Fixation-related potentials in visual search: A combined EEG and eye tracking study

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We report a study of concurrent eye movements and electroencephalographic (EEG) recordings while subjects freely explored a search array looking for hidden targets. We describe a sequence of fixation-event related potentials (fERPs) that unfolds during ~ 400 ms following each fixation. This sequence highly resembles the event-related responses in a *replay* experiment, in which subjects kept fixation while a sequence of images occurred around the fovea simulating the spatial and temporal patterns during the *free viewing* experiment. Similar responses were also observed in a second control experiment where the appearance of stimuli was controlled by the experimenters and presented at the center of the screen. We also observed a relatively early component (~150 ms) that distinguished between targets and distractors only in the *freeviewing* condition. We present a novel approach to match the critical properties of two conditions (targets/distractors), which can be readily adapted to other paradigms to investigate EEG components during free eye-movements.

Keywords: ERP, eye movements, visual search, target detection

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Introduction

When exploring a scene, we systematically move our eyes to produce a discrete sequence of fixations, gathering information in each instance of the sequence. Two non-invasive methodologies—event-related potentials (ERPs) and eye tracking—have largely contributed to our understanding of visual processing (Heinze et al., 1994; Henderson, 2003; Liversedge & Findlay, 2000; Luck, Woodman, & Vogel, 2000; Najemnik & Geisler, 2005; Sereno & Rayner, 2003; Thorpe, Fize, & Marlot, 1996).

In the vast majority of ERP experiments visual stimuli are presented while subjects fixate at the center of the screen. One of the most widely studied paradigms involves the detection of a target stimulus embedded in a sequence of distractors. Target detection elicits a consistent response appearing around 300 ms after stimulus onset (Polich, 2007; Sutton, Braren, Zubin, & John, 1965). Earlier physiologic signatures of stimulus identity have also been reported in fixed gaze tasks in the time window between 150-300 ms (Johnson & Olshausen, 2003; Potts, Liotti, Tucker, & Posner, 1996; Thorpe et al., 1996). Despite the knowledge gained from decades of using these type of paradigms (Dehaene et al., 2001; Heinze et al., 1994; S. J. Luck et al., 2000; Polich, 2007; Thorpe et al., 1996), to date, no studies have investigated the physiologic responses

triggered by target detection in more realistic scenarios (Geisler & Ringach, 2009), where instead of fixating at stimuli transiently shown at the center of the screen, subjects look for a target at their own pace, freely exploring a crowded scene.

Some studies have specifically investigated evoked potentials in relation to fixations or saccades under different eye movement scenarios, using non-invasive electrophysiology (Dimigen, Valsecchi, Sommer, & Kliegl, 2009; Graupner, Velichkovsky, Pannasch, & Marx, 2007; Jagla, Jergelova, & Riecansky, 2007; Keren, Yuval-Greenberg, & Deouell, 2010; Luo, Parra, & Sajda, 2009; Marton & Szirtes, 1988a, 1988b; Ossandon, Helo, Montefusco-Siegmund, & Maldonado, 2010; Parks & Corballis, 2010; Rama & Baccino, 2010; Takeda, Sugai, & Yagi, 2001; Thickbroom, Knezevic, Carroll, & Mastaglia, 1991; Thickbroom & Mastaglia, 1985; Yagi, 1981; Yuval-Greenberg, Tomer, Keren, Nelken, & Deouell, 2008). Most of these studies focused on the early ERP components evoked by saccades or fixations in either controlled saccadic tasks (Kazai & Yagi, 1999; Parks & Corballis, 2010; Thickbroom et al., 1991; Thickbroom & Mastaglia, 1985; Yagi, 1981) or reading (Dimigen, Sommer, Hohlfeld, Jacobs, & Kliegl, 2011; Marton & Szirtes, 1988a, 1988b), where the eye movements are also constrained. Only a couple of studies have investigated ERPs during *free viewing* of an image (Graupner et al., 2007; Luo et al., 2009; Ossandon et al., 2010). For instance, Ossandon et al. (2010) showed that the saccade-related potential was consistent with a model of superposition of phase resetting and evoked responses while subjects observed natural images (Ossandon et al., 2010).

In this study we investigated the brain correlates of target detection in a *free viewing* search task using concurrent eye movements and ERP recordings. Our aim was to compare the dynamics of target detection responses during *free viewing* and during controlled fixation. We show that, while the overall pattern of ERP responses in *free viewing* and in matched foveal presentations during fixation are highly similar, there is an early marker of stimulus identity observed only during *free viewing*. We present a simple analytic methodology based on a fixation-matching procedure which can be effectively used to avoid technical problems related to fERP recordings and can serve as a tool for future fERP experiments.

Materials and methods

Participants

Seventeen participants performed the *free viewing* experiment (11 male / six female, age range: 21–31 years). Twenty-four participants were involved in the two fixed gaze control experiments (*replay*: 10 male / two female; [21–31] years; and *oddball*: 11 male / one female; age: [21–31] years). All participants had normal or corrected to normal vision and gave written informed consent. All the experiments described in this paper were reviewed and approved by the ethics committee.

Apparatus

Stimuli were presented in a CRT monitor, at a screen resolution of 1,024 × 768 pixels and a refresh rate of 75Hz. Participants sat in a comfortable chair at 60 cm from the screen with the head stabilized with an in-house chin rest. Responses were collected with a standard keyboard.

Free viewing experiment: visual search task

Each screen contained 20 patches (18 containing distractors and two containing targets), pseudo-randomly distributed in a centered square of 750 pixels (covering an angle of 25.1°). The center of each patch was at least three patches (2.3°) away from each other (Figure 1A, left panel). Each patch was composed by eight black "#" surrounding an E (Targets) or an inverted E (∃, Distractors) (Figure 1A, right panels) in a slightly darker gray than the background. The size of the patches was 0.74°. We used this experimental design to assure that patches had to be foveated for target identification, since the #s exerted a crowding effect on each stimulus (Toet & Levi, 1992; Tripathy & Cavanagh, 2002). Subjects were instructed to find two targets hidden among 18 distractors and press the space bar in the keyboard with their right hand once they identified the second target. We used two targets (instead of one) to have the first target embedded in a sequence of saccades free of any contamination from the manual response. We asked subjects to search the target comfortably, at a normal pace. Additionally, we told subjects they should try to avoid looking at the same patch (target or distractor) more than one time. Using these simple instructions we obtained: 1) Longer fixations than in other visual search experiments, and 2) Less redundancy between fixations, 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 late evoked potentials and low redundancy prevented fixations in which the subject fixated at the target but might have not identified it.

