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Looking for a face in the crowd: Fixation-related potentials in an eye-movement visual search task [☆]



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ABSTRACT

Despite the compelling contribution of the study of event related potentials (ERPs) and eye movements to cognitive neuroscience, these two approaches have largely evolved independently. We designed an eye-movement visual search paradigm that allowed us to concurrently record EEG and eye movements while subjects were asked to find a hidden target face in a crowded scene with distractor faces. Fixation event-related potentials (fERPs) to target and distractor stimuli showed the emergence of robust sensory components associated with the perception of stimuli and cognitive components associated with the detection of target faces. We compared those components with the ones obtained in a control task at fixation: qualitative similarities as well as differences in terms of scalp topography and latency emerged between the two. By using single trial analyses, fixations to target and distractors could be decoded from the EEG signals above chance level in 11 out of 12 subjects. Our results show that EEG signatures related to cognitive behavior develop across spatially unconstrained exploration of natural scenes and provide a first step towards understanding the mechanisms of target detection during natural search.

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Introduction

A central goal in cognitive psychology and visual neuroscience is to understand how we perceive real-world scenes (for a review see Eckstein, 2011). Real-world scenarios typically include several salient features and thus natural vision involves sophisticated mechanisms to efficiently allocate foveal resources (Itti and Koch, 2000). Several processes, such as behavioral goals, motivational state, and the spatial properties of the visual scene, govern saccadic scan paths during freeviewing tasks. But can classical event related potentials (ERPs) be reliably measured during visual search tasks that involve complex and unconstrained spatial distributions of ocular trajectories? EEG recordings typically involve flashing stimuli at fixation to avoid the large artifacts that eye movements introduce in the ERPs. For this reason, the registration of EEG during eye-movement exploration tasks of natural scenes has been largely avoided in the past, posing a potential difficulty to the study of human vision in more ecological environments.

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Recent reports have shown that it is feasible to concurrently record EEG and eye movements (Kamienkowski et al., 2012a, 2012b; Ossandón et al., 2010; Plöchl et al., 2012). However, in order to restrict eye-movement contaminations, these studies were run in much simplified scenarios compared to the exploration of natural scenes; namely they involved controlled saccade tasks (Brouwer et al., 2013: Dandekar et al., 2012: Kazai and Yagi, 1999: Thickbroom and Mastaglia, 1985: Thickbroom et al., 1991; Yagi, 1981), reading paradigms (Dimigen et al., 2011; Marton and Szirtes, 1988a, 1988b) or visual search tasks with artificial stimuli (Kamienkowski et al., 2012a, 2012b). To our knowledge, only two studies have focused on fixation event-related potentials (fERPs) during the free-viewing of natural images (Graupner et al., 2007; Ossandón et al., 2010). Due to the difficulty in obtaining long fixations (i.e. long EEG traces without contamination of eye movements), these studies did not deal with long latency components typically associated with cognitive processing.

In the present study we sought to understand the full range of events that unfold during the visual exploration of natural scenes. Subjects had to find a hidden target face in a crowded scene while we simultaneously recorded EEG and eye movements. Before the experiment we trained subjects to avoid making fixations of short duration while searching. In this way, we were able to obtain relatively long fixations during the experiment, which allowed the analysis of late cognitive components without contamination of eye movements. Moreover, we designed a

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fixed-gaze experiment akin to a classical oddball paradigm, in order to systematically compare the ERPs obtained in our visual search task with the classic ERPs of paradigms at fixation. This allowed a simple and direct way to compare fERPs and ERPs without the need of ocular correction methods (such as those based on Independent Component Analysis). Developing objective validation criteria (Ossandón et al., 2010; see also Dimigen et al., 2012) would be particularly problematic in this experiment since subjects performed saccades of any size and in any direction.

Our results show that known EEG signatures related to cognitive functions in fixed-gaze paradigms are also present in more ecological settings. Interestingly, we also show that a direct comparison between ERPs and fERPs yields differences in relation to their latency and topography. Furthermore, we show that the information contained in the cognitive fERPs can be used to discriminate target detection in single trials. Altogether, our work provides new insights into the dynamics of brain processes during visual exploration of natural scenes.

Materials and methods

Participants

Twelve subjects (10 males and 2 females, ages 21–31 years old) participated in the experiments. 10 subjects completed both tasks while 2 subjects completed only the eye-movement visual search task. All subjects were naive to the objectives of the experiment, had normal or corrected to normal vision and gave written informed consent according to the recommendations of the declaration of Helsinki to participate in the study.

