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Saccadic context indicates information processing within visual fixations: Evidence from event-related potentials and eye-movements analysis of the distractor effect

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ABSTRACT

Attention, visual information processing, and oculomotor control are integrated functions of closely related brain mechanisms. Recently, it was shown that the processing of visual distractors appearing during a fixation is modulated by the amplitude of its preceding saccade (Pannasch & Velichkovsky, 2009). So far, this was demonstrated only at the behavioral level in terms of saccadic inhibition. The present study investigated distractor-related brain activity with cortical eye fixation-related potentials (EFRPs). Moreover, the following saccade was included as an additional classification criterion. Eye movements and EFRPs were recorded during free visual exploration of paintings. During some of the fixations, a visual distractor was shown as an annulus around the fixation position, 100 ms after the fixation onset. The saccadic context of a fixation was classified by its preceding and following saccade amplitudes with the cut-off criterion set to 4° of visual angle. The prolongation of fixation duration induced by distractors was largest for fixations preceded and followed by short saccades. EFRP data revealed a difference in distractor-related P2 amplitude between the saccadic context conditions, following the same trend as in eye movements. Furthermore, influences of the following saccade amplitude on the latency of the saccadic inhibition and on the N1 amplitude were found. The EFRP results cannot be explained by the influence of saccades *per se* since this bias was removed by subtracting the baseline from the distractor EFRP. Rather, the data suggest that saccadic context indicates differences in how information is processed within single visual fixations.

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1. Introduction

In everyday visual tasks such as reading, search or scene viewing, the oculomotor activity can be described as an interplay between saccades and fixations. Saccades—fast ballistic movements—are executed about three times per second and bring the gaze from one point to another. Visual information uptake and processing are largely suppressed during saccades (Bridgeman et al., 1994; Matin, 1974; Vallines and Greenlee, 2006) and only take place during fixations, i.e., in the period when the eye remains relatively stable. Both the duration of fixations and the amplitude of saccades vary considerably in continuous visual activities. Several factors contributing to this variation have been discovered so far; for instance, the optical quality of an image (van Diepen et al., 1995, 1998), the meaning of a scene (de Graef et al., 1990; Loftus and Mackworth, 1978), but also attention and the task context (Brockmole and Henderson, 2006; Velichkovsky et al., 1997). It has been found that fixation durations and saccadic amplitudes are systematically related (Tatler and Vincent, 2008) and that combining these parameters can provide insights about the mode of information processing (Velichkovsky et al., 2002a, 2005). The present study investigates whether amplitudes of saccades during continuous visual behavior can be used to distinguish between processing differences within fixations.

Velichkovsky et al. (2002a,b) reported differences in visual recognition performance with regard to particular regularities in eye movement behavior and related them to activation of different brain mechanisms such as the dorsal and ventral pathways of the visual system (see e.g. Milner and Goodale, 2008). More specifically, short fixations in combination with long saccades may allow a rapid evaluation of the spatial layout of a scene; therefore, they are correlated to the 'ambient' mode of attention (to borrow the term from Trevarthen, 1968). In contrast, long fixations that are often embedded in short saccades facilitate a close, object-and-features-directed analysis; therefore, such fixations are well-suited to tasks requiring 'focal' attention. In further experiments, differences in the

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recognition of visual stimuli depending on the duration of fixations and the amplitude of adjacent saccades in real-world static scenes were reported (Velichkovsky et al., 2005). Other authors suggested similar functional classifications of eye movement patterns, distinguishing for instance between global and local visual scanning behavior (Tatler and Vincent, 2008; Wedel et al., 2008). However, so far only behavioral evidence has been obtained to support the idea that differences in eye movement behavior are related to particular modes of information processing. The present paper aims to contribute more insight into this question by investigating brain activity during certain fixations in free visual behavior.

The distractor paradigm (Lévy-Schoen, 1969; Walker et al., 1995) was chosen to analyze the effects of brief test stimuli presented during ongoing fixations. This gaze-contingent technique (McConkie and Rayner, 1975) allows us to investigate the influence of distractors in continuous activities, such as free picture viewing (Pannasch et al., 2001). It has been consistently shown that any sudden change in the visual input prolongs the duration of the affected fixation. This effect is related to an inhibition of saccades around 70–140 ms subsequent to the distractor onset (Reingold and Stampe, 1999, 2000), presumably due to a reflex-like process in the superior colliculus (SC), a midbrain nucleus that is responsible for the input to the brain stem saccadic generator (e.g. Dorris et al., 1997; Munoz et al., 2000; Munoz and Istvan, 1998; Sparks, 2002). However, the processing of distracting events also takes place at other levels in the brain and it has recently been suggested that subcortical and cortical structures are involved in this inhibition of saccadic activity (Graupner et al., 2007; Sumner et al., 2006). For instance, Graupner et al. (2007) found evidence of habituation to repeatedly shown distracting events in cortical responses (N1 and P2) as well as in the fixation prolongation.

The finding that cortical structures are also involved in the distractor processing allows us to make another connection: Since particular eye movement patterns indicate distinct processing mechanisms within a fixation (e.g. Velichkovsky et al., 2005), it can be assumed that those mechanisms also modulate the distractor effect. This has recently been tested by Pannasch and Velichkovsky (2009) who found that the influence of a distractor on the affected fixation was modulated by the amplitude of its preceding saccade. Fixations were more prolonged when the preceding saccade was within the parafoveal range, i.e. when the amplitude was below 5° of visual angle. In contrast, a weaker prolongation effect was found for preceding saccades larger than 5°. This approach opens the way to explore changes in visual information processing with regard to specific eye movement patterns.

The present study investigated the time course of distractor-related brain activity with cortical eye fixation-related potentials (EFRPs). Furthermore, the distractor effect was examined regarding the amplitude of the preceding and the following saccade, thus considering a fixation's full saccadic context. We assumed that the saccadic context can distinguish functional processing differences within a fixation. We furthermore expected to replicate previous findings that showed a distinct influence of the preceding saccade amplitude on the distractor effect (see Pannasch et al., submitted for publication; Pannasch and Velichkovsky, 2009) and anticipated a similar relation for the following saccade.