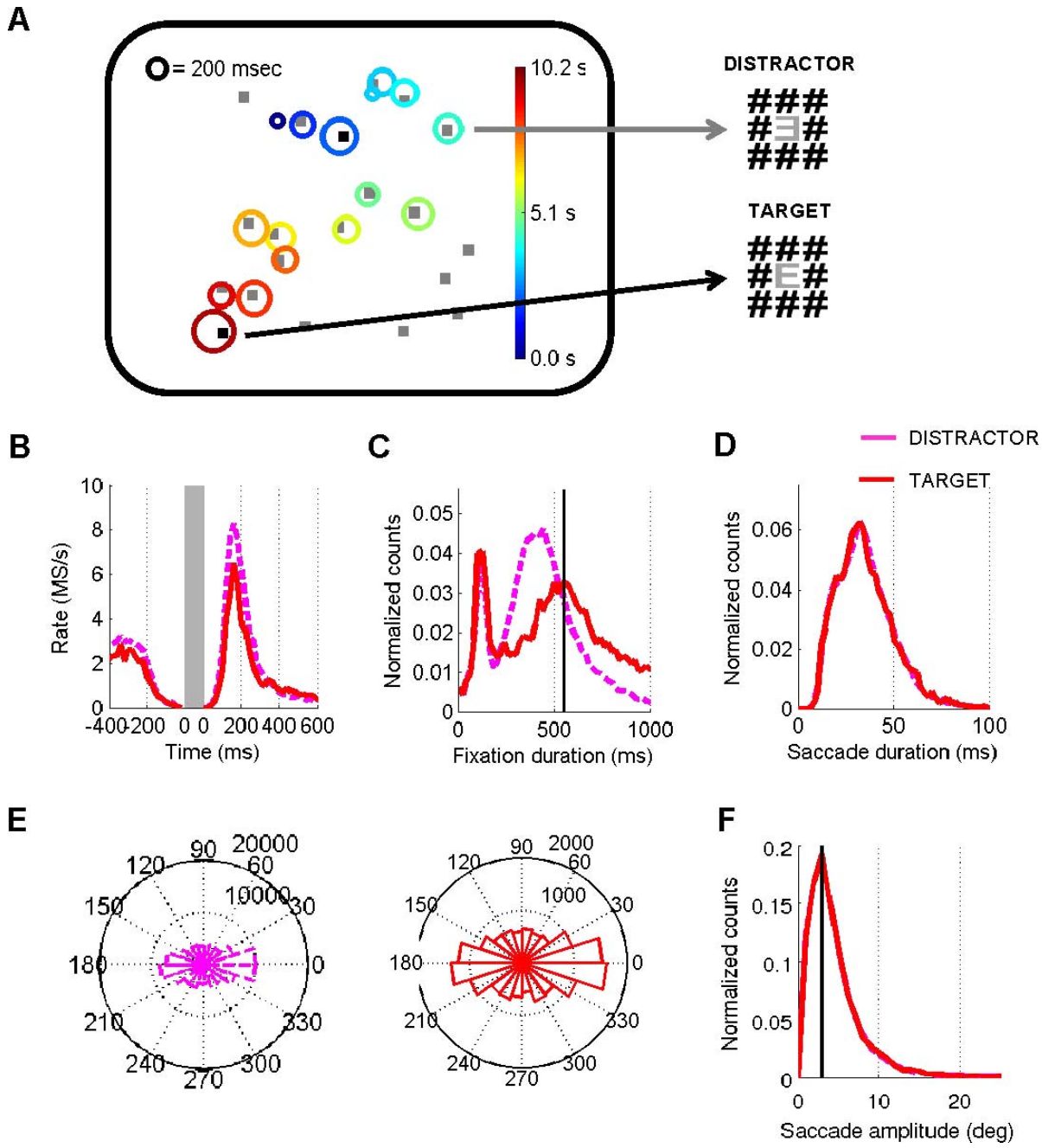

Figure 1. Experimental design and eye movements' statistics. A) Left Panel: Patch location and fixation sequence of a representative trial. The size of the circles represent the duration of the fixation (compared to the black circle on the top left corner). Time course of the trial is color coded. Since it is impossible to visualize the target and distractor patches at this scale, we indicate Distractors (Targets) with grey (black) squares. Right Panel: Zoom of a Distractor and a Target patch B) Microsaccade rate distribution for targets and distractors, exhibiting an early inhibition after the fixation, a peak at approximately 200 ms. An inhibition period is also present before the end of the preceding fixation. C) Distribution of fixation durations for targets and distractors. The black vertical line at 550 ms denotes the threshold we adopted for discarding short fixations. D) Saccade duration distribution for targets and distractors. We selected the baseline taking into account that saccades are shorter than 100 ms (denoted by the vertical black line). E) Saccade angular distribution for targets and distractors. A predominance of saccades in the horizontal direction can be observed for both targets and distractors. F) Absolute saccade distance distribution for targets and distractors. Vertical black line indicates the threshold for large saccades selected for analysis in Supplementary Figure S3D. Red: Target, Magenta: Distractor.

Fixed gaze experiments: replay and oddball

We designed two control experiments with fixed gaze: 1) In the *replay* experiment the sequence of distractors / targets were the same as in *free viewing*, the stimulus duration and the inter-stimulus interval (ISI) were taken from the fixation and saccade durations (Figure 1C and 1D respectively; resulting in stimulus duration of 484 ± 266 ms [mean ± std], and ISI 35 ± 15 ms [mean ± std]). Stimuli positions were slightly displaced with respect to the center of the screen to reflect the displacement of the fixation location relative to the center of the stimulus in the *free viewing* experiment. The distribution of stimulus position was calculated from all fixations inside the patch during the free-viewing experiment. 2) In the *oddball* experiment the sequence of distractors / targets were also the same as in *free viewing*, but all the stimuli were presented in the center of the screen where the subject was fixating, the stimulus duration was set to 100 ms, and the ISI were obtained from the distribution of times between two consecutive fixation onsets, replacing the trials with ISIs shorter than 550 ms by a random value between 550 ms and 1750 ms (resulting ISI [mean ± std]: [633 ± 464] ms). In the two control experiments the subjects' task was the same as in the *free viewing* situation, i.e. to find two targets hidden among N distractors and press the space bar with the right hand. The three experiments were conducted in different sessions and with a different group of participants. The sequence of stimuli was not matched for each individual participant. Conditions were matched pooling together all the trials of the *free viewing* experiment and generating new distributions of ISI and stimulus location from these grand distributions. Since the displayed sequences were constructed from the sequence distributions of subjects performing the *free viewing* experiment, the actual number of distractors displayed depended on the performance of other subjects. Instructions were the same as in the *free viewing* experiment.

General design

All experiments were implemented in MATLAB (Mathworks, Natick, MA) using psychophysics toolbox (Brainard, 1997). Subjects performed between 150 and 250 trials (mean: 209 trials) in the *free viewing* experiment, with resting time and drift corrections every 10 trials, and recalibrations of the eye tracker every 50 trials. In the control experiments subjects performed 180 trials with resting time and drift corrections every 10 trials, but with only one calibration at the beginning of the experiment. Each trial started with a green fixation dot randomly positionedfor 3000 ms mainly to rest and allow blinks, then the dot turned gray for 800 ms (prepare signal), and then all patches were presented until the subject completed the sequence and pressed the space bar.

EEG data acquisition and preprocessing

EEG activity was recorded on a dedicated PC at 1024Hz, at 128 electrode positions on a standard 10–20 montage, using the Biosemi Active-Two system (Biosemi, Amsterdam, Holland). Also, the electrooculogram (EOG) was recorded at the left and right external ocular canti (horizontal EOG), and under the eye and above the eyebrow (vertical EOG); four reference electrodes were placed at both mastoids and ear lobes. After data were recorded, the sampling rate was digitally downsampled to 512Hz using a fifth order sinc filter to prevent aliasing, and imported into MATLAB using the EEGLAB toolbox (Delorme & Makeig, 2004) with the reference in the right ear lobe. The data was filtered between 1Hz and 100Hz (six-order elliptic filter) and the 50Hz line signal was suppressed with a notch filter between 49Hz and 51 Hz. We used average reference for all the results presented in this work. Bad channels were detected by visual inspection of the raw data and the spectra, and replaced by an interpolated signal using all the other channels weighted by the inverse distance to the replaced channel. This was necessary in less than 50% of subjects for one or two channels per subject. We kept only fixations lasting between 550 ms and 1750 ms (Figure 1C and Eye Movement data acquisition and preprocessing). Data were cropped between 250 ms before and 550 ms after the onset of each fixation. For the trials considered, no additional saccades were present during this period. Since the artifact of the previous saccade was restricted from 100 ms to 0 ms before the fixation onset (Figure 1D), the baseline for each channel was defined between 200 ms and 100 ms before the onset of the current fixation, and subtracted. We only considered intervals without blinks. From the eye movement data, we also discarded periods containing microsaccades (Figure 1B) to avoid any potential bias in the interpretation of results (Dimigen et al., 2009; Yuval-Greenberg et al., 2008). To further eliminate artifacts we applied an amplitude threshold of amplitude 75 μV to each channel x epoch from the onset of fixation (0 ms) to the end of the considered interval (550 ms). Hence this elimination procedure does not include the artifact of the last saccade. If less than five channels in one epoch exceeded the threshold those channels were interpolated in that epoch, and if more than five channels in one epoch exceeded the threshold the trial was rejected. All the subjects contributed with more than 20 epochs in the target condition after the rejection/artifact correction process

and were kept for further analyses. The average number of target epochs after all rejections was 55 ± 34 trials per subject (range: [21–145]). The same criteria were also used for the preprocessing of data from the control experiments (average number of target epochs: *replay*: 67 ± 23 trials per subject (range: [32, 114]), and *oddball*: 137 ± 33 trials per subject (range: [74, 194])). ERPs shown in all figures were calculated as the median value of the all the subject-level ERPs, where each subject-level ERP was itself computed as the median of all epochs of a participant.

Eye Movement data acquisition and preprocessing

Data acquisition

Eye Movement data was recorded with an EyeLink1000 system (SR Research, Ontario, Canada). For 39/41 subjects the eye tracker was used in binocular mode with stabilized-head and sampling rate of 1 kHz in each eye. Data from two participants in the main experiment were acquired in a monocular and remote configuration of the eye tracker, with a sampling rate of 0.5 kHz in each eye. Exclusion of these subjects from the analysis did not change any of the results presented in this work. The data was recorded with a sampling rate of 1 kHz and downsampled to 500 Hz before saccade detection. The eye tracker was calibrated in 13 points spanning the central part of the screen, where the stimuli were presented.

The quality of the calibration was verified comparing the mean error during the first 25 trials after each calibration for all subjects with the last 25 trials of the main experiment. No significant differences were found ($P = 0.95$, Wilcoxon rank-sum test), suggesting that the calibration procedure was adequate.

Saccade detection

We used an adapted version of the algorithm of Engbert and Kliegl (http://www.agnld.uni-potsdam.de/~ralf/MS/) to detect the saccades and separate the microsaccades as done in previous studies (Laubrock, Kliegl, & Engbert, 2006; Moller, Laursen, Tygesen, & Sjolie, 2002; Otero-Millan, Troncoso, Macknik, Serrano-Pedraza, & Martinez-Conde, 2008; Rolfs, Kliegl, & Engbert, 2008; Troncoso, Macknik, & Martinez-Conde, 2008) and in particular as in the previous EEG – Eye Tracking works (Dimigen et al., 2009; Yuval-Greenberg et al., 2008). This algorithm has three critical parameters that need to be defined empirically: The minimum duration of the (micro)saccade, the velocity threshold, and the minimum inter-saccadic interval. This last parameter was added to prevent detecting corrective movements as new saccades (Moller et al., 2002; Troncoso et al., 2008). Based on bibliography and inspection of the raw data we set these parameters to: *minimum duration of the (micro)saccade*: 3 ms, *velocity threshold* = 6 times the mean velocity and *the minimum inter-saccadic interval* = 50 ms. To reduce noise (Engbert & Mergenthaler, 2006), we only considered binocular (micro)saccades defined as (micro)saccades that occur simultaneously in both eyes for at least one sample (2 ms) (Engbert & Kliegl, 2003; Engbert & Mergenthaler, 2006; Laubrock, Engbert, & Kliegl, 2005; Moller et al., 2002; Otero-Millan et al., 2008; Rolfs, Laubrock, & Kliegl, 2006; Troncoso et al., 2008). Microsaccades were distinguished from saccades based on their amplitude using a 1° threshold (Engbert & Mergenthaler, 2006; Otero-Millan et al., 2008).