Stimuli

The image database contained 60 gray scale images of crowds at stadiums downloaded from Internet or obtained at football stadiums. Images were 800×768 pixels in size and each one contained between 23 and 35 distractor faces (30.68 faces on average). From all the faces in each image 3 were chosen as targets. Images were made isoluminant in order to avoid areas of increased saliency.

Experimental procedures

Stimuli were presented on a 21" liyama CRT monitor, with a screen resolution of 1024×768 pixels and a refresh rate of 75 Hz. Participants sat in a comfortable chair inside a darkened room at 60 cm from the screen, their heads stabilized via an in-house chin rest. All experiments were implemented in MATLAB (Mathworks, Natick, MA) using the Psychophysics toolbox (Brainard, 1997). Manual responses were collected with a standard keyboard. Ocular responses were obtained from the eye position of subjects via the on-line information provided by an eye tracker. During task execution in both experiments, we simultaneously recorded EEG and eye movements.

Visual search experiment

At the beginning of each trial subjects pressed the space bar and were presented with a target face for 3 s. On each trial we resized the original target face to a random value between $2 \times 2^{\circ}$ and $3 \times 3^{\circ}$. This prevented subjects from using target size to guide their visual search strategy. After this time a fixation point was presented on the screen at a random location. Subjects needed to fixate at the new dot location for 1 s for the image of a crowd to appear on the screen. The subjects' task was to search for the target face within the crowd and to fixate on it for 1 s once they have found it (Fig. 1). Trials ended when subjects found the target or after 20 s of visual search. The 60 images were presented in pseudo-random order as a block. Between blocks subjects took 5 min resting breaks. In each block the target face for each image was different from previous blocks. The target faces varied in size

from 2° to 4° across trials to prevent subjects from making inferences about the face position on the following image presentation. In total subjects performed 180 trials (3 different targets per crowd image for the whole experiment). Before the experiment started, subjects were trained to search the target without rushing and gave them an indicative pace with a metronome clicking at 1 Hz. The metronome was only used during their training session, not during the actual experiment; it served to train subjects not to rush during the visual search. During the experiment, we provided subjects with visual feedback at the end of a trial only if they had produced less than 2 fixations of at least 0.5 s throughout the trial. The feedback consisted of the sentence "too fast" shown on a gray background screen. The rationale of this was to encourage larger fixation times in order to study late latency fERPs related to cognitive processes, as described below. The images used during the training sessions were not used during the experiment. On 59% of trials (980/1663 trials, over all subjects and experiments) subjects made at least 2 fixations of 0.5 s to distractors. In total, subjects made 1561 fixations to targets and 4655 fixations to distractors. Using these simple instructions we obtained: 1) longer fixations than in other visual search experiments, and 2) less redundancy between fixations (less number of repeated fixations on the same faces), very common when subjects are allowed to freely explore without any instruction. Both properties of the eye movements were important for the analysis: longer fixations opened the possibility to observe clean late evoked potentials and low redundancy prevented fixations in which the subject fixated at the target but might have not identified it.

Visual Oddball experiment

Subjects had to fixate at the center of the screen, where target and distractor images were flashed in pseudo-random order (Fig. 1, Supplementary Materials). From each image of crowds in the dataset we extracted 11 faces. We extracted these faces by cutting a rectangular area of $2 \times 2^{\circ}$, keeping the target face original size. Before each trial we selected 1 of these images of faces as the target and the other 10 as distractors. In each trial the target face was presented before the beginning of the trial for 3 s as in the visual search experiment. The sequence of 11 faces was then presented, each one for 0.5 s with a random inter-stimulus interval in the range of 0.2-0.3 s. Subjects were asked to fixate constantly on the sequence of images. In total we presented subjects with 220 trials consisting in 3 blocks of 60 trials each and one final block of 40 trials. Between blocks subjects took 5 min resting breaks. The target was present in the sequence on 80% of the trials (180 trials). Targets appeared with the same frequency at any position from 2 to 11 in the sequence and were never presented as the first image in the sequence. The subjects' task was to report with a keyboard press at the end of the trial whether they had detected the target in the sequence

Eye movements and EEG recordings

Eye movements were registered with an EYELINK 1000 system (SR Research, Ontario, Canada). The eye tracker was used in binocular mode with stabilized-head and sampling rate of 500 Hz in each eye. Saccades and fixations were detected using an adapted version of the velocity-based Engbert and Kliegl's algorithm (Engbert and Kliegl, 2003) using the parameters described in Kamienkowski et al. (2012a, 2012b). We only kept saccades larger than 1° for the analyses of the data. We considered as fixations to targets all those fixations that landed on an area of $2 \times 2^{\circ}$ of visual angle from the center of the target face. For all the experiments we ran drift corrections every 10 trials and a recalibration of the eye tracker every 60 trials (before the beginning of a new block). The nine-point calibration was kept with an average error below 1° (typically below 0.5°). EEG data were recorded on a standard 64-channel 10-20 montage using a Biosemi Active-Two System (Biosemi, Amsterdam, Holland) at 1024 Hz. Data was imported into MATLAB with EEGLAB toolbox (Delorme and Makeig, 2004) using

