated a significant decrease from group 1 to groups 3 and 4. No interaction with fatigue as a covariate, $F \leq 1$, was obtained.

< insert Figure 2 about here >

Fast habituation was analyzed by examining fixations influenced by the first seven distractors within pictures. A variation was found within the baseline of the visual modality, $F(6, 270) = 2.23$, $p < .05$, $\eta^2 = .05$, but could not be confirmed by post hoc comparisons. Figure 2B illustrates the results for fast habituation. For both modalities a clear decrease from distractor 1 to distractor 2 and a stabilization for the following distractors were observed. Statistical testing revealed significant effects for visual, $F(6, 270) = 8.01$, $p < .001$, $\eta^2 = .15$, and auditory distractors, $F(6, 258) = 2.87$, $p < .05$, $\eta^2 = .06$. As expected, post hoc comparisons yielded significance only for distractor 1. An increase in fixation duration following the presentation of the deviant distractor was found compared to the two preceding and following distractors (see Figure 2C). This was obtained for both modalities: visual (17 ms) $F(4, 180) = 3.29$, $p < .05$, $\eta^2 = .07$ and auditory (33 ms) $F(4, 172) = 11.3$, $p < .001$, $\eta^2 = .21$. Post hoc testing revealed significance only for the deviant distractor, which supports the hypothesis of response recovery and not that of a dishabituation in the strict sense.

An illustration of the distractor effect can be provided by the frequency distributions of saccadic latency depicting the proportion of terminated fixations within certain intervals. As can be seen in Figure 3, at the beginning (0-70 ms) the distributions are identical to the baseline. The

next segment of the distribution is different for each modality and is characterized by a clear dip, in particular for fixations affected by visual distractors (left panels in Figure 3). The distributions look very similar for all conditions until the maximum of the dip is reached (70-110 ms). In the following interval (110 up to ~220 ms), the chronological order of the distractor presentation seems to become important. The influence of auditory distractors is different: for all conditions it was weaker and generally faster than in the visual modality (right panels in Figure 3).

< insert Figure 3 about here >

To estimate any influence of the chronological order of distractor presentation on the shapes of the distributions, we analyzed intervals before and after the dip. For these exploratory analyses, we calculated the proportion of fixations terminated within 68-116 ms (before) and 117-212 ms (after). Due to the fact that such a clear dip could not be found for the auditory modality, statistical analyses were applied only to the visual distractor condition.

For slow habituation, our analysis revealed no effect in the interval before the maximum dip, $F \leq 1$, and a significant increase in frequency values after the dip, $F(3, 132) = 14.6, p < .001, \eta^2 = .25$. However, only the increase between picture groups 1 and 2 reached significance in post hoc testing. The interaction with fatigue as covariate was in both cases not significant, $F \leq 1$. For fast habituation and for the deviant distractor, non significant results were again found before the dip, $F < 1$. Fast habituation after the dip revealed significance, $F(6, 270) = 22.0, p < .001, \eta^2 = .33$, based solely on the increase from distractor 1 to distractor 2. Presentation of the deviant distractor led to a significant decrease of frequency values after the dip, $F(4, 180) = 7.39, p < .001, \eta^2 = .14$. Post hoc testing indicated significance only for the deviant distractor.

ERP Data

The ERPs for all electrode locations are presented in Figures 4 and 5 for visual and for auditory distractors respectively. ERPs are plotted with reference to the onset of a distractor. Conditions are depicted columnwise: slow habituation on the left, fast habituation in the middle and deviant distractor on the right. Our ERP data show features reflecting typical and specific characteristics of fixation related potentials. Firstly, there is a peak at the fixation onset (-100 ms) indicating the offset of the previous saccade (e.g. Kazai & Yagi, 2003). Secondly, there is a large positive peak over occipital sites about 90 ms after the fixation onset, which was suggested to be a correlate of the occurrence of eye movements in the visual cortex (the so-called lambda response, see Skrandies & Laschke, 1997). Following the time course of the ERPs N1 and P2 components were found for all conditions. Furthermore, a N2 component and a late P3 component were found mainly for the deviant distractor condition. A late negativity is also visible at about 400 ms for the auditory modality in the deviant distractor and the fast habituation condition. The maximum amplitude of this component is at vertex, resembling the so-called reorienting negativity (Schröger & Wolff, 1998).

