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Contributions
GE, RVR and PC designed the research. GE performed the experiments. GE analyzed the data. GE, RVR, & PC wrote the manuscript.

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Abstract

We examine whether peripheral information at a planned saccade target affects immediate post-saccadic processing at the fovea on saccade landing. Current neuroimaging research suggests that pre-saccadic stimulation has a late effect on post-saccadic processing, in contrast to the early effect seen in behavioral studies. Human participants (both male and female) were instructed to saccade toward a face or a house that, on different trials, remained the same, changed, or disappeared during the saccade. We used a multivariate pattern analysis (MVPA) of electroencephalography (EEG) data to decode face versus house processing directly after the saccade. The classifier was trained on separate trials without a saccade, where a house or face was presented at the fovea. When the saccade target remained the same across the saccade, we could reliably decode the target 123 ms after saccade offset. In contrast, when the target was changed during the saccade, the new target was decoded at a later time-point, 151 ms after saccade offset. The "same" condition advantage suggests that congruent pre-saccadic information facilitates processing of the post-saccadic stimulus compared to incongruent information. Finally, the saccade target could be decoded above chance even when it had been removed during the saccade, albeit with a slower time-course (162 ms) and poorer signal strength. These findings indicate that information about the (peripheral) pre-saccadic stimulus is transferred across the saccade so that it becomes quickly available and influences processing at its expected, new retinal position (the fovea).

Significance Statement

Here we provide neural evidence for early information transfer across saccades. Specifically, we examined the effect of pre-saccadic sensory information on the initial neuronal processing of a post-saccadic stimuli. Using electroencephalography and multivariate pattern analysis, we found that: 1) the identity of the pre-saccadic stimulus modulated the post-saccadic latency of stimulus relevant information, 2) a post-saccadic neural marker for a saccade target stimulus could be detected even

when the stimulus had been removed during saccade. These results demonstrate that information about the peripheral pre-saccadic stimulus was transferred across the saccade and influenced processing at a new retinal position (the fovea) directly after the saccade landed.

Introduction

Humans make up to four saccadic eye-movements per second to direct the high-resolution fovea to locations of interest in the visual environment (Schiller, 1998). As efficient as this process may seem, it is unclear how the successive snapshots of information are combined across saccade sequences. One possibility is that information is carried across saccade to compensate for the eye movement, so that it can integrate with the information on the next fixation (McConkie & Rayner, 1976; Trehub, 1977; Paeye et al., 2017). However, many studies have demonstrated that changes to a scene made during a saccade are rarely detected (Grimes, 1996, O'Regan, Rensink, & Clark, 1999, Simons & Rensink, 2005), indicating that little, if any, perceptual information is transferred across saccades. Even though much is lost, information about attended items may be preserved (Higgins & Rayner, 2015): for example, Grimes (1996) demonstrated that changes to more salient, attention-grabbing objects of a scene were noticed in 40% more trials than changes to background objects. Furthermore, information preservation across saccade has been demonstrated behaviorally in motion perception (Fracasso et al., 2010; Szinte & Cavanagh, 2011), detection of line interception (Prime et al., 2006; Paeye et al., 2017), object completion (Hayhoe et al., 1991), color biasing (Wittenberg et al., 2008) and identification performance (De Graef & Verfaillie, 2002). These studies have indicated that pre-saccadic information is available within 20-140 ms following the saccade landing. Even though behavioral signatures of trans-saccadic memory have been reported before, the early neurophysiological correlates of this information transfer remain largely unexplored. A series of studies from one group (Dimigen et al., (2012); Niefind & Dimigen (2016); Kornrumpf et al., (2017)), find a relatively late marker with electroencephalography (EEG) for parafoveal-to-foveal information transfer in reading (from 140 ms lasting until 300 ms). However, the initial post-saccadic

92 processing was unaffected. The dissociation between the trans-saccadic information findings for
93 behavioral versus neuroimaging measures motivated our interest in the effect of pre-saccadic
94 sensory information on the early neuronal processing of post-saccadic stimuli.

95 We employed EEG and multivariate pattern analysis (MVPA) to address this question. Specifically, we
96 hypothesize that accuracy and / or latency of decoding a post-saccadic stimulus will depend on
97 whether the pre-saccadic stimulus at the same spatial location was either the same or different (on
98 separate trials). The time course of decoding accuracy indicates when there is sufficient information
99 to identify the stimulus. Trans-saccadic information transfer should improve decoding accuracy
100 and/or decrease the latency of the peak decoding performance when the same stimulus was present
101 prior to the saccade, compared to when a different stimulus was present. In contrast, if there is no
102 memory or information transfer across saccades, the decoding of a post-saccadic stimulus should
103 operate identically, regardless of the pre-saccadic information.

104 We also included a condition where no stimulus was present after the saccade. Early studies
105 reported the presence of spatiotopic, persisting target information even when the stimulus had been
106 removed during saccade (Wolf et al. 1980; Jonides et al., 1982). These studies were later overturned
107 when the phosphor persistence was properly controlled and no effect was found (Jonides et al.,
108 1983). Nevertheless, trans-saccadic integration studies have suggested the presence of a spatiotopic
109 information transfer, a “ghost” illusion that may in some cases be perceptual as well as memory-
110 based (Wolf, 1980; Deubel et al., 1996; Wolf & Schultz, 2015; Ganmor et al., 2015; Paeye et al.,
111 2017). We therefore examined the timing and strength of information in the post-saccadic time-
112 period in additional trials where the target had been removed during saccade.