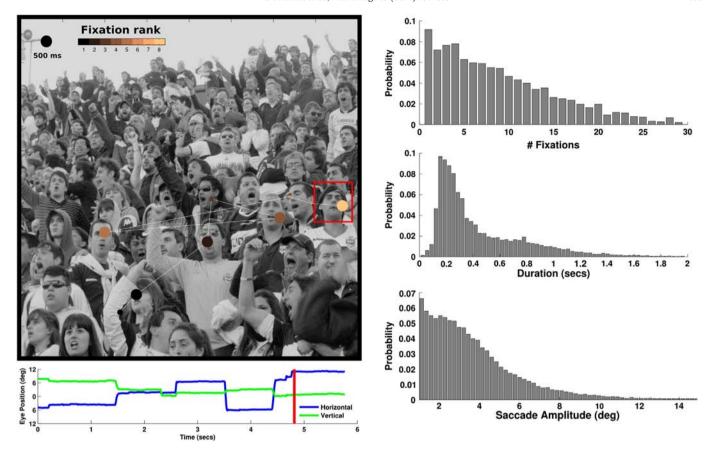


Fig. 1. Experimental design and eye movements' statistics. Upper left panel: Sequence of fixations during an exemplary trial. The red square shows the position of the target in the crowd. Each dot in the image represents a fixation. Dot colors, from darker to brighter, represent the order in which fixations were produced while dot size represents the duration of fixations. Trials ended when subjects fixated on the target face for 1 s or after 20 s visual search. Bottom left panel: Traces of the eye position as recorded by the eye tracker during the trial shown in the upper panel. The final vertical red line shows the beginning of the fixation on the target and the start time of the EEG epoch. Behavioral responses for the free-viewing condition. Upper right: Distribution of the number of fixations across trials. Middle right: Distribution durations. Bottom right: Saccade amplitude distribution.

linked mastoids as reference. Datasets were down-sampled at 256 Hz and bandpass filtered at 0.1–40 Hz (sixth order elliptic filter). We considered the start of the fixation on each face as the trial onset (Fig. 1). For each crowd scene we analyzed the response to the target image (the last image in which the subject fixated > 1 s to indicate finding the target) and to fixations to distractors. In the later case we only considered fixations longer than 500 ms. EEG data were aligned to fixation onset and cropped between .200 ms and 500 ms from the fixation time. We applied a baseline correction to each epoch in the time window [-200–100] ms from fixation onset. Epochs were visually inspected and non-saccadic artifacts were manually removed. An analog card was used to convert and output the digital eye position as analog voltage channels. The temporal offset between the signals was corrected by realigning the eye tracking data to the frontal electrodes, which showed a sharp saccadic spike potential shortly after saccade onset.

Statistical analysis of ERPs

We mainly focused our statistical analysis on midline channels Fz, Cz, Pz and Oz. In order to run statistical comparisons between targets and distractors, we applied a non-parametric Wilcoxon rank-sum test to each (channel, time) sample of the average ERP. We ran separate tests for each channel and data point to compare the two conditions across all subjects. In order to correct for multiple comparisons we applied a false discovery rate procedure. We considered samples as statistically different between the two conditions when the p-value of the Wilcoxon rank-sum test was below the threshold that set the expected proportion of falsely rejected null hypotheses to 5%.

EEG single trial classification

We applied Support Vector Machines to the EEG data to conduct a single-trial classification between fixations to targets and distractors. Data classification was performed with the FieldTrip software (Oostenveld et al., 2011). Classification performance was assessed with five-fold cross-validation, the classifier being fed with 64×128 features corresponding to the voltage values of the 64 channels and the whole post-fixation epoch (0 to 500 ms after fixation onset). For each single trial we performed baseline correction in the range [-200-100] ms before running the classification procedure. Since we had 3 times more fixations to distractors than targets we selected a random subset of distractors to match the number of targets for a given participant (between 110 and 150). We report the mean and SEM accuracy for each subject. The significance was estimated using a binomial test (Quiroga and Panzeri, 2009).