So far, only few studies have tackled the problem of combined EEG/ERP and eye tracking methods, especially in the paradigm of gaze-contingent stimulus presentation. Graupner et al. (2007) reported a modulation of the N1–P2 pattern in the EFRPs by the appearance of distractors. A link between activity in the P2 time window and the inhibition of irrelevant or distracting information was also suggested in other studies (Alain et al., 1994; Freunberger et al., 2007; Kotchoubey, 2006). Both N1 and P2 were therefore at the focus of the electrophysiological part of this study.

2. Methods

2.1. Subjects

Forty-six 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 ($M=23.4$, $SD=6.1$). They were naive with respect to the purpose of the study and were either paid €5 or received course credits for participation. Informed consent was obtained according to local ethical guidelines.

2.2. Apparatus and stimuli

Subjects were seated in a dimly-illuminated, sound-attenuated room. Images were displayed using a 19-inch CRT monitor (Iiyama Vision Master 452) with a screen resolution of 1152 by 864 pixels and a refresh rate of 100 Hz. Viewed from a distance of 80 cm, the resulting visual angle was 26° horizontally and 18° vertically in total.

Eye movements were recorded at 250 Hz using an SR Research Ltd. EyeLink I eye tracker (SR Research, Osgoode, Ontario, Canada). 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 4 ms. Fixations were defined by the absence of a saccade.

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 bipolarly recorded supra- and infra-orbitally (vertical EOG) and from the outer canthus of each eye (horizontal EOG). Linked earlobes served as reference and an electrode at AFz was used as ground. Impedances were kept at 5 kΩ or below. EEG was recorded continuously, sampled at a rate of 1000 Hz and bandpass-filtered by the amplifier from 0.3 to 70 Hz.

Forty-five digitized copies of paintings by different 18th century European artists illustrating scenes of daily routines with one or more people (see Fig. 1) were used as stimuli for the image inspection task.

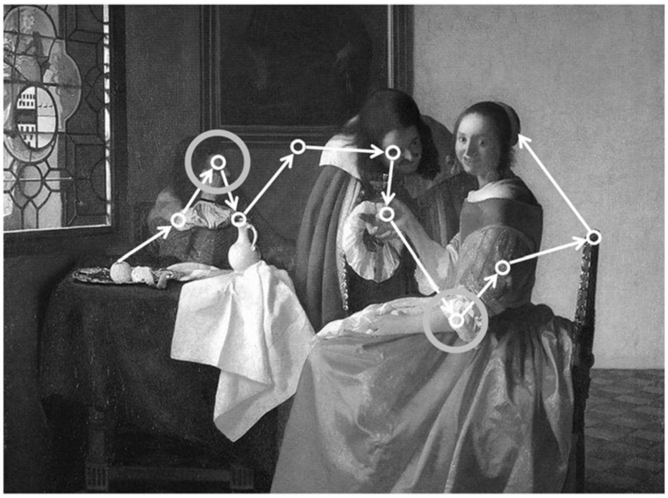

Fig. 1. Schematic illustration of the distractor presentation. The example shows Jan Vermeers "Girl with a wine glass" overlaid with a 3 s eye scanning sequence. Saccades and fixations are illustrated as white lines and circles, respectively, together with two distractors at different locations shown in gray (Note that distractors were of light blue color in the experiment).

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They were displayed in monochrome colors. A light blue annulus (2.7° in diameter, 0.3° margin width) served as a temporally and spatially gaze-contingent visual distractor stimulus.

2.3. Procedure

Eye movements and EEG were recorded throughout the experiment. Before the start of the experiment, participants were informed about the distractor presentation, but instructed to ignore them. Participants were asked to study the images in order to answer five questions regarding scene content which were shown after the picture offset (e.g. "Was the woman wearing a bracelet?" is an example for the image in Fig. 1).

The experimental session was run in one block, containing 35 pictures with and 10 pictures without distractors, shown in random order. The 10 non-distractor pictures were later used to generate a fixation-locked baseline for the EFRP analysis. The picture presentation began with an initial period (5 s) without distractors, followed by a period containing 17 distractors. Individual distractors were triggered by the onset of each 5th fixation. Distractors were overlaid on the image, thus leaving the content in the middle of the annulus visible (see Fig. 1). Distractors appeared with a stimulus onset asynchrony (SOA) of 100 ms centered on the actual coordinates of the selected fixation and were visible for 80 ms. If fixations were terminated before reaching the SOA, the program waited for the next suitable fixation. Once the last distractor was presented, the image remained for two more seconds and then was replaced by the questions regarding the picture content. On average, the presentation of an image lasted for about 34 s, resulting in approximately 1 h for the full experiment.

2.4. Data analysis

The statistical analysis of eye movement data was performed with the SPSS 17.0 software package and EEG data preparation and analysis was performed with EEGLAB (Delorme and Makeig, 2004). All fixations preceded or followed by a blink outside the screen area or with durations of less than 120 ms were excluded from further analysis. Experimentally manipulated fixations were removed if the distractor presentation exceeded the SOA by ±10 ms. Due to the right-skewed distribution of fixation durations, all analyses of this parameter were performed using the median score for each subject and condition.

Prior to data analysis, all valid fixations were classified according to their preceding (P) and the following (F) saccadic amplitudes. The criterion for classification was set at 4 deg of visual angle according to conservative estimations of the radius for parafoveal vision of the adult human eye (Wyszecki and Stiles, 1982). This distinction between short (S) and long (L) saccades resulted in four conditions of saccadic sequences (henceforth termed saccadic context) in which a fixation could have been embedded; short-short (PS-FS), short-long (PS-FL), long-short (PL-FS) and long-long (PL-FL).