Correction of displacements

The locations of the fixations recorded with the eye tracker were corrected by applying a fixed displacement in each separate trial. The value of the correction was calculated as the mean displacement of all the fixations during the trial relative to the closest patch, for all displacements lower than 1.15° to prevent correcting the position of fixation to patches with fixations to the empty space. If less than half of the total fixations were considered in a certain trial, the procedure was repeated with 2.3° instead of 1.15°. If this procedure failed, the trial was discarded.

Fixation/trial rejection criteria based on eye movements

We applied the following criteria to reject fixations for the present analysis: The duration was shorter than the epoch limit (550 ms) to analyze data free from saccade artifacts. We also discarded fixations larger than 1750 ms (Figure 1C). Whenever two successive fixations were directed near the same patch (<1.15° from the center), the second fixation was removed from analysis. We also discarded from analysis all the fixations that were preceded by very short fixations (< 100 ms). Fixations that included blinks or microsaccades inside the epoch limits were also discarded.

In the *Free viewing* experiment we also matched the properties of the preceding saccade –horizontal (*dx*) and vertical (*dy*) amplitudes and duration (*dt*)– across conditions, to prevent potential differences in baseline (Luo et al., 2009). For each fixation in one condition we looked for the most similar fixation in the other condition, i.e. the one closer in the sense of the quadratic distance in the (*dx*,*dy*,*dt*) space normalized by the sum of the standard deviations. Since the distributions of these variables were initially very similar (Figure 1D, E) and we had 10 times more distractors than targets, we were able to find a pair for each target. This procedure also equated the number of fixations considered in each condition. To

Parameter	Fixations to distractors	Fixations to targets	*p*-value
Saccade duration (*dt*) (ms)	31.0 ([27.0 34.0])	32.0 ([27.8 34.5])	0.7420
Horizontal saccade amplitude (*dx*) (deg)	0.51 ([0.033 1.275])	0.43 ([0.200 0.973])	0.7829
Vertical saccade amplitude (*dy*) (deg)	0.09 ([-0.046 0.752])	0.23 ([-0.049 0.739])	0.8363

Table 1. Comparison between matched parameters. Values are expressed as median [inter-quartile interval]. *P*-values were the result of a Wilcoxon rank-sum test between the median fixation to distractors and targets across all participants for each parameter.

further test that the distributions of *dx*, *dy*, and *dt* were matched for both conditions and were not different, we performed a paired rank-sum tests across participants for each individual parameter. The same procedure was applied for all controls in all supplementary figures. None of these comparisons showed significant differences (Table 1 and Supplementary Table S1).

Eye tracking and EEG synchronization

To synchronize the eye movements and EEG data the display computer sent a clock signal through the parallel port to the EEG and a clock signal through the Ethernet port to the eye tracker. We sent synchronization signal at different events (preparatory signal, start of trial, subject response, end of trial).

The synchronization of the two signals was assessed offline by comparing the onset of the saccades detected with the EOG channels (with a derivative and peak of the derivative procedure) with the onset saccades detected by the Engbert and Kliegl algorithm (Engbert & Kliegl, 2003). The realignment was in all cases smaller than 20 ms.

Statistical analysis

Early visual component latencies

Statistical analysis was carried out by the Kruskal-Wallis test, an extension of the Wilcoxon rank sum test to more than two groups, with "experiment" as the independent factor for each early visual component (Table 2). Differences of $p \leq 0.05$ were considered significant.

Comparisons between targets and distractors

In all cases we submitted each (channel, time) sample to a non-parametric Wilcoxon rank-sum test to compare the two conditions (target versus distractors) across all subjects. This implies over 36,096 comparisons for each pair of conditions. We filtered these multiple comparisons across time samples and recording sites with the following criteria: 1) We kept only samples with $p < 0.01$; 2) For each channel, a given time point was considered significant if it was part of a cluster of 10 or more consecutive significant consecutive time points (19.5 ms time window) (Dehaene et al., 2001; Steven J. Luck, 2005; Murray, Foxe, Higgins, Javitt, & Schroeder, 2001; Thorpe et al., 1996); 3) Each sample was considered significant for a given electrode if, for the same time point, at least one of its neighboring electrodes also fulfilled 1) and 2).

Comparisons between targets and distractors on a subject-by-subject basis

Similar to the grand average analysis, we submitted each (channel, time) sample to a non-parametric

	Free viewing	Replay	Oddball	χ^2	*p*-value
Occipital left channels					
First positive peak	86 ([71 104])	80 ([74 87])	99 ([90 111])	6.12	0.0468
First negative peak	133 ([88 142])	130 ([116 138])	135 ([131 158])	2.66	0.2648
Second positive peak	156 ([121 197])	165 ([140 188])	203 ([167 222])	5.26	0.0722
Occipital right channels					
First positive peak	102 ([91 120])	88 ([76 90])	98 ([90 105])	4.83	0.0892
First negative peak	156 ([139 179])	139 ([119 146])	143 ([126 166])	2.13	0.3439
Second positive peak	209 ([188 221])	183 ([164 201])	208 ([155 224])	1.13	0.5680

Table 2. Latencies of early visual potentials. Values are presented as median [inter-quartile interval]. The *first positive peak* was required to exhibit latencies larger than 40 ms and amplitudes larger than 0.25 μV. The *second positive peak* was considered as the next positive peak with a minimum distance between peaks of 31 ms. The *first negative peak* was considered as the first negative valley after the *first positive peak*. Statistical analysis was carried out by the Kruskal-Wallis test with "experiment" as the independent factor for each early visual component (see Statistical analysis section). Differences of $p < 0.05$ were considered significant.

Wilcoxon's rank-sum test to compare the two conditions (target versus distractors) across all trials in each subject. We filtered these multiple comparisons with the same criteria as in the between subjects comparison. To assess the latency of the early discrimination in each subject, we selected the channel with the lowest p-value between 150 and 250 ms, and looked for the first time point in which the p-value for this channel crossed the 0.01 threshold.

Comparisons of difference waves among the three experiments

For each channel considered in Figure 5 (Fz, Cz, Pz, Oz) we submitted each time point to a non-parametric Kruskal-Wallis test to compare the three experiments. We filtered these multiple comparisons across time with the following criteria, similar to the comparisons between targets and distractors: 1) We kept only samples with $p < 0.05$; 2) A given time point was considered significant if it was part of a cluster of 15 or more consecutive significant consecutive time points (29 ms time window) (Dehaene et al., 2001; Steven J. Luck, 2005; Murray et al., 2001; Thorpe et al., 1996).

Regression on principal components

We used the first two principal components that resulted of the decomposition of the ERPs for the differences between targets and distractors in the three experiments. On a single-trial basis we performed a regression analysis on these components plus an offset, and then averaged for each subject and over all subjects to obtain the grand-average (Duda, Hart, & Stork, 2000; Sigman & Dehaene, 2006). Significant differences between targets and distractors were assessed as in the 128-channel space, and filtered in time with a window of 29 ms.

Onset times

We defined the onset as the first time at which there is a significant difference between the waves of targets and distractors and the significance was estimated with the method described previously (Dehaene et al., 2001; Steven J. Luck, 2005; Murray et al., 2001; Thorpe et al., 1996). We mostly focused on the onset time estimated from the principal component analysis. Note that different onset times are present (in the principal component space, and in the electrodes space both for all participants and for each participant separately).

Source modeling

Cortical current density mapping was obtained using a distributed model consisting of 10,000 current dipoles. Dipole locations and orientations were constrained to the cortical mantle of a generic brain model built from the standard brain of the Montreal Neurological Institute, and warped to the standard geometry of the electroencephalogram (EEG) sensor net. The warping procedure and all subsequent source analysis and surface visualization were processed with the BrainStorm software package (Tadel, Baillet, Mosher, Pantazis, & Leahy, 2011; http://neuroimage.usc.edu/brainstorm). EEG forward modeling was computed with an extension of the overlapping-spheres analytical model (Huang, Mosher, & Leahy, 1999). Cortical current maps were computed from the EEG time series using a linear inverse estimator (weighted minimum-norm current estimate, Baillet, Mosher, & Leahy, 2001). Evoked responses in each region of interest (ROI, Figure 7) were shown as the power of all current sources in the ROI.

Results

Behavior and eye-movement analysis

Participants explored a sequence of visual patches. Each patch contained an object, which could be either a target or a distractor, masked by a texture. The mask forced subjects to fixate in order to determine whether the object in the patch was a target or a distractor (Figure 1A). Two patches contained a target (the letter E) while the remaining 18 patches in the screen contained distractors (the horizontal mirror image ∃). Participants scanned the image freely. Once they had seen both targets they responded with a key press. This experimental design allowed us to compare responses to the first target and to distractors without a motor response confound.