Results

Behavioral results for the eye-movement visual search task

On average subjects found the target in 138 out of 180 trials (SD: 15.36). Only trials that ended with a fixation on the target were considered valid and were kept for further analysis. Subjects made an average of 8.4 fixations (SD: 1.84) and took a mean time of 8.5 s before fixating on the target (Fig. 1). The distribution of fixation durations was skewed with a peak at \sim 0.22 s and a long tail to longer times. Even though the peak was earlier than 0.5 s, there were still a large number of fixations with a duration longer than 0.5 s to run the statistical analysis on the

full sequence of ERP events. The saccade amplitudes had a skewed distribution with an average amplitude of 3.7° (SD: 2.3°). To assess the presence of training or memory effects across the task (the fact that subjects could potentially remember the images and use this information to improve their performance) we compared the response times of subjects across blocks. We ran an ANOVA with response time as dependent measure and block (1, 2 or 3) as factor. This analysis showed no statistical difference between the response times of the three blocks (F = 0.66, df = 2, p = 0.51). Potential differences in the physical properties of saccades (such as saccade amplitude and angular distribution) to targets and distractors could lead to spurious differences in the fERPs. To avoid this issue, we tested the hypothesis that the angular distribution or the amplitude of saccades might vary between saccades to targets and distractors. We could not find any statistical evidence to support this hypothesis (Kuiper test for circular statistics, p = 0.15).

Behavioral results for the visual oddball task

Subjects had an average of 95.27% correct detections of the target and an average of 7.35% false alarms in those sequences when the target was not present. Only correct trials were used for analysis.

Analysis of fixation event-related potentials during the eye-movement visual search task

Fixation-event related potentials (fERPs) during the visual search experiment generated similar patterns for targets and distractors in the first 250 ms following fixation onset (Fig. 2). We observed a saccade-related artifact before fixation onset, an initial frontal positivity at the start of the fixation (t=0 ms) followed by a positive occipital P1 component at ~100 ms and a vertex positive potential at ~170 ms. Conversely, late potentials showed a large difference between fixations to target and distractors. Only fixations to targets elicited a sustained positive P3 component starting from 250 ms, with a centro-parietal topography (see Fig. 2).

Analysis of event-related potentials for the oddball task

For the oddball experiment we compared the ERPs elicited by targets to the ERPs triggered by the distractors preceding the target in the sequence. As in the visual search task, the spatial topographies of the ERPs showed that the early ERPs generated by the faces were identical for the targets and distractors (Fig. 3). After ~250 ms a P3 target-related component was observed occurring first over the main frontal and central electrodes and later spreading to parietal and occipital electrodes.

Comparison between the visual search and the oddball tasks

From a direct comparison between the fERPs obtained in the free-viewing with the ERPs from the oddball experiment, it is clear that, despite showing similar trends and a significant difference between targets and distractors, there were also some differences in the shape of the P3 component (Fig. 4). The P1 for the visual search task occurred earlier than the P1 for the oddball task, with a peak at 96 ms (SEM: 2.13 ms) after stimuli onset as compared to the 115 ms (SEM: 4.8 ms) for the oddball. For the visual search task the P3 appeared as a single centro-parietal component with a maximum at 372 ms. Instead, in the oddball task this component presented an increased fronto-central amplitude at a latency of 305 ms and a centro-parietal maximum at 440 ms (Fig. 4, right panel). In addition, the P3 component was more posterior for the oddball task than for the visual search task, encompassing also occipital channels (Fig. 4, bottom panels).

Single trial classification of stimulus identity

The classification of target vs. non-target faces was significantly above chance (binomial test, p < 0.05, against the null hypothesis that subjects were performing at chance level) in 11 out of 12 subjects for the visual search experiment and in 10 out of 10 subjects for the oddball experiment. Mean accuracy, shown in Fig. 5A, was significantly higher in oddball (O) than in free viewing (FV) (O: (0.72 ± 0.02) , FV: (0.63 ± 0.01) ; t-test: t = 4.70, p = 0.0002). The largest contribution to the classifier originated from centro-parietal channels at around 450 ms (Fig. 5B). In the oddball task, an earlier contribution from more frontal electrodes was observed. Both the time window and the location of the most informative electrodes for classification using a blind analysis were consistent with the P3 obtained from the ERP analysis (Fig. 5B, compare with Fig. 2).