Regarding the eye movement behavior, we calculated for each saccadic context the difference between the duration of distractor fixations and unaffected baseline fixations. The baseline consisted of the respective second fixation before and after the distractor and had to belong to the same saccadic context. Since a habituation of the distractor effect was shown during a picture presentation (Graupner et al., 2007), fixations related to the first distractor of each picture were excluded. The statistical analysis of difference values was performed with a repeated measures analysis of variance (ANOVA).

Data of four subjects (two male and female) had to be discarded from the statistical analysis of EEG data due to technical problems with the recording. All valid distractor fixations were used to generate epochs from the EEG data. Due to the short interstimulus intervals between successive distractor presentations (~1.5 s) the EFRP baseline was created using valid fixations from the ten images without distractors. This was to avoid any corruption of the baseline EFRP signal by preceding and following distractor presentations. Because this baseline is different from the one used for the eye movement analyses, we compared the fixation durations as well as preceding and following saccade amplitudes of both baseline populations but found no differences. Two-second epochs were extracted beginning 800 ms prior to the baseline or distractor fixation onset. Segments with strong muscle activity and other artifacts were excluded by manual inspection. An independent component analysis (ICA) was run on the dataset to identify and remove components related to eye-movement artifacts, punctual muscle artifacts or line noise (especially components with frontal and temporal sources). Activity 50–250 ms before the fixation onset was used as baseline to correct the epochs. Subsequently, the EEG segments were averaged to obtain separate EFRPs for the distractor and baseline fixations of each saccade context.

It is known that the saccade before and after a fixation generates systematic activity patterns in the EFRP. The most prominent saccade-related patterns are the spike potential, a positive peak around 10 ms before the saccade onset, and the lambda response, a large positive peak about 100 ms after the saccade offset. The amplitude of the lambda response is modulated by the size of the preceding saccade (Yagi, 1979). Due to this influence, we expect different activity patterns in the EFRPs regarding the saccadic context mixed up with the activity related to the processing of the distractor. Therefore, calculating the difference between distractor and baseline EFRPs for each saccadic context individually should remove the influences of the saccades but maintain the activity that is related to the distractor processing.

As a precondition for this approach and the validity of subsequent statistical analysis, it is important that classifying preceding/following and short/long saccades is based on similar amplitudes for distractor and baseline fixations within each group. If this requirement is not fulfilled, additional variance would be introduced to the EFRPs which cannot be related to the distractor processing. Therefore, we conducted pair wise *t*-tests on the saccadic amplitudes for each saccade condition between baseline and distractor. No differences were obtained for the preceding saccade. The following saccade amplitudes were about 0.1° shorter in the distractor sample for PS–FS and PL–FS, all $p < .001$. It is not clear if and how this difference affects the EFRPs but it needs to be considered when interpreting the results.

Statistical testing was performed on indices derived from baseline and distractor EFRPs. Mean activity values of N1 (130–170 ms after distractor onset) and P2 (200–250 ms after distractor onset) were analyzed at O2 and averaged Cz/Pz, respectively. This selection was motivated by previous results using a similar paradigm (Graupner et al., 2007), where the largest amplitudes were found at these electrode positions. Data obtained from these preprocessing steps were analyzed with repeated measures ANOVAs using treatment (baseline vs. distractor), preceding saccades (short vs. long) and following saccade (short vs. long) as within-subject factors. Separate analyses of the difference EFRP components and pair-wise Bonferroni-corrected comparisons (including adjusted *p*-values) were provided to further evaluate the effects of saccadic context. Finally, we were interested in the relation between behavioral (fixation lengthening) and cortical (EFRP components) effects induced by distractor presentation. This was examined by a correlation analysis contrasting saccadic context related changes in the distractor effect and in ERP components.

3. Results

3.1. Eye movement data

The mean durations of distractor and baseline fixations in Table 1 were obtained by averaging the medians for each subject and

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Table 1
Mean fixation duration for baseline and distractor fixations for the effect of preceding saccade alone and for the combined influence of preceding and following saccades.

		Preceding saccade			
		Short		Long	
		Baseline in ms	Distractor in ms	Baseline in ms	Distractor in ms
Alone		265.3 (30.9) N = 555	344.0 (33.0) N = 280	257.9 (29.0) N = 350	322.9 (30.7) N = 187
Following saccade	Short	273.8 (30.9) N = 344	354.3 (31.8) N = 173	255.5 (28.4) N = 216	325.1 (32.8) N = 118
	Long	250.2 (29.5) N = 211	326.0 (40.4) N = 106	262.7 (33.9) N = 133	321.0 (32.4) N = 69

Note: Standard deviation of fixation duration is given in parentheses. Mean number of fixations per subject belonging to this condition are shown on the second line in each cell.

condition. While the first row displays the influence of the preceding saccade, the second and third rows depict the combined effects of preceding and following saccades. For the subsequent statistical testing, the respective difference values (distractor–baseline) were used as a measure of the behavioral distractor effect.

The repeated measures ANOVA conducted to determine the influence of the preceding saccade amplitude (short vs. long) revealed a significantly stronger fixation prolongation for short preceding saccades, $F(1,45) = 24.7$, $p < .001$, $\eta^2 = .35$. Adding the following saccade as a separate factor for statistical testing revealed significant effects for the preceding, $F(1,45) = 23.9$, $p < .001$, $\eta^2 = .34$, as well as for the following saccade amplitudes, $F(1,45) = 5.69$, $p < .05$, $\eta^2 = .11$, with no interaction, $F < 1$. For both factors, short saccades elicited a stronger distractor effect. Consequently, the prolongation of fixation duration was strongest for PS–FS ($M = 80.5$ ms, $SD = 21.6$) with PS–FL ($M = 75.7$ ms, $SD = 31.7$), PL–FS ($M = 69.6$ ms, $SD = 20.0$) and PL–FL ($M = 58.2$ ms, $SD = 23.5$) in order. According to pair-wise Bonferroni-corrected post-hoc t-tests, the values for PS-FS were significantly larger for PL–FS and for PL–FL (all $p < .01$), and PL–FL was smaller compared to all others (all $p < .015$).