< insert Figure 4 about here >

< insert Figure 5 about here >

In order to analyze slow habituation, components of the ERPs in picture groups 1 and 2 were compared using a method described by Blair and Karniski (1993). Only the earliest significant differences identified at each electrode are discussed here due to their importance with respect to our analysis of the inhibition of saccades. The earliest indications of the ERPs difference between picture groups 1 and 2 were found at Cz within 140-175 ms following the onset of visual distractors and within 94-150 ms following the onset of auditory distractors

(Figure 6A top and middle panel). Mean ERP activity values for the designated intervals were entered in the statistical analysis and yielded a significant decrease of the N1 component for visual, $F(3, 126) = 13.3, p < .001, \eta^2 = .24$, and auditory distractors, $F(3, 120) = 39.9, p < .001, \eta^2 = .50$ (Figure 6A bottom panel). Interactions with fatigue were non significant, $F \leq 1$. Post hoc comparisons revealed significant differences for visual distractors between picture groups 1 and 2 and for auditory distractors between groups 1, 2 and 3.

< insert Figure 6 about here >

For fast habituation, we compared the ERPs of distractors 1 and 2 within pictures. The earliest indications of significant differences were found at P8 within 199-265 ms following the onset of visual distractors and at Cz within 105-154 ms following the onset of auditory distractors (Figure 6B top and middle panel). In both cases a decrease in negativity was found from distractor 1 to distractor 2. Mean ERP values for these intervals were entered in the statistical analysis and yielded a significant decrease for visual, $F(6, 252) = 18.8, p < .001, \eta^2 = .31$, and auditory distractors, $F(6, 240) = 44.3, p < .001, \eta^2 = .53$ (Figure 6B bottom panel). Post hoc testing revealed significant differences for distractor 1 only, in both modalities.

The ERPs for the deviant distractor were compared to the ERPs of the preceding distractor. The earliest significant differences were found at O2 within 172-231 ms following the onset of visual distractors and at Cz within 89-140 ms following the onset of auditory distractors (Figure 6C top and middle panel). In both cases negativity increased from the preceding to the deviant distractor. Mean ERP activity values for the designated intervals were entered in the statistical analysis and yielded a significant increase for visual, $F(4, 168) = 15.8, p < .001, \eta^2 = .26$, and auditory deviant distractors, $F(4, 160) = 24.37, p < .001, \eta^2 = .36$ (Figure 6C

bottom panel). Post hoc testing revealed significant differences for the deviant distractor only, in both modalities.

To examine the relationship between distractor influences on eye movements and ERPs, we performed a correlation analysis. This analysis was based on difference values between picture groups 1 and 2 for slow habituation, distractor 1 and 2 for fast habituation and deviant and preceding distractors for the deviant distractor condition. Differences in ERP activity were calculated for the same electrode location and intervals that had been used for the statistical analysis of mean ERP activity (see above). For the eye movement data relating to visual distractors, we used the same indices which were employed in the analysis of the shapes of the frequency distribution after the dip. For the auditory modality, frequency values for an interval with similar length but an earlier onset (69-164 ms) were used to assess the difference values. The subsequent analyses revealed a significant correlation, $r = .338, p < .05$, for slow habituation in the visual modality only. Larger ERP differences were related to larger differences in the probability of terminated fixations, i.e. a decrease in negativity for the N1 component was related to a decrease in visual distractor effect.

Discussion

The present study confirmed previous findings concerning the distractor effect (cf. Pannasch et al., 2001) and revealed new facts on a sensitivity of the distractor effect to the novelty of stimulation. With reference to the main task of this study, that is the analysis of a possible habituation of the distractor effect, significant results were obtained along three lines: (i) long-term habituation over groups of pictures, (ii) short-term habituation within single picture (iii) response recovery and dishabituation in response to a deviant distractor. An explanation in terms of fatigue, vigilance or arousal can be rejected because no interaction with data on fixation

duration and on ERPs was demonstrated when fatigue was used as a covariate (Näätänen & Picton, 1987; Parasuraman, Warm, & See, 2000). With respect to the multimodality of this effect, the acoustic distractor effect was less pronounced than the visual one and had a number of qualitative differences, which will be commented on later.