Influence of saccade amplitude in the fERP P1 component

In order to further understand the properties of the early freeviewing P1 component; we realigned the data to the start of the saccade and compared the latency and amplitude of the fERP P1 component for both alignments (fixation aligned versus saccade aligned, Fig. 6). To assess the contribution of the saccades to the P1 component we studied the amplitude of the saccades preceding the fixation. We divided the trials into 3 classes according to the amplitude of the preceding saccade: 1–2°, 2–3° and saccades larger than 3° of visual angle. For each class of trial we averaged the EEG epochs and obtained an ERP for each subject. We then ran ANOVAs on the P1 peak amplitude and P1 peak latency across subjects and classes. Our analysis showed that fixations with

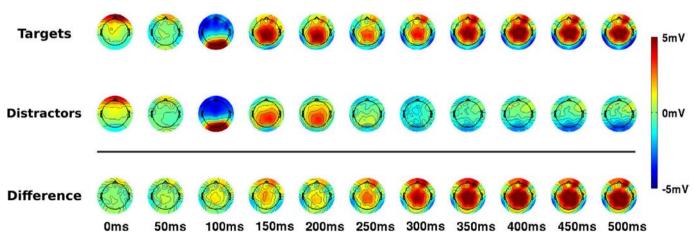


Fig. 2. Topographical maps for the free-viewing condition. Fixations to targets and fixations to distractors generated almost identical early visual components up to ~250 ms after fixation onset. The neural correlates of target detection appeared after 250 ms with a strong P3 component only for the fixations on targets. Time '0' in the topographical plots corresponds to fixation onset.

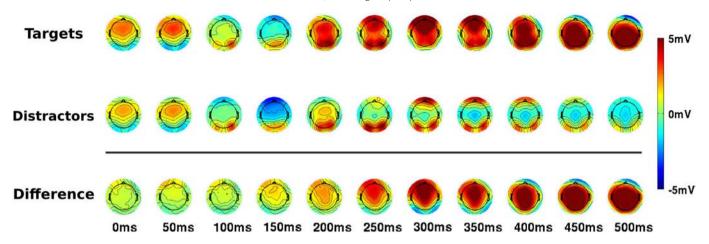


Fig. 3. Topographical maps for the oddball condition. As with the free-viewing experiment, fixations to targets and distractors generated similar early visual components up to ~250 ms after fixation onset. The differences between targets and distractors appeared after 250 ms with a strong component present only during the presentation of targets.

preceding short saccades generated smaller P1 amplitudes, compared to the fixations with preceding large saccades. From these subsets of ERPs we observed a main effect of the preceding saccade on the P1 amplitude for fixation aligned trials (F(2,33) = 4.12, p = 0.0003) as well as for saccade aligned trials (F(2,33) = 8.33, p = 0.0012, Fig. 5). Post-hoc Tukey's HSD tests showed that preceding saccades in the

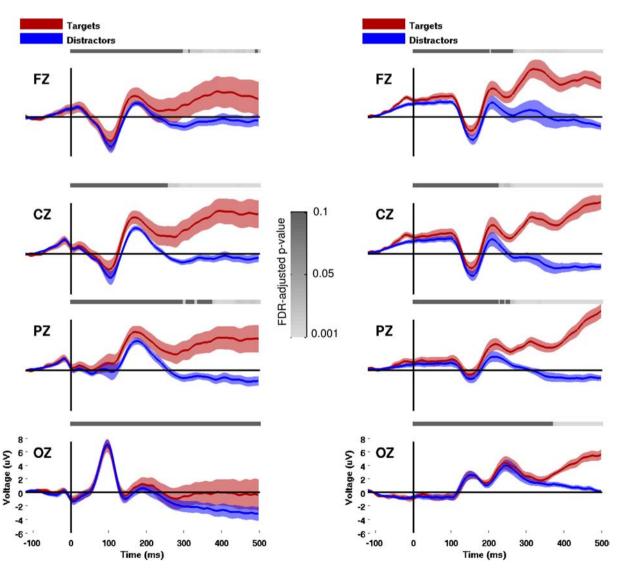


Fig. 4. Main fERP and ERP components for the free-viewing and oddball experiments. Targets elicited a clear P3 component in the two experiments. The P3 component for the oddball task could be further separated into two subcomponents. Shaded areas depict SEM and gray scale bars show the p-values for the comparison between conditions at each time point (Wilcoxon rank sum test, p < 0.05 corrected for multiple comparisons; see section 'Statistical analysis of ERPs').