Fig. 2 shows the frequency distributions of baseline (Fig. 2A) and distractor fixations (Fig. 2B) for the four saccade conditions. The distributions were compiled by collapsing data of all subjects for each condition using a bin size of 12 ms. Dividing all bins of the distractor distribution by the baseline fixation frequency resulted in a normalized ratio plot (Fig. 2C). While a value of 1 in this graph demonstrates an identical proportion of terminated fixations in both the distractor and the baseline distribution, smaller (larger) values represent a relative inhibition (facilitation) of saccades in the distractor distribution.

Up to about 70 ms after distractor onset, the corresponding distributions of distractor and baseline fixations had an equal dynamic (Fig. 2A and B) as also indicated by values closely around 1 in the ratio plot (Fig. 2C). In the time window of 70–140 ms, the distractor fixations distributions showed a pronounced dip indicating inhibition of new saccades (Fig. 2B), which was very similar for all saccadic context conditions. In the subsequent phase, the patterns of saccadic activity differed between the saccadic context conditions (Fig. 2B and C), similar to the effects observed in difference values of fixation duration.

According to Fig. 2C, there is a shift in latency of the first dip which seems to be related to the amplitude of the following saccade. To further analyze this effect, we computed, for each subject and condition, histograms with bin size of 4 ms (Reingold and Stampe, 2002). To allow for a reliable detection of the dip latency, we required that histograms of a single condition had to contain at least 40 fixations. Due to this criterion, we discarded data of six subjects. Histograms were smoothed with a 7-bin box average filter. Next, the smoothed values of all distractor bins were divided by their corresponding baseline values, resulting in normalized histograms for each subject and condition. Subsequently, we extracted the latency values of the dip (i.e. the minimum within the 70–140 ms period following the distractor onset). The obtained latencies were entered into a 2 (preceding saccade: short, long) × 2 (following saccade: short, long) repeated measures ANOVA. We found a significant main effect for following saccade, $F(1,39) = 37.1$, $p < .001$, $\eta^2 = .49$, demonstrating that the latency of the dip was larger for short ($M = 118$ ms, $SD = 9.5$) than for long ($M = 110$ ms, $SD = 9.4$) following saccades. No effect was found for preceding saccades, $F < 1$, but there was a significant interaction, $F(1,39) = 4.36$, $p < .05$, $\eta^2 = .10$, mainly related to shorter latencies for PL–FL in contrast to PS–FL ($p = .054$).

3.2. EFRP data

The influence of saccadic context on EFRP activity for baseline and distractor fixations is illustrated in Fig. 3A and B for the four saccadic context conditions at four selected electrode positions. The additionally plotted difference wave EFRPs (baseline subtracted from distractor) in Fig. 3C clearly shows the influence of saccadic context on distractor induced N1 and P2 activity. For the statistical evaluation of the influence of saccadic context and distractor presentation on N1 and P2 of the EFRP, repeated measures ANOVAs were performed with treatment (distractor vs. baseline), preceding saccade (short vs. long) and following saccade (short vs. long), all three serving as within-

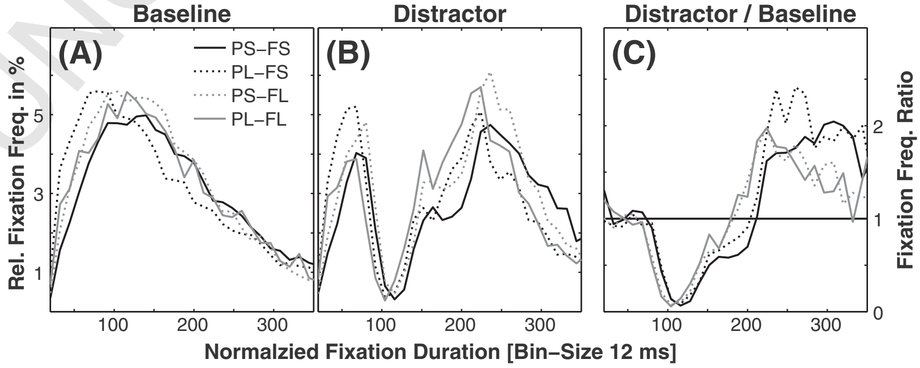

Fig. 2. Fixation frequency for baseline (A) and distractor (B) fixations for the saccadic context conditions. The plots show the distribution of new saccades as function of time. Please note the x-axes is normalized with regard to the time of distractor presentation in distractor fixation, i.e. effective fixation duration minus 100 ms. The distractor-to-baseline ratio of fixation frequency is shown in panel C. In this plot, values below 1 indicate a relative inhibition and values above 1 a relative facilitation of new saccades in the distractor as compared to the baseline distribution. Values of 1, as marked by a horizontal line, correspond to the baseline level i.e. an equal dynamic in both distributions.