During task execution, we recorded simultaneously the high-density electroencephalogram (EEG) and eye movements. Seventeen participants scanned on average (8 ± 1) patches before finding the first target and (18 ± 2) before concluding the search occurring at (9.8 ± 1.6) seconds on average. An average of 3,723 fixations (range: [2,360–4,740]) were obtained in approximately 200 trials per experiment. The distribution of fixation durations was bimodal (Figure 1C) with very short fixations, typically followed by a corrective saccade towards the same patch. Only fixations with a duration exceeding 550 ms and free of blinks and microsaccades were included in the EEG analysis (see Materials and methods).

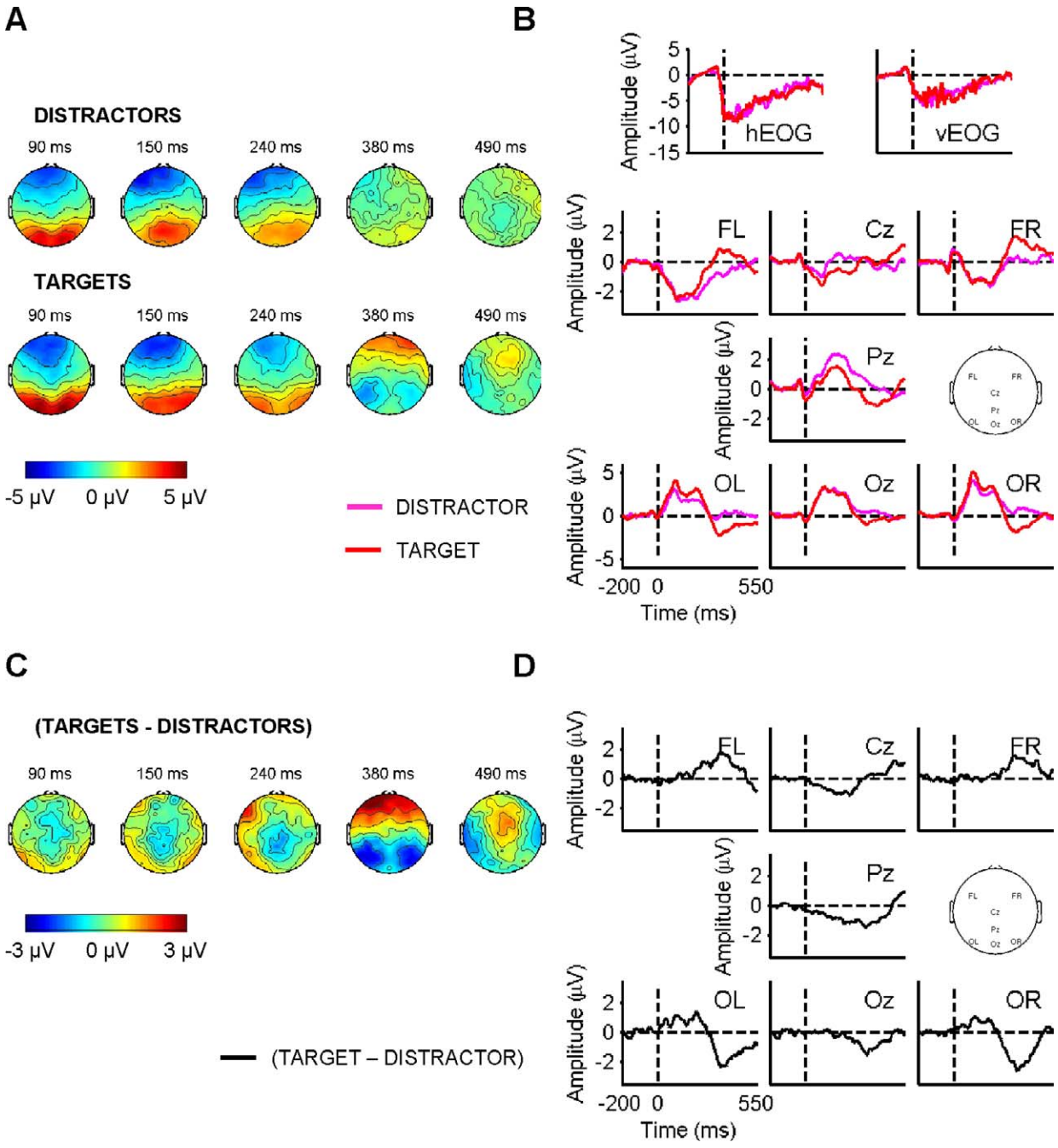

Figure 2. Fixation-event related potentials (fERPs). A) Temporal course of scalp distributions for Targets and Distractors, and B) fERPs at six scalp locations (FL, Cz, FR, OL, Oz, OR) and the vertical and horizontal EOG. Red: Target – *free viewing*, Magenta: Distractor – *free viewing*. C) Temporal course of scalp distributions of the difference between Targets and Distractors, and D) differential responses of the fERPs at six locations (FL, Cz, FR, OL, Oz, OR). Color scale in A: Blue-Red: [-5 5] μV, and in C: Blue-Red: [-3 3] μV.

Fixation-event related potentials to target and distractors

Fixation-event related potentials (henceforth referred to as fERPs) unfolded as a sequence of discrete components. Responses evoked by distractors were mainly positive at occipital electrodes, showed a first peak at a latency of 100 ms (Figure 2A). In contrast, fixations to targets also elicited a sustained late response lasting at least 550 ms (lower panel of Figure 2A, B and Supplementary Figure S1). This shows that ERPs obtained during free eye movements can reliably distinguish between target and distractor categories (Figures 2C, D and Supplementary Figure S1, S2).

To compare responses during *free viewing* and during gaze-fixation (as done in the vast majority of EEG

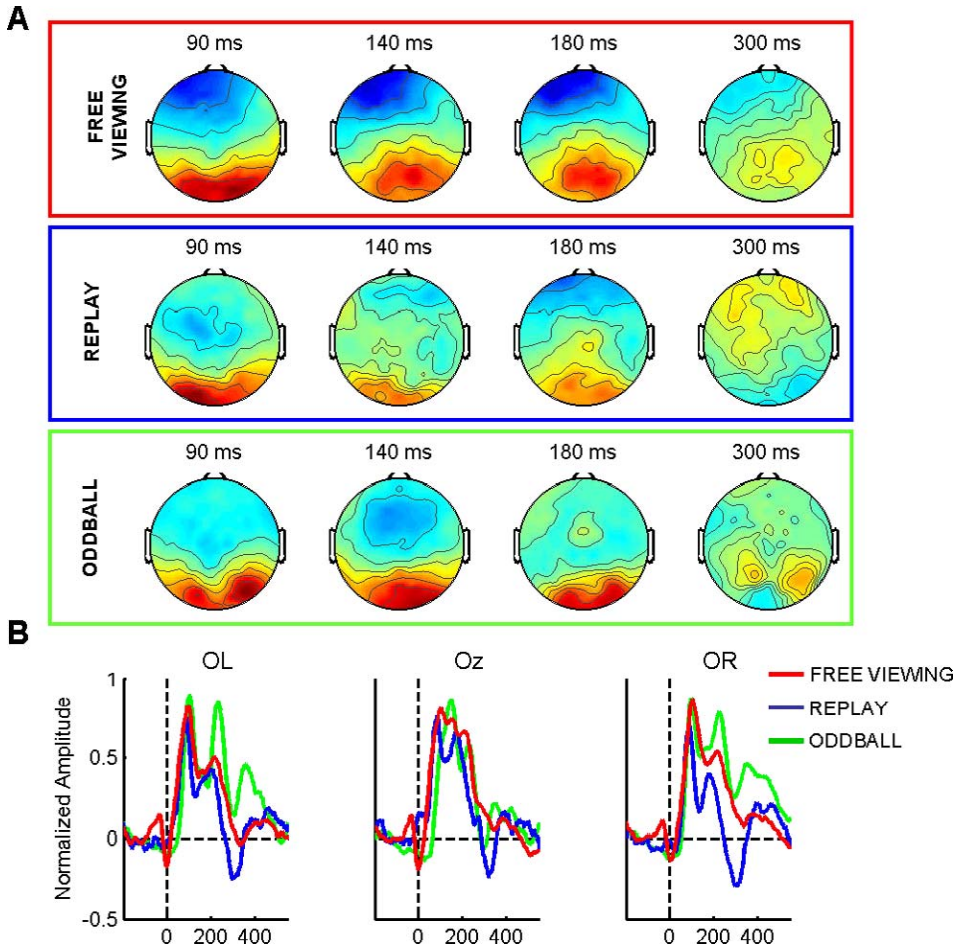

Figure 3. Early evoked potentials. A) Sequence of scalp distributions. Amplitudes were normalized by the maximum range across all samples (channels x data points) in each task. B) ERPs for the three experiments in three occipital channels. Each curve corresponds to an average of three neighboring electrodes. Curves represent the median across subjects. Red: *free viewing*, Blue: *replay*, Green: *oddball*.

studies), we investigated two control experiments: 1) An *oddball*, in which sequences of patches (identical to those used in the *free viewing* experiment) were presented at the center of the screen with an inter-stimulus interval between 550 and 1750 ms. The precise sequence (i.e., the order of targets and distractors) was obtained from the *free viewing* experiment. 2) A *replay* experiment in which the sequence order, the inter-stimulus interval, the stimulus duration, and the position of the center of the patch relative to the fovea were matched to the distribution of the corresponding parameters in the *free viewing* experiment. This control experiment simulated the situation where the content of the retinal image around the fovea during sustained fixation mimics the projection of the central patch during *free viewing* without the presence of eye movements.