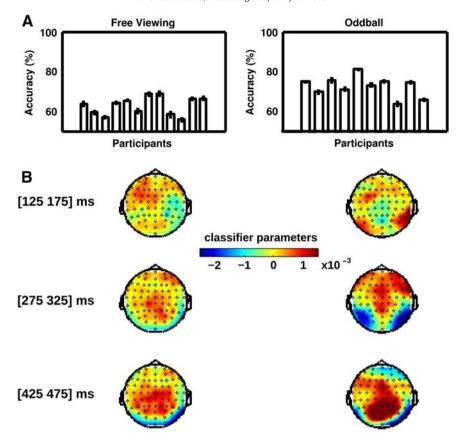


Fig. 5. Single-trial analysis of target versus distractor responses. A: Average accuracy (\pm SEM) over 10 repetitions of the single-trial classification procedure for each participant for both experiments. In each repetition we randomly selected a subset of distractors of the same size as the targets set for a given participant (between 110 and 150 trials), and we ran a five-fold cross-validation. The classification was successful in 11 out of 12 subjects for the free viewing experiment and in 10 out of 10 subjects for the oddball task. Accuracy was significantly higher in Oddball than in Free Viewing (0: (0.72 ± 0.02) , FV: (0.63 ± 0.01) ; t-test: t = 4.70, p = 0.0002). B: Scalp distribution of the classification parameters at three 50 ms time-windows around 150 ms, 300 ms and 450 ms, for both experiments. The data from all the channels during the whole epoch was submitted to the classifier. The most discriminative time points and channels selected by the classification algorithm (classifier parameters or weights of the classifier) matched the times and channel locations of the ERPs P3 components.

range of $1-2^\circ$ of visual angle generated a modulation on P1 amplitude that differed statistically from the saccades in the range of $2-3^\circ$, and those larger than 3° . All other comparisons were not significant. To further validate these results, we conducted a regression analysis of the P1 peak amplitude on the preceding saccade amplitude, at the single trial level for all subjects. We epoched each trial and applied a baseline

correction to each epoch in the time window [-200-100] ms from fixation onset. After epoching the data, we calculated the peak amplitude of the P1 component in each single trial for each subject. With these data we ran regression analyses of the P1 amplitudes as a function of the amplitude of the saccade preceding the fixation. As with the previous analysis, we found a significant positive correlation between the P1

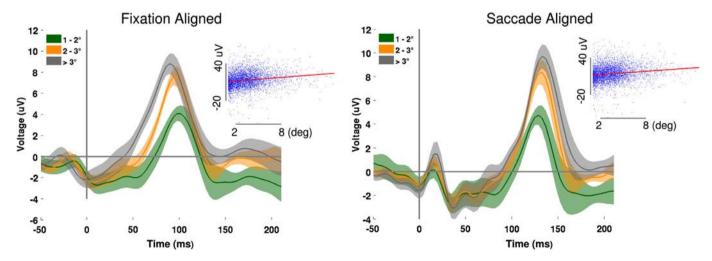


Fig. 6. Preceding saccades modulate P1 amplitude. fERPs/ERPs at channel Oz. Left panel: trials aligned to the beginning of fixation; Right panel: trials aligned to the beginning of saccade. Both panels show only fixations to distractors. Fixations with preceding short saccades generated a smaller P1 amplitude compared to the fixations with preceding large saccades (see Results). These effects were observed in the average ERPs as well as in the single trial analysis. The small insets in the panels show the P1 peak amplitude as a function of preceding saccade amplitude at the single-trial level. The difference in the P1 latency peak between the fixation-aligned and the saccade-aligned events was 39 ms and matched the median duration of saccades across all trials during the experiment.

amplitude and previous saccade amplitude for fixation aligned (Pearson $r=0.17;\, p=10^{-10})$ and saccade aligned trials (Pearson $r=0.15,\, p=10^{-9})$.

Discussion

In the present study we showed fERP components associated with the perception of faces in a search task involving natural scenes. Two previous studies analyzed fERPs during exploration of natural scenes focusing on source models of ongoing and evoked EEG activity (Ossandón et al., 2010) and on the fERPs related to short-term habituation (Graupner et al., 2007). Due to the difficulty in obtaining long fixations, these authors restricted their data analysis to the early components of the fERPs. Building up from these studies the design of our paradigm allowed us to have access to both early sensory and late cognitive potentials during the visual search task and to compare these potentials with the components of a control oddball task. Our findings demonstrate that it is possible to obtain robust cognitive ERP components during visual search tasks with crowded and complex natural images. The remarkable similarities between the evoked responses in both tasks link the results we obtained during free exploration with the large literature describing evoked responses with stimuli flashed at fixation (Fisch et al., 2009; Gaillard et al., 2009; Hillyard et al., 1973; Kranczioch et al., 2003; Navajas et al., 2013; Picton, 1992; Polich, 2007; Polich and Kok, 1995; Quiroga et al.,