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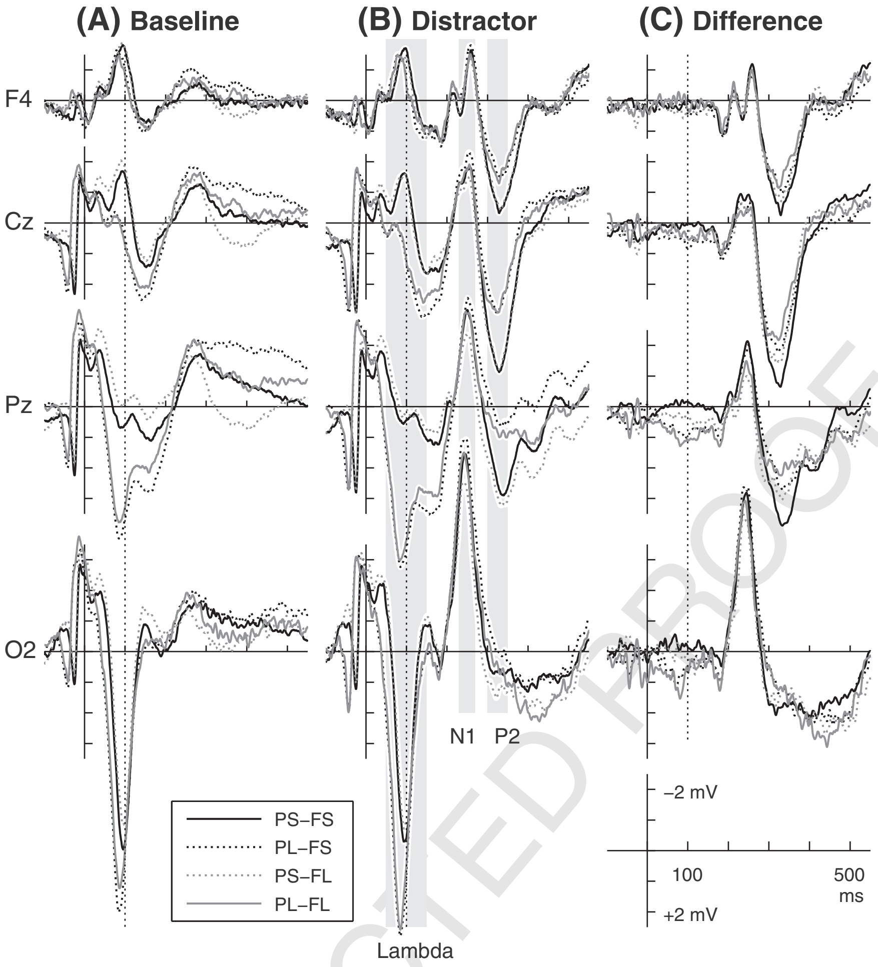

Fig. 3. Grand mean EFRPs of baseline (A) and distractor fixations (B) and for the difference wave (distractor minus baseline, C). Saccadic context conditions are shown at electrode positions F4, Cz, Pz, and O2. The ordinate axis represents the fixation onset; the dotted vertical lines indicate the time when distractors were presented in distractor fixations. Time windows and components of interest for the statistical analysis (lambda, N1 and P2) are indicated in grey.

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subjects factors. Results for the main effect of treatment will characterize the distractor influence. Possible influences of the saccadic context on the EFRPs will be expressed by the main effects for preceding as well as for following saccades. Furthermore, the degree of interaction between treatment and preceding (and/or following) saccade will answer to what extent the saccadic context modulates N1 and P2 activity beyond the simple influence of different saccade amplitudes.

3.2.1. General effects of saccadic context on the EFRP

An influence of the saccadic context was found in the EFRPs of the baseline (Fig. 3 A). This is evidenced by shorter latencies and larger amplitudes of the lambda response, especially for long preceding saccades at O2. At Pz and Cz sites, this stronger positivity persisted until about 200 ms after fixation onset. At around 300–500 ms after the fixation onset, baseline and distractor EFRPs showed a second positive deviation in the activity which was more pronounced for long following saccades, particularly at Pz. This, however, can also be read as a prevailing influence of the preceding saccade, indexed as a stronger positivity for short preceding saccades which were more prominent at Cz.

Results of the ANOVAs for N1 and P2 are shown in Table 2. We obtained significant main effects for preceding and following saccade in the N1 time window. The first main effect results from stronger N1 activity for long preceding saccades while the second is determined by stronger N1 activity for short following saccades. Moreover, significant main effects for preceding and following saccade were found in the P2 time window. Here the pattern is reversed: the P2 activity is stronger if preceding saccades are short and if the following saccades are long.

3.2.2. Effects of saccadic context and distractor processing on the EFRP

For the distractor EFRPs we observed similar influences of saccadic context as for the baseline EFRPs. Additionally, a superposed

Table 2
Results of ANOVAs for N1 and P2 activity.

	Factor	F(1,41)	p	η^2
N1	T	65.17	.000	.614
	P	20.10	.000	.329
	F	8.91	.005	.178
	T×P	1.97	.168	.046
	T×F	11.18	.002	.214
	P×F	0.03	.872	.001
	T×P×F	0.44	.513	.010
P2	T	149.1	.000	.784
	P	106.6	.000	.722
	F	29.08	.000	.415
	T×P	27.54	.000	.402
	T×F	6.58	.014	.138
	P×F	0.38	.539	.009
	T×P×F	0.93	.340	.022

Note. T = treatment (baseline vs. distractor); P = preceding saccade; F = following saccade.

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distractor-related activity pattern was found: A negative peak occurred at about 140 ms after distractor onset with the largest amplitudes at O2, resembling the N1 component, and a positive peak occurred at ~225 ms with the largest amplitude at Cz, probably reflecting the P2 component. Concerning this influence of distractors on the EFRP the statistical analyses revealed significant main effects of the factor treatment for both N1 and P2 (see Table 2). Amplitudes for the N1 as well as for the P2 were larger in the distractor compared to the baseline EFRP.

3.2.3. Saccadic context and the EFRP to distractor stimuli

The difference wave in Fig. 3C shows the activity remaining after subtracting the baseline EFRP from the distractor EFRP. Given that the influence of saccades in the baseline and distractor EFRP of each saccadic context are equal, the difference wave reveals the impact of saccadic context on distractor processing itself. Most prominent in the EFRPs are the N1 and the P2 components. Especially for P2, a saccadic context-based variation in the amplitude can be observed at Pz and Cz. This is illustrated in Fig. 4 showing the P2 scalp distributions in the difference waves for PS-FS (largest P2) and PL-FL (smallest P2). While the largest P2 amplitude in both conditions can be found at Cz, the modulation induced by saccadic context, i.e. the difference between PS-FS and PL-FL (right panel of Fig. 4), seems to have a maximum at a more parietal region.