The assumption of long-term habituation was confirmed for the visual modality only: the influence of visual distractors on eye movements decreased over the first three groups of pictures. The absence of a similar adaptation to auditory distractors may be due to their generally smaller effect. There was clear evidence of a slow habituation effect in N1 of the ERP data for both modalities. This latter finding is in line with several reports (Laurian & Gaillard, 1976; Näätänen & Picton, 1987; Sambeth et al., 2004; Woods & Elmasian, 1986) promoting the idea that the long-term decrease of N1 reflects a genuine habituation process. Since it evolves in a similar way for the ERPs of both modalities over the same electrode sites, it could even reflect a modality-independent process (Lehtonen 1973, Näätänen & Picton, 1987).

Concerning short-term habituation effects, our analysis of eye movements demonstrated a decrease of distractor effect for both modalities, with a drop from the first to the second distractor within a picture. The ERP data also revealed a short-term habituation for both modalities. As in the case of fixation durations, the decrement showed a rapid drop from the first to the second distractor and a stabilized effect afterwards. The ERP changes for auditory and visual distractors are consistent with many other studies of short-term habituation (Bruin et al., 2000; Kenemans et al., 1989; Näätänen & Picton, 1987; Ritter et al., 1968; Romero & Polich, 1996; Rust, 1977; Verbaten et al., 1986; Wastell & Kleinman, 1980). The decrease of the N1 component for visual distractors was slightly delayed, which made an interpretation in terms of mismatch negativity plausible (Pazo-Alvarez, Cadaveira, & Amenedo, 2003).

Our assumption about the efficiency of a deviant distractor has also been confirmed with the response recovery in eye movements for both modalities. Furthermore, comparable changes were found in ERP data. The introduction of a deviant was in part motivated by the proposed differentiation between a response recovery and dishabituation (Thompson & Spencer, 1966). Neither fixation durations nor ERP data showed any indication of dishabituation in the strict sense. This result is consistent with a number of previous studies which showed evidence for response recovery only (Barry et al., 1992; Ritter et al., 1968; Woods & Elmasian, 1986). The recovery is however undisputed suggesting that the short-term decrease of distractor effects in our study is a genuine habituation rather than a process like refractoriness. In a preliminary way, the short term habituation and response recovery could also be considered in terms of a fast reaction to novelty, as will be discussed in the following.

The present study aimed at disentangling two explanations of the distractor effect: as a low level (SC, see Reingold & Stampe, 2000) oculomotor reflex and as an early component of the OR (Pannasch et al., 2001). A closer inspection of data reveals that both explanations can be correct. To demonstrate this, we rephrased data from Figure 3 (left) in a slightly idealized form. Figure 7 illustrates distributions of fixation durations for visual distractors as it can be inferred from the present results. The distributions reveal two deviations: the first one, with latency of about 110 ms, is similar to one reported in previous studies (Pannasch et al., 2001; Reingold & Stampe, 1999). It is labeled “first inhibition”. The second deviation, which occurs ~180 ms after the distractor onset, is described here as “second inhibition”. Only this latter inhibition demonstrated habituation effects in the present study. An inhibition similar to this second dip in the visually-evoked distractor effect was also observed for auditory distractors. However, it

occurred ~70 ms earlier and was modifiable for the two short-term conditions only, i.e. for the fast habituation and for the deviant distractor.

< insert Figure 7 about here >

In order to explain this pattern of results, it is necessary to discuss the relationship between the habituations in ERPs and in eye movements. We found that both parameters correlated in the case of long-term habituation of visual distractors. This long-term habituation to visual distractors was also the only condition where the decrease of N1 occurred within the temporal range of the second wave of inhibition, in terms of Figure 7. In all other cases, changes in eye movements preceded even such early cortical indices of distractor processing as N1. It means that a pathway, independent of the cortical processing and fast enough to precede it, may mediate short-term habituation.