Early potentials evoked by distractor stimuli

Early visual potentials evoked by distractors showed qualitatively similar waveforms for the three independent experiments (*free viewing*, *replay*, and *oddball*) (Figure 3). We identified a sequence of three main components (located at approximately 100 ms, 130 ms, and 200 ms) in each of them. Latencies of these early potentials measured for each individual subject did not differ significantly among experiments. Except for the P1 at occipital left channels (Kruskal-Wallis test: $p = 0.0482$), all comparisons between experiments for different peak latencies and channels were not significant (Kruskal-Wallis test: $p > 0.05$, Figure 3B and Table 2). Despite this overall resemblance in the dynamics of evoked components, we observed some differences between experiments. For instance, the second peak (at ~200 ms) was more pronounced in the *oddball* experiment with a topography which mapped to bilateral posterior channels, consistent with an off response since the stimulus was present for only 100ms in the oddball experiment whereas in the other experiments stimuli durations were both variable and lasted during all the fixation in *free viewing*, and almost during all the epoch in the *replay* condition.

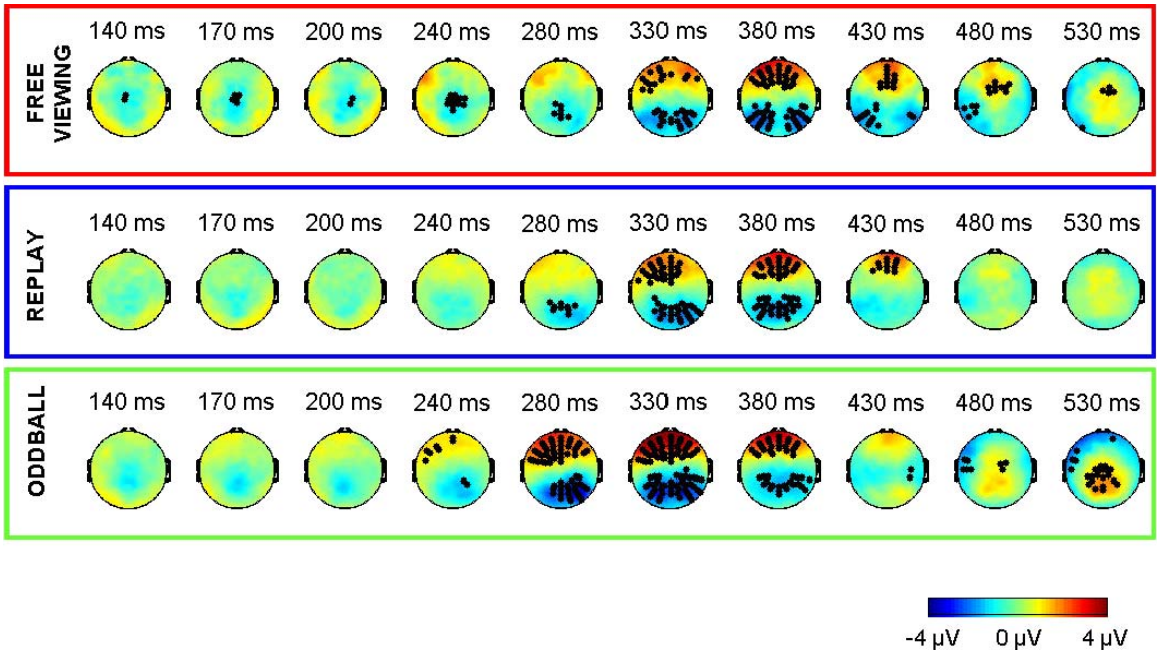

Figure 4. Discrimination between Targets and Distractors. Temporal course of scalp distributions for the difference between Targets and Distractors in the three experiments. Black dots indicate the channels where we found a significant discrimination between Target and Distractors ($p < 0.01$; see Materials and methods). Color scale: Blue-Red: [-4 4] μV.

Medium-latency and late target effects

We then compared the responses to target and distractors in free viewing and fixed gaze experiments. In all three experiments we observed a relatively late (>270 ms) component that distinguished fERPs of targets and distractors. This difference was significant for the three experiments in frontal and occipital channels (Figure 4; $p < 0.01$, Wilkoxon rank-sum test with window-based correction, see Materials and methods section). The topography was similar for the three conditions; the correlation coefficient across all channels between experiments at 330 ms and 380 ms were above 0.9, for all combinations of experiments (at 330 ms: $r_{(\text{FreeViewing/Replay})} = 0.96$; $r_{(\text{FreeViewing/Oddball})} = 0.95$; $r_{(\text{Replay/Oddball})} = 0.96$). However, this medium-latency target effect in the *oddball* experiment peaking around 310 ms in frontal and occipital electrodes (Figure 5A) did not only appear to be stronger, but also begins earlier in conventional ERPs than in *free viewing* since potentially different target effects overlap at least for the *free viewing* experiment; the onsets were defined below (Figure 4). Comparing directly the target effects for the different experiment we found significant differences from 258 ms and 271 ms in Fz and Pz electrodes respectively (Figure 5B; $p < 0.05$, Kruskal-Wallis test with window-based correction, see Materials and methods section) and was also hinted in Oz, consistent with the previous observations (note that the onset of the target effect for the *oddball* experiment in Figure 4 [bottom row] was 230 ms). This potential was followed by a central/parietal positivity, usually referred as a P3 (Polich, 2007), starting around 480 ms after the initiation of the fixations and reaching significance for the *free viewing* and *oddball* paradigms at central channels ($p < 0.01$, Wilkoxon rank-sum test with window-based correction).Although the late target effect seemed to be larger and maybe faster for the *oddball* experiment, this effect did not reach significance (Figure 5).

In brief, while early visual evoked potential and medium-latency (~300 ms) and late (~500 ms) target effects seemed to be almost similar between the three experiments, we found two main differences that distinguish mainly between the oddball experiment and the other two: 1) A larger second positive visual response in the oddball experiment, consistent with an off response due to shorter stimulus duration; and 2) larger and faster medium-latency and late target effects in the *oddball* experiment.

Early target effects

Interestingly, when further comparing target versus distractor responses in *free viewing* and gaze-fixation experiments we observed an early potential projecting to central/parietal electrodes which was only significant in the *free viewing* but not in the fixed gaze controls (Figure 4; the onset of the target effect for the *free viewing* experiment [top row] was 133 ms, but a more precise value of the onset is given below). This early

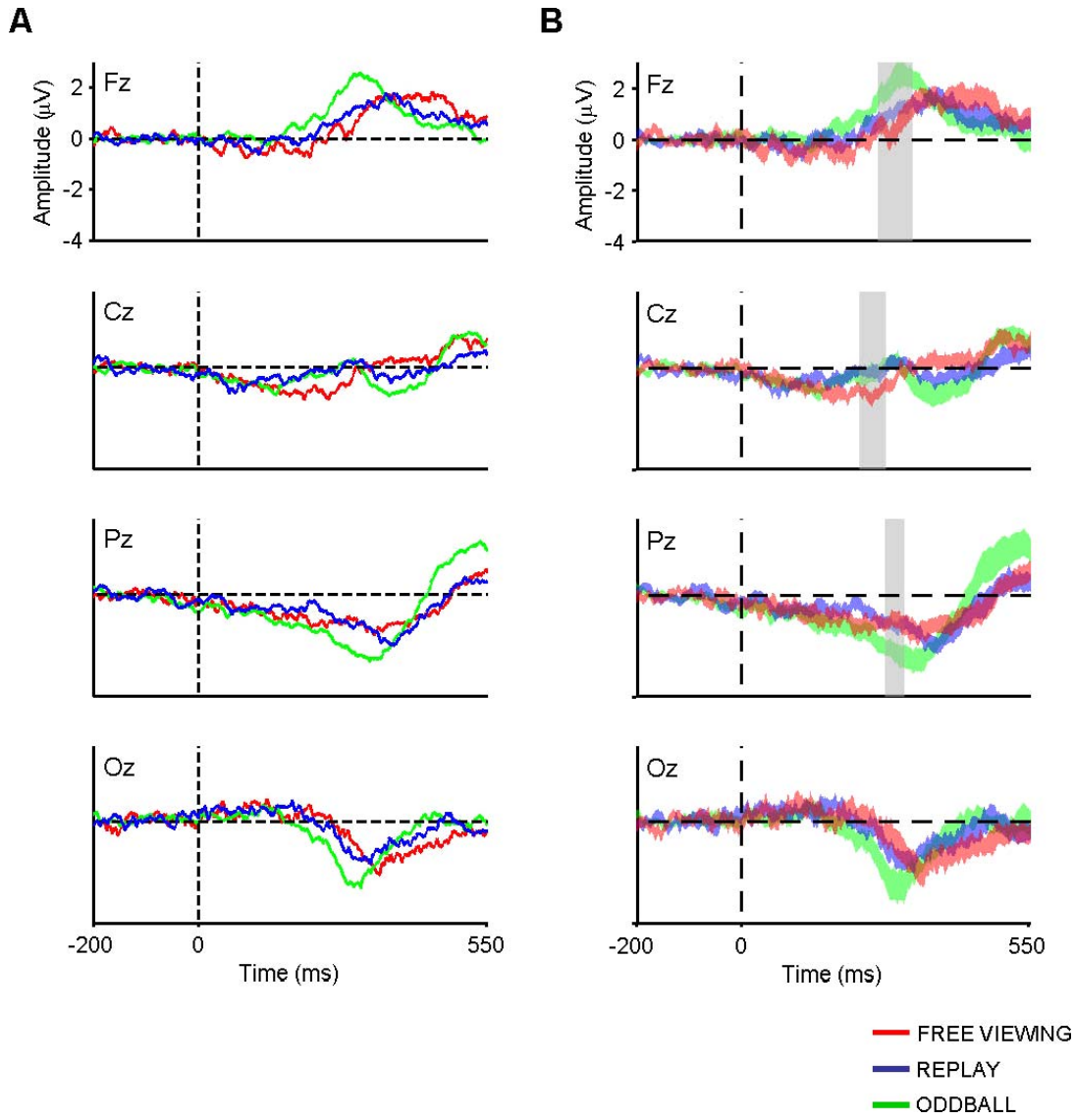

Figure 5. Target minus distractor effect on central electrodes. A) Differential responses (Target – Distractor) at four central scalp locations (Fz, Cz, Pz, Oz) for the three experiments. B) Same as A, including the variance and the periods in which the responses in the three experiments differed significantly (gray shadows; Kruskal-Wallis test with window-based correction; $p < 0.05$).