The modulation of distractor related N1 and P2 activity by saccadic context is evidenced by the significant interactions between treatment and preceding/following saccade. For N1 we only found a significant interaction between treatment and following saccade (see Table 2). Bonferroni-corrected post-hoc comparisons revealed a stronger N1 activity for short following saccades ($p<.001$) while there are no differences in the baseline EFRP (see Fig. 5A and B). For P2 both interactions—treatment and preceding saccade as well as treatment and following saccade—are significant (see Table 2). Bonferroni-corrected post-hoc comparisons demonstrated a stronger P2 activity for short preceding saccades in both EFRPs (baseline and distractor). This was, however, more pronounced in the distractor condition (see Fig. 5C). Regarding the interaction of following saccade the pattern is more complex. While the main effect of following saccade suggested a smaller P2 activity for short saccades, post-hoc comparisons revealed significance for this trend only for the baseline ($p<.001$) but not for the distractor EFRP ($p=0.16$). As can be seen in Fig. 5D the latter was related to a larger difference in P2 between baseline and distractor EFRP, i.e. a larger P2 for short compared to long following saccades. To undermine these findings we calculated a further ANOVA on P2 amplitude of the difference wave, using following and preceding saccade as within-subject factors. In line with the previous results we found main effects for preceding, $F(1, 41)=27.5$, $p<.001$, $\eta^2=.40$, and following saccades, $F(1, 41)=6.58$, $p<.05$, $\eta^2=.14$, but no interaction effect ($F<1$). Short compared to long preceding and following saccades were related to larger P2 amplitudes. It is noteworthy that the general pattern of effects on P2 amplitude was similar to the results obtained for the behavioural distractor effect measure, i.e. largest amplitudes for the PS–FS and smallest amplitudes for PL–FL condition.

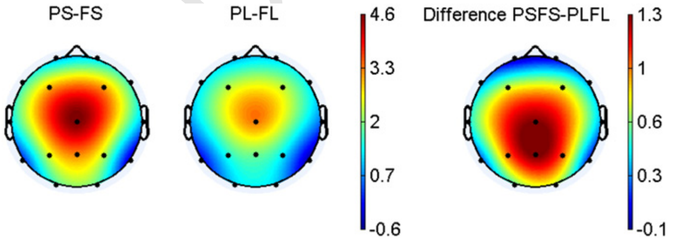

Fig. 4. Scalp distribution for activity in the P2 time window (200–250 ms after the distractor onset) for difference waves of saccadic context for PS-FS (short preceding and short following saccades; left panel) and for PL-FL (long preceding and long following saccades; middle panel). The right panel depicts the difference between left and middle panels.

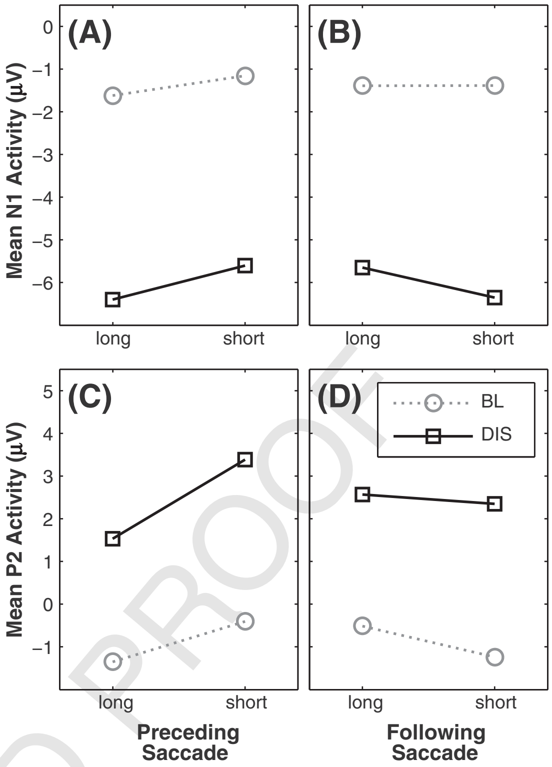

Fig. 5. Mean EFRP activation of baseline (BL = dashed line) and distractor (DIS = solid line) fixations at N1 and P2 time range as a function of the influence from preceding (A and C) and following saccade (B and D). N1 activity was measured at O2 electrode site 130–170 ms after distractor onset and P2 reflects averaged Cz/Pz activity 200–250 ms after distractor onset. Please note that different origins of ordinate axes were used in the plots for N1 and P2 activity.

Fig. 3C also revealed a difference at the Pz and O2 sites about 50–150 ms after fixation onset, i.e. the time window of lambda wave. To evaluate this effect a similar statistical analysis as for N1 and P2 was performed for the lambda component (O2/Pz averaged activity at 50–150 ms after fixation onset). We found an effect of treatment, $F(1,41)=10.8$, $p<.01$, $\eta^2=.20$, showing pronounced activity in the distractor compared to baseline EFRP. Moreover, significant main effects for preceding, $F(1,41)=245$, $p<.001$, $\eta^2=.86$, and following saccade, $F(1,41)=22.9$, $p<.001$, $\eta^2=.36$, were found. Lambda was stronger for long preceding saccades and short following saccades, respectively. Finally, an interaction between treatment and preceding saccade was observed, $F(1,41)=13.9$, $p<.001$, $\eta^2=.25$. All other interactions were not significant ($F<2.5$). Bonferroni-corrected post-hoc comparisons revealed stronger lambda activity for long preceding saccades in the distractor compared to the baseline EFRP ($p<.001$) but no difference for short saccades. It is unlikely that this effect is due to variations in preceding saccadic amplitude, since control analyses (see the methods section) found no differences in this parameter between baseline and distractor fixations for all saccadic context conditions.