The neural correlates of object detection have been explored with different techniques in humans including EEG (Hillyard et al., 1973; Navajas et al., 2013; Polich and Kok, 1995), fMRI (Kanwisher et al., 1997), EcoG (Fisch et al., 2009; Gaillard et al., 2009), single cell recordings in humans (Quiroga et al., 2008) and animals (Sigala and Logothetis, 2002). The visual and auditory oddball tasks are two well-known paradigms that researchers employ to study target detection with EEG (Hillyard et al., 1973; Polich and Kok, 1995). Several previous studies using rapid serial visual presentation, attentional blink or oddball paradigms have shown that targets and distractors are best separated by the evoked P3 component (Hillyard et al., 1973; Kranczioch et al., 2003; Polich and Kok, 1995). In our experiments we used a variation of the classical oddball task; we employed faces as stimuli and asked subjects to respond at the end of the sequence, rather than immediately after seeing the target. These differences with respect to the classical oddball task allowed us to control for the EEG activity related to button responses after the presentation of the target stimuli; plus a more direct comparison with the results of the free-viewing experiment. We tested the hypothesis that a P3-like component is elicited upon target detection during visual exploration. For the visual search and the oddball tasks the fERPs/ERPs found in the first 250 ms were equivalent in latency and amplitude for targets and distractors, while a robust P3 only associated with the detection of targets appeared after ~300 ms. There were differences in the scalp topographies between both paradigms; while in free viewing targets elicited a P3 component with maximum amplitude over parieto-central recording sites, the oddball exhibited an earlier peak with a frontal topography, followed by a later peak that also reached central, parietal, and occipital channels.

Analysis of single trial epochs can potentially reveal more information than average event-related potentials. Single trial analysis of event-related potentials has previously been used to address different problems such as the decoding of stimulus identity or subject's response from the neural signals (Blankertz et al., 2011; Parra et al., 2008; Sajda et al., 2009), the effects of trial-to-trial variability (Quiroga and Garcia, 2003; Ratcliff et al., 2009), and the neural mechanisms underlying average responses (Jung et al., 2001; Navajas et al., 2013). The signal-to-noise ratio in the fERPs allowed single trial predictions: we were able to distinguish fixations to targets and distractors from the EEG signals for 11 out of 12 subjects well above chance (mean accuracy of 63%). Although the performance was significantly lower than the one obtained with the control oddball paradigm, the information that was used by the classifier for both

tasks originated from the P3 component. Our results show that this component, one of the landmarks of cognitive processing in EEG recordings, is present in visual search tasks with unconstrained spatial ocular movements.

In addition to the cognitive components that emerged in the visual search task, we also found artifact-related and sensory potentials. Near fixation onset, we observed a frontal component that was generated by the superposition of the spike potential (SP), caused by the contraction of extra-ocular muscles, and the corneo-retinal dipole (CRD) that originates from the rotation of the eyes (Dimigen et al., 2009; Plöchl et al., 2012; Yuval-Greenberg et al., 2008; see Figs. 2 and 3). As expected, this potential peaked a few milliseconds after saccade onset, displayed a biphasic shape, and increased its amplitude with saccade size (see Fig. 6) (Carl et al., 2012; Keren et al., 2010). We also observed prestimulus activity for the oddball task, which is likely to contain a contribution from the offset of the previous stimulus. Several characteristics of sensory fixation-related potentials have been the subject of many recent investigations. In particular, a recent study focusing on early potentials in a free-viewing task showed that the amplitude of early fERP components is modulated by differences in luminance between successive fixation locations (Ossandón et al., 2010). Previous studies recording from V1 neurons of macagues examined the phase of neuronal oscillations after fixation onset (Schroeder and Lakatos, 2009), and reported an enhancement in the amplitude of the transient responses to visual stimuli; this has been interpreted as a consequence of the increment in phase coherence (Rajkai et al., 2008; Schroeder and Lakatos, 2009). Such findings have led to the hypothesis that fixation-related responses to visual stimuli should have a higher signal-to-noise ratio than ERPs obtained under fixed-gaze paradigms. Our results favor this hypothesis by showing an increase in amplitude of the P1 component for the fERPS compared to conditions without eye movements. This modulation is characteristic of the visually evoked lambda response (Thickbroom et al., 1991), which appears approximately 100 ms after fixation onset, depending on the saccade size, low level features; such as luminance and contrast, and has been interpreted as the P1-equivalent in free-viewing (Dimigen et al., 2012). Given the existence of a strong P1 response after fixation and that the modulation of its peak amplitude is given by the amplitude of the preceding saccade; our results suggest that for fERPs the P1 is generated by a perceptual component related to the processing of a stimulus at fixation, and by a saccade component or lambda potential generated by brain activity associated with eye movements (Thickbroom et al., 1991; Yagi, 1981). This is consistent with previous neurophysiological reports in humans and monkeys that show the existence of saccadic related responses locked to the onset of eye movements (Fourment et al., 1976; Rajkai et al., 2008; Skrandies and Laschke, 1997; but see also Ossandón et al., 2010, for an experiment in which clear visual components were absent when subjects performed saccades on a homogeneously gray screen).