negativity was also apparent in the oddball experiment, although it was more parietal and it didn't reach significance (compare top and bottom rows in Figure 4). Direct comparison of the difference waves between experiments in Figure 5B showed a significantly larger negativity at Cz for the *free viewing* experiment (Figure 5B; $p < 0.05$, Kruskal-Wallis test with window-based correction), starting at 223ms earlier than the differences in favor to the *oddball* experiment in electrodes Fz and Pz (Figure 5B). Interestingly, this early negativity in Cz for the *free viewing* experiment seemed to be a qualitatively different event from the medium-latency potential, not present in the other experiments. On the contrary, the early parietal negativities (see first scalps of the bottom row in Figure 4) were more likely the onset of the medium-latency potentials and were present in all experiments (Figure 5).

The early component reached significance in the grand average fERP in the 128-electrode space at 133 ms and was sustained at least until 250 ms, when it overlapped with the medium-latency potential (Figure 4, top row; $p < 0.01$, Wilkoxon rank-sum test with window-based correction). Next, we performed a series of control analyses to investigate possible confounds which might explain this early difference between target and distractors for the free-viewing conditions.

First, we investigated whether the effect persists for shorter fixations. All the analyses reported here were done considering relatively long fixations (550–1750 ms) where we could investigate and compare all the observed potentials during the course of each individ-

ual fixation. For the specific case of this early central fERP which was observed only in the *free viewing* condition we could investigate whether it persisted in short fixations. We observed that in short fixations fewer electrodes showed a significant difference. Despite the reduction in the effect, it remained significant and showed similar topography (Supplementary Figure S3A).

Second, we investigated whether the difference between target and distractors in the free viewing condition might be explained by the fact that targets were preceded, on average, by more fixations than distractors. Previous studies have shown that the amplitude and latency of P1 and N1 components at fixation onset (following a saccade) change with each consecutive saccade (Rama & Baccino, 2010). To safely conclude that the imbalances in the history cannot explain the differences between target and distractors, we directly compared target and distractors which were preceded by an equal number of distractors. To conduct this analysis we balanced the fixations, comparing each target with a distractor that was matched so that it showed the same number of previous fixations (in addition to being matched to the direction, amplitude and duration of the previous saccade as done for all other analyses, see Material and Methods). This comparison revealed a very similar pattern with central electrodes showing a sustained early difference (130–50 ms) between targets and distractors for the free viewing condition (Supplementary Figure S3B).

Third, while our matching procedure accounts for possible contributions of the saccades it does not preclude the possibility of a spillover of the potentials of the preceding fixation which may cause the early effect. To account for this possibility we performed the same analysis, matching simultaneously the saccade amplitude in both directions as well as the duration of the previous fixation. This analysis yielded almost an identical pattern with the same difference in early potentials for targets vs distractors observed in the *free viewing* condition (Supplementary Figure S3C).

Fourth, although parafoveal processing was precluded by the hash symbols and a minimum separation between stimuli of 2.3°, which is far in terms of the classical crowding results of Toet and Levi (1992) for instance, a possible explanation of the early discrimination could be that the target was detected in the previous fixation from the parafovea. To exclude this possibility we conducted an additional behavioral experiment in which we tested target visibility at 2.3° eccentricity. Five participants maintained fixation in the center of the screen while patches were shown at an eccentricity of 2.3° for 500 ms with an inter-stimulus interval between 550 ms and 1750 ms. The sequence of targets and distractors were obtained from the *replay* experiment. Participants were asked to report whenever they saw a target with a key press, i.e. they did not had to report after each stimuli if there was a target or not. Each participant performed 100 trials and visibility was essentially zero: One participant reported a target but had two false positives and the other four participants reported not seeing the target in all 100 trials of the experiment (10 of which contained targets). Furthermore, we accounted for this potential confound by repeating the matching procedure only for fixations preceded by large saccades (>3°; Figure 1F). Again, this analysis yielded almost an identical pattern of early difference in the fERPs as in the previous matching selections (Supplementary Figure S3D).As mentioned in the Materials and methods section, we had excluded all double fixations to the same target. However, this did not exclude the possibility of the participant coming back to a patch that was already fixated several saccades before. These events were extremely rare in our paradigm (2% of the fixations) and could not account for the effect.

Fifth, we verified that these observations also hold when a relatively different procedure for multiple comparisons is used (*cluster-based permutation test* [Maris & Oostenveld, 2007]; Supplementary Figure S4).

Finally, a possible concern is that the number of subjects in both experiments is not the same which may affect the significance. To discard this possible confound, we repeated the analyses selecting only the group of eleven participants which had sufficient trials to be matched in all possible parameters described above (Supplementary Figure S3). As expected, the significant power of the effect decreases when considering a smaller group of subjects, but the early distinction between targets and distractors remains significant only in the free viewing condition (Supplementary Figure S5). An individual analysis also supports the robustness of this result. We could detect a difference in this early potential in 12 of the 17 subjects who participated in this experiment. When measuring the first significant difference between targets and distractors for each individual subject we measured an onset latency of 148 ± 13 ms (mean ± s.e.m.).

Dynamics of projections of the data to relevant components

To further explore the reliability of early target discrimination during *free viewing* we reduced the dimensionality of the data using principal components analysis (PCA). For each individual participant, the 128 electrodes were projected into principal components, which maximized the variance of the data in each orthogonal direction. The first two components had very similar topographies across all participants and