Finally, the influence of the following saccade on the latency of the initial saccadic inhibition that was observed in the eye movement behavior could be due to a generally prioritized (or speeded) processing of distractors which might also affect the latency of later cortical responses. This motivated an additional analysis of N1 latency in the distractor EFRPs. The N1 latency values were determined at the minimum activity within 100–190 ms after distractor onset at the O2 electrode site. In contrast to the behavioral data, statistical analysis

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Table 3
Correlations between the behavioral distractor effect and the distractor-related EFRP.

	r	*p*	N
	Full saccadic context		
Lambda | DE	.123	.438	42
N1 | DE	.126	.426	42
P2 | DE	.404	.008	42
	Preceding saccade		
Lambda | DE	−.103	.518	42
N1 | DE	−.172	.459	42
P2 | DE	−.042	.803	42
	Following saccade		
Lambda | DE	.030	.851	42
N1 | DE	−.073	.645	42
P2 | DE	.287	.065	42

Note: Indices of behavioral distractor effect (DE) and of cortical responses in the EFRP (lambda, N1 and P2) were calculated as difference between the saccadic context conditions (see text for details).

showed no effect of preceding and following saccades (both $F<1$) on N1 latencies.

3.3. Correlation between eye movement and EFRP data

We found a similar pattern of results for the behavioral distractor effect and for P2 amplitude (fixation prolongation and P2 amplitude was largest for PS-FS and smallest for PL-FL). This motivated a correlation analysis to examine the relation between both parameters. Therefore, differences were calculated between PS–FS and PL–FL for the behavioral distractor effect and for the indices of the difference EFRP (N1 at O2, P2 at Pz/Cz, and lambda-response at Pz). The obtained values were correlated and revealed a significant relationship only between the behavioral distractor effect and the amplitude of P2 but not for lambda and N1 components (see Table 3). Furthermore, we were interested in identifying the individual contribution of preceding and following saccades to this relationship. Therefore, the same measures as above were calculated, in one case only with regard to the distinct saccade length of the preceding saccade, and in the other case only with regard to the distinct following saccade length. None of these additional correlation analyses revealed a significant correlation (see Table 3), suggesting that the full saccadic context is of importance.

4. Discussion

The present study confirmed previous findings on the relation between amplitude of the preceding saccade and behavioral distractor processing (Pannasch and Velichkovsky, 2009), but also extended them by considering effects of both the preceding and following saccades. The largest distractor influence on the fixation duration was found if the affected fixation was preceded and followed by saccades of short amplitudes. In contrast, the smallest prolongation of fixations was obtained in the context of large-amplitude saccades. Therefore, the length of both the preceding and the following saccades are related similarly to the saccadic inhibition. Accordingly, examining these parameters can provide access to differences in the underlying processing mechanisms within a fixation.

Furthermore, using eye-tracking with a concomitant EEG/EFRPs recording enabled us to investigate electrophysiological correlates of these processes. As expected, the saccadic context strongly modulates the EFRPs of fixations. However, the difference wave of distractor and baseline EFRPs allows evaluation of the effect of saccadic context on distractor processing appropriately since it is free of the general influence of saccades on the EFRP. Distractor processing was indexed by an additional N1–P2 wave pattern similar to our previous findings (Graupner et al., 2007). We observed an effect of the following saccade on N1 and a modulation of P2 by preceding and following saccades. In particular, the P2 component seems to be related to the effect in eye movement behavior: Longer fixations and larger P2 amplitudes were found for PS-FS with PS-FL, PL-FS and PL-FL, in descending order. The idea that the different fixation prolongations and the variation in the P2 amplitude are connected was supported by a positive correlation between both parameters. However, no relationship was found when the same parameters were correlated separately for the preceding or for the following saccade. This suggests that considering the complete saccadic context is a promising approach to access differences in the mode of visual attention.

Furthermore, we obtained two other results that shall be discussed according to their temporal occurrence regarding the distractor onset. The difference EFRP showed a deviation related to preceding saccade already about 50–150 ms after the fixation onset, which is in part even before the distractor appearance. For long preceding saccades we observed a stronger lambda positivity in the distractor EFRPs than in the baseline. While it is known that the lambda component is related to the size of the preceding saccade (Yagi, 1979), the current finding could be based on a selection bias between baseline and distractor conditions introduced by the relatively crude saccade classification. However, this does not seem to be the case since a control analysis ruled out such a bias. At present, we have no plausible explanation for this result; still, it can be argued that the early modulation of the lambda amplitude is not related to parameters of subsequent EFRP components. For instance, N1 is affected by the following saccade only. Also, the lambda amplitude is not related to the distractor effect (see Table 3).

A closer examination of the eye movement data revealed a difference in the latency of the distractor effect early (70-140 ms) after the distractor onset. This latency difference is related to the amplitude of the following saccade; for long saccades, the latency was ~8 ms smaller compared to short ones. Apart from that latency shift, the behavioral modulation of the distractor effect by the full saccadic context evolves at a later time, i.e. 140 ms after distractor onset. This finding supports the view of temporally dissociable contributions to distractor-induced saccadic inhibition, similar to that for habituation components of the distractor effect (see Graupner et al., 2007).

What could be the source of this latency shift in the saccadic inhibition? Stimulation studies in primates suggest a delay of ~20 ms between the saccade signals in SC and the overt saccadic behavior (Munoz et al., 1996). Given this estimation, the latency effect must originate in a time window from 50-120 ms after distractor onset which is well before the appearance of N1 (130–170 ms) and P2 (200–250 ms) components of the cortical EFRPs. Furthermore, although an influence of the following saccade on the N1 amplitude of the difference EFRP was found, no effect of saccadic context on N1 latency was detected. Thus, the latency shift does not necessarily reflect an accelerated processing of distractors. As noted above, a modulation of EFRP lambda activity was observed 50–150 ms after fixation onset, i.e. approximately at the moment of distractor presentation. However, this lambda effect is related to the preceding and not the following saccade which makes its causal role in the latency shift of initial saccadic inhibition implausible. Altogether, this indicates that the early latency shift of the distractor effect results not from activities indexed by cortical lambda or N1 components, but rather seems to derive from processes at a lower level. Besides SC which has already been related to the oculomotor distractor effect (Munoz et al., 2000; Sparks, 2002), there could be other subcortical regions such as cerebellum, striatum, and thalamus (see McDowell et al., 2008). In addition, freezing reactions similar to the distractor effect can be produced by stimulation of paleocortex structures such as the amygdala (Panksepp, 1998).