For comparison, we implemented a simple fixed-gaze paradigm using faces taken from the visual scenes. Although we tried our best to make the paradigms as similar and comparable as possible, some visual properties have not been preserved and some cognitive processes might have differed between the tasks. For example, the enhancement in the amplitude of the P1 component during the visual exploration task in comparison to the oddball task could reflect an increasing effort in selecting the target from surrounding peripheral distractors, a higher attentional demand (as demonstrated by Hillyard et al., 1973), the influence of the preceding saccade amplitude (as shown in Fig. 6), or perceptual differences between the stimuli in the tasks (one face presented in isolation during the oddball task compared with one face surrounded by other faces during free exploration). Requiring participants to make fixations with sufficiently long durations (in order to analyze latelatency fERP components) might have also introduced some additional neural activation linked to executive control or motor functions, which could have also contributed to the differences between ERPs and fERPs. Despite these differences due to the particular paradigm implemented

here, central aspects of visual processing could be intrinsically different between passive (fixed-gaze) search and active (free viewing) search. First of all, in active search the decision of identifying the identity of a stimulus is linked to the decision of where to look next; several models of control of eye movements have been developed to explain that sequence mainly in visual search, scene perception and reading (Engbert et al., 2005; Findlay and Walker, 1999; Nuthmann et al., 2010). Secondly, the segmentation of the cognitive tasks could be different. Indeed, the discrete stucturing of attention in an RSVP task (Wyble et al., 2009, 2011), has been recently shown to fit naturally into fixations using an attentional blink task embedded in eye movements (Kamienkowski et al., 2012a, 2012b). Finally, the expectation is also intrinsically different in both fixed-gaze and free viewing; in natural viewing participants can have a glance of the following position using peripheral vision (Kliegl et al., 2006), and they are continuously updating information about the whole scene, estimating the likely position of the target (Najemnik and Geisler, 2005). We acknowledge the need of further studies to assess those very interesting issues on fERPs in more ecological environments; but we note that, in spite of the differences between the tasks, remarkable similarities in the late cognitive fERPs that distinguish targets from distractors offer a novel bridge between fixed-gaze and free exploration paradigms.

Understanding brain responses under the presence of eye movements is a challenging question, with theoretical and practical implications (Dandekar et al., 2012). However, the few studies that have previously investigated saccade or fixation potentials have mostly used constrained eye movement tasks with subjects moving their eyes at restricted locations and at fixed times set up experimentally. These works have focused on a wide spectrum of questions; such as the technical challenges concerning artifacts related to eye movements and microsaccades (Dimigen et al., 2009, 2011; Keren et al., 2010; Yuval-Greenberg et al., 2008), early evoked potentials or "lambda waves" (Thickbroom et al., 1991; Yagi, 1981) and reading (Dimigen et al., 2011). To date, only a handful of studies have looked at fixation-elicited ERPs in tasks allowing eye movements (Brouwer et al., 2013; Dimigen et al., 2011; Graupner et al., 2007; Kamienkowski et al., 2012a, 2012b; Ossandón et al., 2010) and, to our knowledge, no study has previously focused on cognitive ERP components appearing in tasks involving natural scenes.

While several algorithms have been proposed to mitigate the effects of ocular artifacts in the EEG signal, most of them have been largely restricted to the occurrence of rare eye movements occurring in fixation tasks (Jung et al., 1998). Two recent studies have extended ICA-based methods to the field of reading (Dimigen et al., 2011) and to correct for ocular artifacts occurring in saccades across two dimensions (Plöchl et al., 2012). Although these methods were successful in allowing some types of analyses, their application to tasks involving natural scenes, which involve saccades of a wide variety of amplitudes and that are unconstrained in their spatial directions, has remain elusive. This occurred because the number of ICA coefficients related to the artifacts present in the signal increases if eye movements are to be performed freely. Importantly, our experimental design allowed us to avoid this data processing and to directly compare the fERP responses with a control oddball paradigm.

Here we presented a first approach towards brain responses in natural vision. We did so by showing that it is possible to obtain robust cognitive components across spatially unconstrained eye-movements in a real-world-like scenario. We believe our results will encourage further work to understand the mechanisms of object processing and target detection during visual exploration of natural scenes.

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