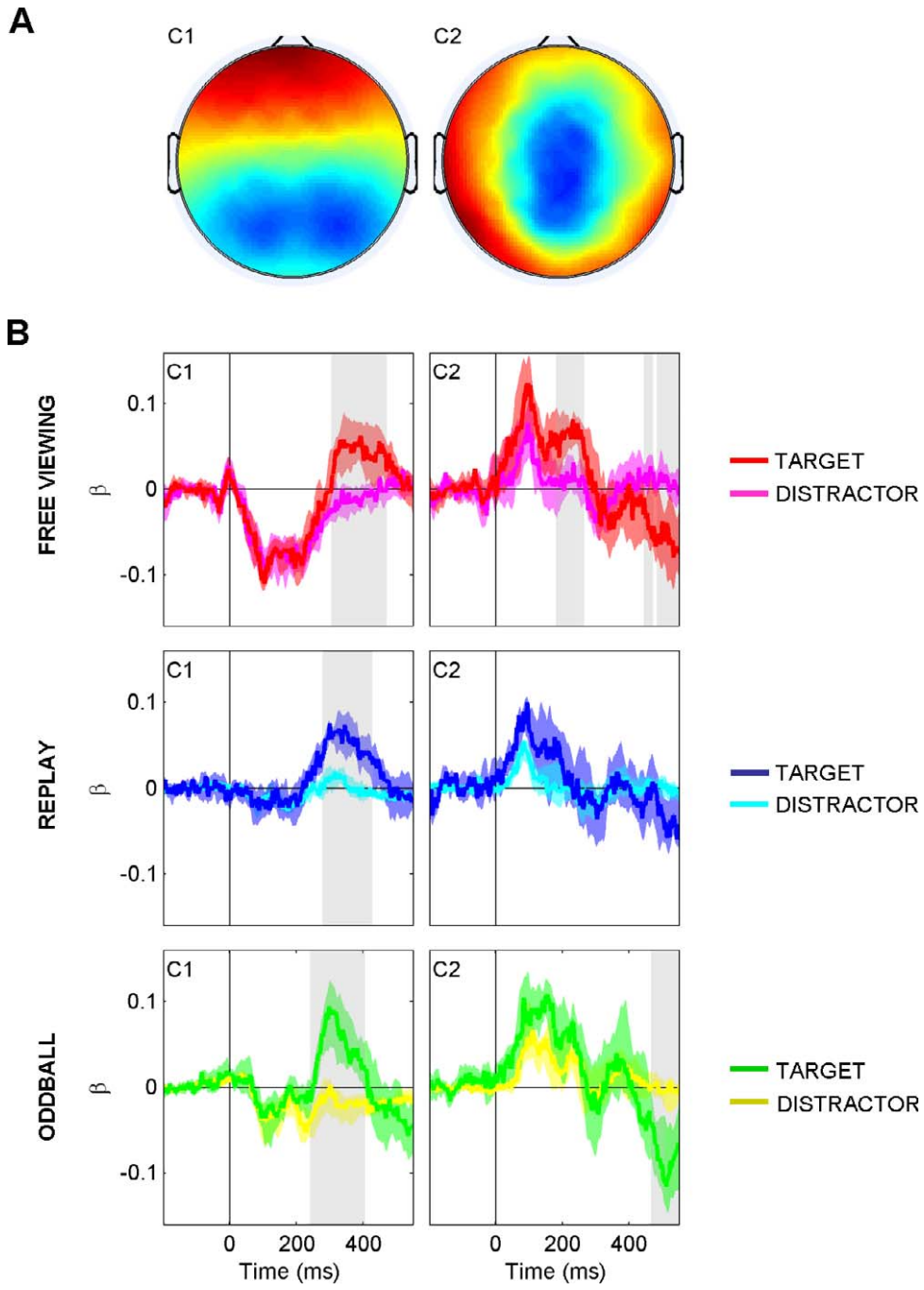

Figure 6. Projection of the evoked responses on the first two principal components (PC) subspace. A) Spatial distributions of the first two PCs. Amplitudes were normalized by the maximum range across all samples (channels x data points) in each task. B) Dynamics of the coefficients of responses to Targets and Distractors in the (C1, C2) subspace, in the three experiments: *free viewing* (left panels), *replay* (central panels) and *oddball* (right panels). Black bars represent the intervals in which the discrimination in each PC was significant ($p < 0.01$). Curves represent the median and interquartile range across subjects. Red: Target – *free viewing*, Magenta: Distractor – *free viewing*, Blue: Target – *replay*, Cyan: Distractor – *replay*, Green: Target – *oddball*, Yellow: Distractor – *oddball*.

were capable of explaining the bulk of the variance (more than 90%; Figure 6A). We investigated the temporal course of the first two components, i.e., the projection of the data to the first two principal components throughout the course of the fixation (Figure 6B). The topography of the first principal component (C1) was very similar to the topography of the difference between target and distractors around 300 ms, which was significant in all experiments (Figure 6B, left panels). Indeed, when the data was projected to this component we observed a significant discrimination between 303 ms and 406 ms for the three

experiments ($p < 0.01$, Wilkoxon rank-sum test with window-based correction, see Materials and methods section). Consistent with our previous observations, the onset in the *oddball* experimentals occurred slightly earlier than in the other experiments, but in this case we could also separate, in the case of *free viewing*, this medium-latency target effect from the early target effect (Figure 6B, left panels; onsets: *free viewing* = 303 ms, *replay* = 277 ms, and *oddball* = 238 ms).

The time course of the second principal component (C2) showed a significant difference between targets and distractors after 463 ms for both the *free viewing* and *oddball* experiments (Figure 6B, right panels; $p < 0.01$, Wilkoxon rank-sum test with window-based correction; onsets: *free viewing* = 441 ms, and *oddball* = 463 ms). Consistent with our previous observation, we found an early window of significance in the C2 signaling stimulus identity only for the *free viewing* condition, between 180 ms and 264 ms, (Figure 6B, right panels; $p < 0.01$,Wilkoxon rank-sum test with window-based correction). Thus, PCA's representation of the raw ERP data allowed us to identify three different non-overlapped spatiotemporal windows of significance, and define the onset of the otherwise overlapping effects.

To tentatively localize sources of early and late signals of target-distractor discrimination we explored the neural generators of the scalp-recorded electrical fields, modeling the fERPs using a large number (10,000) of distributed dipoles spread throughout the cortical surface (see Materials and methods for details and (Baillet et al., 2001). Despite the limited spatial resolution of this method (Baillet et al., 2001), it can be used to obtain an approximate activity distribution on the cortical surface and allow and estimation of the activation dynamics in various regions of interest (Del Cul, Baillet, & Dehaene, 2007; Rudrauf et al., 2008). Source analysis revealed that markers of target-distractor discrimination are first observed in the occipital cortex and only later, at a latency of about 200ms, in the frontal cortex (Figure 7A). A finer analysis, investigating the dynamics of scouts located at each Brodmann Area (BA) (Rudrauf et al., 2008) revealed a spatial gradient of latencies of the late (300 ms component) with latencies progressing towards more anterior regions (Figure 7B). This progression was most evident in the *oddball* experiment.

Discussion

Previous studies investigating eye movement-related potentials have described saccade or fixation related potentials. These studies have focused in a wide variety of fields as: the study of early evoked potentials themselves usually called "lambda waves" (Thickbroom et al., 1991; Thickbroom & Mastaglia, 1985; Yagi, 1981), reading (Dimigen et al., 2011; Marton & Szirtes, 1988a, 1988b), remapping (Parks & Corballis, 2010), the potential confound introduced by microsaccades in measuring gamma oscillations (Yuval-Greenberg et al., 2008) and ERPs (Dimigen et al., 2011; Dimigen et al., 2009), and technical issues concerning the artifact introduced by eye movements (Dimigen et al., 2011; Keren et al., 2010). Most of them have used constrained eye movements tasks, where the subjects move their eyes between very few places at a pace fixed experimentally, or used only the last (first) fixation in the sentence. In contrast, only very few studies have looked at all the fixations in free eye movement tasks (Dimigen et al., 2011; Graupner et al., 2007; Luo et al., 2009; Ossandon et al., 2010; Rama & Baccino, 2010; Takeda et al., 2001; Yagi, 1981).

A direct comparison of our results with previous findings is difficult because of the many experimental differences among paradigms (the number of electrodes and electrode layout, the reference, baseline correction and the specific task settings). Despite these differences, there are consistent emerging observations: a sequence of early visual potentials, peaking at 100 ms (P1), 150 (N1) and 200 (P2), on the occipital electrodes relative to saccade offset (Jagla et al., 2007; Thickbroom et al., 1991; Yagi, 1981). Since it was a free eye movement task and we aligned our evoked potentials to the saccade offset (i.e., to the onset of the fixation), we expected the presaccadic potentials, i.e. the presaccadic spike (SP), the premotor negativity (PMN) and the premotor positivity (PMP) (Jagla et al., 2007; Thickbroom & Mastaglia, 1985, 1990) to be somewhat blurred. In the PMN and PMP, since there was no fixed preparatory period and we also used the period between 200 ms and 100 ms before the saccade offset as baseline for averaging, we did not expect to see any deflection. Some previous studies have also shown late cognitive responses, mostly in reading (Marton & Szirtes, 1988a, 1988b). Interestingly, early markers of fixation content have been reported (Marton & Szirtes, 1988b). Marton and Szirtes (1988) presented a P370 or N370 that indexed if the last word of a sentence was correct or incorrect. These responses started to diverge at around 220 ms locked to saccade onset, thus near 160 ms after saccade offset, and comparable to our study (Marton & Szirtes, 1988b). Since in fixed gaze experiments in reading some effects of word frequency, context and semantic category have been described in early potentials such as N170 (Pulvermuller, Assadollahi, & Elbert, 2001; Scott, O'Donnell, Leuthold, & Sereno, 2009; Sereno, Brewer, & O'Donnell, 2003; Sereno & Rayner, 2003; Sereno, Rayner, & Posner, 1998; Skrandies, 1998), and these studies did not have a replay situation, it is impossible to discriminate if these