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Next, a modulation of N1 amplitude was found in terms of a smaller N1 for large compared to short following saccades. However, no correlation between the behavioral measures and distractor-related N1 activity was observed. An explanation for this finding is that preceding and following saccades differentially reflect the dynamics of attention during natural viewing. A number of studies have demonstrated an influence of attention allocation on early sensory potentials (e.g. Heinze et al., 1990; Luck et al., 1990; Mangun and Hillyard, 1990; Van Voorhis and Hillyard, 1977), and an increase of N1 in this context can reflect a facilitation in sensory processing at the attended location. It can be argued that attention is covertly shifted to the next fixation location prior to the saccade (Deubel and Schneider, 1996; Findlay and Walker, 1999). In the case of short-range following saccades, the appearance of a distractor nearby the current locus of fixation might still fall into the covertly attended area. In contrast, for long saccades there is a higher chance that spatial attention is already engaged somewhere else in the scene. Thus, the larger distractor-related N1 amplitude for short compared to long following saccades could reflect a facilitation of sensory processing due to the difference in distribution of covert spatial attention. This is corroborated by the active vision perspective of attention as proposed by Findlay and Gilchrist (2001) suggesting that covert attention to a peripheral location supplements but not substitutes for actual movement of the eyes.

Finally, the relation between the behavioral effect of fixation lengthening and P2 amplitude needs to be discussed. Not only was the data for P2 similar to the main effect of distracting events in eye movements, both parameters were also correlated with each other. This strongly suggests a relation between the cortical processes and the inhibitory influence on saccade generation. Indeed, a link between activity in the P2 time window and distractor-related processing has been suggested in a number of studies (Alain et al., 1994; Freunberger et al., 2007; Kotchoubey, 2006). Accordingly, the P2 component may express enhanced processing demands or active inhibition, particularly in situations when targets and irrelevant stimuli appear simultaneously. Further support for this functional role comes from research on visual search where it was found that the allocation of attention to stimuli in a visual search array is reflected by the N2pc component of ERPs (N2–posterior–contralateral, Luck and Hillyard, 1994a,b). Attention to targets in a search task requires simultaneous suppression of distracting information. Recent evidence indicates that N2pc is dissociable into components of target processing and distractor suppression (Hickey et al., 2009). The activity pattern related to the distractor suppression as reported by Hickey et al. (2009) was very similar to the P2 modulation in our study because it occurred in the same time window and with a similar spatial distribution. Taken together, the P2 amplitude probably reflects the active suppression of distractor-related information in cortical areas. Therefore, larger P2 amplitudes in the short saccade context may express an increased effort to protect an attentive processing of the actual target from conflicting and irrelevant signals.

It is, to some degree, surprising that a stronger inhibitory response at the cortical level occurs with a stronger inhibition in the observed behavior. One would expect the contrary pattern, i.e. if the cortical effort is high in order to suppress irrelevant information, then the behavioral effect of distraction should be less pronounced. An explanation could be that these effects are not causally related but rather indicate the parallel work of related but functionally distinct processing mechanisms. The connection between P2 activity and saccadic inhibition therefore warrants further in-depth investigation to elucidate this relation and its underlying brain mechanisms.

The idea that eye movement behavior can be used to identify the mode of visual attention can be extended to previous work which analyzed visual task performance (Velichkovsky, 2002; Velichkovsky et al., 2005) and relationships between saccadic amplitudes and fixation durations in perception of complex images (Tatler and Vincent, 2008; Unema et al., 2005). This view in particular agrees with the two attentional networks approach: Changes in the environment require increased activity in the ventral frontoparietal network of visual attention by interrupting the ongoing selection in the dorsal network (Corbetta et al., 2008). One can expect, therefore, that the processing and suppressing of distractors requires special efforts, accompanied by increased P2 activity in the dorsal segment of the frontoparietal network of visual attention (Hickey et al., 2009).

An additional analysis (see method section) revealed differences in saccadic amplitude between the baseline and distractor fixations that were used for EFRP analysis but only for conditions with short following saccades. So far, influences of distractors on the following saccade have not yet been investigated in free visual exploration. In a study analyzing inhibition/facilitation of return in free viewing, it was found that the locations of sudden irrelevant stimulus onsets—those events appeared not at the position of the current fixation—were more likely to be the target of the following saccade (Smith and Henderson, 2009). These findings give a hint that sudden events might also influence the spatial programming of the next saccade. Further research is needed to disentangle if such effects can contribute to modulations of the EFRP.

To summarize, the analysis of eye movements provides a viable approach to infer the mode of processing in ongoing visual behavior. We showed that processing of a distractor presented within a fixation is modulated—behaviorally and neurophysiologically—by the pattern of saccades surrounding the fixation. The gaze-contingent distractor presentation paradigm as deployed here offers a methodological perspective to study the phenomena of attention and visual processing in conditions of continuous natural viewing, also potentially accessing different stages and levels in the functioning of the neurophysiological mechanisms. As noted above, the saccadic inhibition which is believed to underlie the distractor effect is commonly related to processing in mid-brain areas as the SC. Together with earlier neurophysiological evidence (Graupner et al., 2007) and behavioral data (Reingold and Stampe, 2004; Sumner et al., 2006), the current findings strongly suggest a cortical involvement in this multilevel process.

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