Research in recent years has brought up the notion of a subcortical pathway (Dolan, 2003; Doron & Ledoux, 1999; Linke, De Lima, Schwegler, & Pape, 1999; Öhman, 2002; Pessoa, 2005; Vuilleumier, Armony, Driver, & Dolan, 2003), which promotes a fast processing of visual information on the basis of low spatial frequencies. The amygdala, as the terminal structure on this route, is particularly involved in the evaluation of fearful and threatening stimuli and in the preparation of related behavioral responses like freezing or escape (Panksepp, 1998). A similar pathway for auditory information has also been postulated (Campeau & Davis, 1995; Doron & Ledoux, 1999). In the present context, the auditory distractor effect can be considered as a manifestation of only the second wave of inhibition, mediated by the amygdala and temporally shifted to the interval where the first wave of inhibition is observed in the case of visual distractors. It is generally known that auditory information is processed faster than visual, which is also seen in our ERP data. An additional advantage may arise from the fact that structures for

auditory processing are anatomically close to the amygdala. An analysis of the time course of the distractor effect for other modalities, e.g. elicited by tactile stimulation, could shed light on this issue.

The present notion implicates the construction of a stimulus model to which following stimuli can be compared. Such a comparator function is essential in the concept of OR and is also necessary to explain a differing response to the following stimuli. Although many aspects of the fast distractors' processing are still unknown, we hope that our results provide an approach for its experimental investigation, for instance, with respect to the role of amygdala in surprise-induced effects on learning (Holland & Gallagher, 2006). It is of particular interest that in a previous study of hazard-related changes in fixation durations (Velichkovsky, Rothert, Kopf, Dornhoefer, & Joos, 2002), no habituation in fixation-freezing reaction was found despite the numerous repetitions of dangerous stimuli across five weeks of the experiment.

In summary, the current study found a variety of habituation-like processes in eye movements as well as in the N1 component of the cortical ERPs. The habituation found in eye movements can be attributed to an inhibitory process, which is temporally (latency of ca. 180 ms) and functionally dissociable from the first reflex-like wave of inhibition (with the maximum at 110 ms after distractor). The existence of two distinct components in the distractor effect has not been reported before. Conflicting explanations of the distractor effect, either as a midbrain-level oculomotor reflex (Reingold & Stampe, 2000; 2004) or as a manifestation of the OR (Pannasch et al., 2001) can be specifically related to only one of these components. Despite this new understanding, the origins of the habituation in delaying saccadic eye movements remain somewhat unclear. We assume that especially short-term habituation can be related to information processing within a fast subcortical pathway and may also involve limbic structures,

first of all, the amygdala. There is a growing acceptance in the literature that such stimulus qualities as change and novelty trigger activation of more or less the whole brain. With the two distinct components of the visual distractor effect, we may be at the very roots of this important biological mechanism.

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Table 1.

Mean durations and standard deviations (in ms) of fixations around the distractor appearance for both modalities (0 = distractor influenced fixation).

Distractor Modality	Fixation Relative to Distractor				
	-2	-1	0	1	2
Visual	258.9 (30.4)	261.0 (29.8)	334.3 (31.6)	263.9 (29.8)	259.6 (29.4)
Auditory	259.4 (27.7)	260.3 (31.1)	267.1 (26.9)	257.8 (30.9)	258.8 (30.0)

Figure Captions

Figure 1. Example of an image for the free viewing picture task with a visual standard distractor.

Figure 2. Difference values of fixation duration for slow (A) and fast (B) habituation and the deviant distractor (C) for both modalities.

Figure 3. Frequency distributions of fixation duration after distractor onset for visual and auditory distractors for slow habituation, fast habituation and the deviant distractor condition (bin size = 12 ms).

Figure 4. Grand mean ERPs (N=43) of visual distractors for slow (left) and fast habituation (middle) and the deviant distractor (right). The distractor onset was at 0 ms and the start of fixation at -100 ms.

Figure 5. Grand mean ERPs (N=41) of auditory distractors for slow (left) and fast habituation (middle) and the deviant distractor (right). The distractor onset was at 0 ms and the start of fixation at -100 ms.

Figure 6. Grand mean ERPs of the electrode site with the earliest significant effects of slow habituation (A), fast habituation (B) and deviant distractor (C), presented separately for visual (top panel) and auditory (middle panel) modalities. The intervals of the significant difference are given in grey. The bottom panels plot mean ERP activity of both modalities for the observed interval.

Figure 7. A simplified model of inhibitory processes as the basis for the visual distractor effect. While the first inhibition is independent from the distractor novelty, the second inhibitory process varies with the repetition of a distractor, being most pronounced for the first distractor in a sequence.