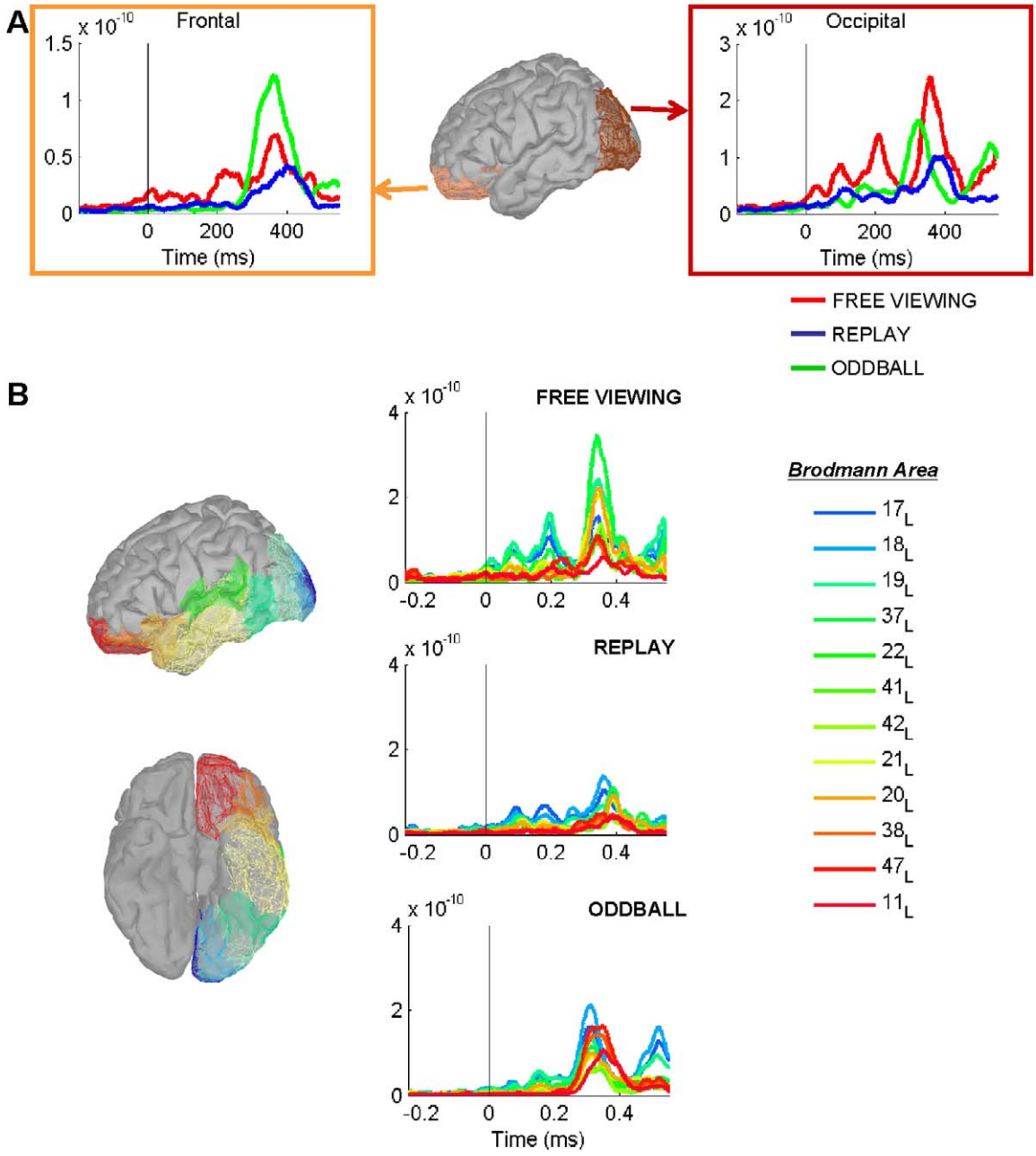

Figure 7. Cortical localization of the discrimination between Targets and Distractors. Source-localization over the cortical mantle. A) Two Regions of Interest (ROIs) were defined in areas that showed evoked responses. Left panel: Absolute power of the current density for the three experiments in a left frontal inferior area (BA: 11+47). Center panel: ROIs localization represented on a standardized cortex in left view. Right panel: Absolute power of the current density for the three experiments in a left occipital area (BA 18+19). Red: *free viewing*, Blue: *replay*, Green: *oddball*. B) Twelve regions of interest (ROIs) were defined from Brodmann areas across the occipito-temporo-frontal stream. Left panels: ROIs localization represented on a standardized cortex in left and bottom views. Right panels: Absolute power of the current density in the twelve defined ROIs for the three experiments (Top: *free viewing*, Middle: *replay*, Bottom: *oddball*).

early responses were characteristic of the eye movement situation or they were related to the spatial and temporal features of the statistical distribution of the stimuli. An important difference of our study is that we explicitly compared the evoked potentials during eye movements with a control in which we tried to match all variables while fixing eye-movement.

Category information has been shown to be conveyed in noninvasive scalp EEG recordings with a latency of ~ 150 ms (Rousselet, Fabre-Thorpe, & Thorpe, 2002; Thorpe et al., 1996). Identity stimulus information (contingent upon recognition) has also been found to be present in the EEG signal quite early, ranging from 150 to 300 ms (Johnson & Olshausen,

2003, 2005; VanRullen & Thorpe, 2001). The focus of these studies has been the detection of objects in natural complex scenes (Johnson & Olshausen, 2003, 2005; Rousselet et al., 2002; Thorpe et al., 1996; VanRullen & Thorpe, 2001). In contrast, in our study the distinction between the target and the distractor was quite subtle (E vs ∃ at low contrast) and required fixating to the patch to determine whether the contained object was a target (due to a crowding mask). Under these circumstances we showed an early potential, which indexes target presence observed only in the free viewing is consistent with rapid processing of target identification enhanced by presaccadic attentional engagement.

While we designed three experiments that controlled several experimental variables, there are numerous effects, which may explain our observation since free viewing activates in conjunction a series of mechanisms. Tearing apart these effects certainly requires further investigation but here we speculate on possible contributions of different effects in relation to previous observations.

A possible concern on the early responses to stimulus identity is that using a relatively strong high-pass filter (1Hz) could lead to a smearing of the late P3 response into an early time window. If this was the case, we would expect that different electrodes with similar late potentials showed the same pattern on early latencies. However, looking at the Fz electrode in Figure 5 we do not seem to observe any trend even when there is a subsequent peak of comparable latency, magnitude and width to the one observed in Pz. Hence, this does not seem to be a pure filter-induce artifact but rather a reflection of different dynamics in electrodes. In addition, it has been shown that eye movement artifacts have a significant contribution to the ERPs at low frequencies (see Funase, Yagi, Kuno, & Uchikawa, 1999; Keren et al., 2010). Based on this evidence we adopted a conservative choice by using a relatively high high-pass filter (1Hz). However, future works may shed light to optimal filtering procedures by explicitly analyzing the effect of different high-pass filters and the relative contribution of ERPs and eye movement artifacts on different frequency bands.

A possible theoretical source that needs to be considered to account for the differences observed in free viewing is the temporal modulation of attention. A relevant distinction between the *free viewing* condition, where the temporal control of saccades is under subjects' control, and the replay experiment is that even if the statistics are matched, in the latter the precise occurrence of each stimulus has significant temporal uncertainty. Indeed, high attentional engagement is naturally present in *free viewing* from fixation onset or even earlier (Corbetta et al., 1998; Melcher & Colby, 2008). Previous experiments have shown that a cue which signals the presence of a stimulus has a perceptual effect, which may be effective even for subliminal stimuli (Naccache, Blandin, & Dehaene, 2002). Temporal attention affects the amplitude and latency of N2 (Correa, Lupianez, Madrid, & Tudela, 2006) and P3 components (Miniussi, Wilding, Coull, & Nobre, 1999), and the amplitude of the P1 component.Targets appearing at attended moments elicit a larger P1 (Correa et al., 2006). Hence, temporal attention may be an important factor accounting for the observed early differences between *free viewing* and fixation paradigms.

Experiments in *free viewing* non-human primates may shed light on the precise biophysical mechanisms by which eye movements may dynamically control the speed of processing. For instance, Schroeder and colleagues, recording from V1 neurons of macaques, showed that the phase of neuronal oscillation organizes coherently just after fixation onset, which is accompanied by increased spectral power in several frequency bands. A consequence of this increased coherence is that the amplitude of transient visual responses is enhanced at the specific oscillatory phase associated with fixation (Rajkai et al., 2008; Schroeder & Lakatos, 2009). These results led them to hypothesize that fixation-related responses to visual stimuli should have a higher signal-to-noise ratio than traditional measures (Rajkai et al., 2008). Similarly, Maldonado and colleagues found that 30 ms after a fixation, synchronization between neurons in V1 builds up. This process is followed by an increase in firing rate starting from 90 to 200 ms, nicely coincident with the early marker of target detection in our ERP data. Interestingly, the excess in synchronization is not observed when the animals scanned a blank screen (Maldonado et al., 2008). The final piece of the puzzle comes from observations showing that oscillations can function as an instrument of attentional selection (Ding, Sperling, & Srinivasan, 2006; Kim, Grabowecky, Paller, Muthu, & Suzuki, 2007; Lakatos, Karmos, Mehta, Ulbert, & Schroeder, 2008; Morgan, Hansen, & Hillyard, 1996; Schroeder & Lakatos, 2009).

We described medium-latency and late target effects which were larger and begin earlier in the *oddball* condition than in the other conditions. Previous studies (Gonsalvez et al., 1999) have shown that the target-to-target interval (TTI) affects both the amplitude and the latency of the P3 component, i.e., long TTIs resulted in shorter latencies and larger amplitudes. Moreover, Gonsalvez and colleagues have also shown that many previous results on the dependence of the P3 component on sequence structure, ISI and probability could be explained on the basis of the TTI hypothesis (Gonsalvez et al., 1999; Gonsalvez & Polich, 2002). The present results are consistent with those findings since the *replay* and the *free viewing* conditions had

similar TTIs by construction, but we artificially prolonged the inter-stimulus interval (ISI) in the *oddball* condition keeping the sequence constant, which resulted in longer TTIs (presentation time of the first target [median (interquartile interval)]: *Oddball*: 5.5 sec [4.8, 5.9] vs. *Replay*: 2.8 sec [2.7, 3.0]; and time between consecutive targets: *Oddball*: 7.0 sec [6.8, 7.1] vs. *Replay*: 4.2 sec [4.1, 4.3]).

An important aspect, which occurs naturally from these results, is that not everything is faster in *free viewing*. It may not be that just a more efficient encoding decreases all latencies, instead we observed a difference in a nearly potential while later potentials are delayed. Interestingly, late potentials, more likely related to higher cognitive functions, appeared to be roughly preserved in free viewing. For instance, Dimigen and colleagues replicated robust effects of word predictability on the N400 component in natural reading (Dimigen et al., 2011). Thus, we propose that during the first quarter second after fixation the observer could extract some features that guide following saccades in times consistent with typical fixation durations. And in the next half second, the observer continues processing the information roughly in the same way as if their eyes were fixed looking for a target in a sequence of distractors or reading a word in a sentence, as it has been described in previous works (Grodzinsky & Friederici, 2006; Polich, 2007).

Our findings contribute towards the emerging field of studying human physiology and cognition in more natural environments, where the subject's gaze position is not fixed. The methodology presented here is a contribution in this direction and can be readily adapted to other paradigms to uncover the neural underpinnings of natural vision.

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