113 **Method & Materials**

114 *Participants.* Seventeen volunteers including author GE (10 female; 19-40 years) participated in the
115 experiment. All participants had normal or corrected-to-normal vision. Three participants were
116 rejected from the analysis (leaving 14), as we were unable to efficiently decode between the neural

117 signals of faces and houses when the stimuli were presented in the peripheral visual field (for further
118 details see *Criteria* section).

119 *Stimuli.* Stimuli were presented with a 16-inch Sony Triton Monitor (resolution: 1024 x 768; refresh
120 rate: 85 Hz) at 50 cm distance from the participants. The stimuli were designed and presented using
121 MatLab 2009a and Psychophysics Toolbox extension (Brainard, 1997). The stimuli were presented in
122 separate saccade and fixation blocks. Fixation blocks contained the trials used to train the
123 multivariate pattern classifier, and the trials in the saccade blocks were fed to the classifier as the
124 test set. Each block contained 20 trials in a randomized order. Five fixation blocks were interleaved
125 with six saccade blocks across one run of 15 minutes. Participants performed four runs in total.
126 Therefore, there were 480 saccade trials and 400 fixation trials presented to each participant.

127 *Fixation blocks.* There were two fixation conditions: "central" and "peripheral" (Figure 1a). In the
128 "central" condition, participants fixated a fixation marker which was presented 6° to the right of the
129 screen center. After 200 ms, either a face or a house (3.4° height, 3.3° width) was then presented for
130 500 ms, replacing the fixation marker. Low-level stimulus features (i.e. global luminance, contrast,
131 spatial frequencies and 2D Fourier power spectrum) of the two possible images were equalized by
132 spectral normalization (Senoussi et al., 2016). In the "peripheral" condition, the trials began with the
133 same fixation marker as in the "central" condition. After 200 ms, a face or a house was presented in
134 the periphery (10° to the left of the fixation marker) for 500 ms while the participants remained
135 fixated on the fixation marker. In order to keep the participants' attention on the image in both
136 conditions, participants were required to perform a one-back task to determine if the image
137 presented in trial n was the same as or different from the image presented in n-1 (regardless of
138 stimulus position).

139 *Saccade blocks.* There were three saccade conditions: "same", "change", and "disappear" (Figure 1b).
140 In each condition, the trial began with a fixation point presented 6° to the right of the screen center.
141 After 200 ms, a gray-scale image (either a face or a house, 3.4° height, 3.3° width) was presented to

the left of the screen, 10° from the fixation point. The fixation point was removed 500 ms later, which cued participants to perform a saccade toward the image. In the "same" condition, the image remained on screen throughout the saccade and for 45 ms after saccade landing. In the "change" condition, the image changed during the saccade (which was detected online) so that the participant's saccade would land on a new image, which remained on screen for 45 ms post saccade. The change was made once the saccade crossed a 1.5° boundary to the left of the fixation dashes. The trial was restarted if participants initiated saccade prior to the removal of the fixation dashes. The new image would be a house if a face was presented prior to saccade (as in Figure 1a), or the new image would be a face if a house were presented prior to saccade. In the "disappear" condition, the image would disappear once the saccade was initiated, meaning that the saccade would land on the blank, gray background. Phosphor persistence was measured using an oscilloscope and photodiode and the signal from a light spot on a black background was found to drop to below 1% of its peak luminance by a maximum of 11ms after stimulus offset. Therefore stimulus, which was light and dark on a grey background had faded from the phosphors long before the saccades landed in the "disappear" condition (mean saccade duration = 51.5 ms). All saccade trials were performed with a leftward saccade. The participants' behavioral task was to determine if the image presented prior to the saccade was the same as or different from the image presented after saccade. Importantly, participants were not made aware that the saccade target could disappear during saccade.

Experimental Design & Statistical Analyses. The experiment was performed as a within-subjects design; each participant completed all conditions of the experiment. There were three test conditions in the saccade block and two training conditions in the fixation block, described in detail above. Using the training conditions, we analyze the participants' EEG signal for different neural signatures in the three test conditions. The post-saccadic neural signals were expected to be different dependent on whether an image remained the same, changed, or disappeared during a saccade. Repeated measures analyses (ANOVA and paired t-tests) were used to compare neural signatures across the three saccade conditions. 1-sample t-tests were performed on each condition

to determine those with a significant difference from chance (50%). Multiple comparisons were based on Bonferroni corrected p-values from paired t-tests performed at each time-point (Shaffer, 1995). Behavioral analyses were also performed using repeated measures. Specific details of each analysis are presented below.

Behavioral Data analysis. Analysis on the saccade task and fixation task was performed in MatLab 2016a. For the saccade task, mean correct responses and reaction times were calculated across participants for each saccade condition. A correct response was defined as responding 'same' in the "same" condition, 'different' in the "change" condition, and 'same' in the "disappear" condition where the participant might perceive the pre-saccadic stimulus as still present (Wolf et al., 1980), but a priori would have no reason to report the opposite stimulus. A fixed effect one-way ANOVA was performed on the percentage correct responses and mean reaction times across participants and conditions. Responses were performed in a designated response period 300 ms after each trial was concluded. A designated response time-window was employed to reduce motor response noise during the post-saccadic time-period. This constraint ruled out their use for reaction time analyses. For the fixation task, subjects performed a one-back task and the mean correct responses were calculated across participants. A t-test was conducted for the group analysis.

Eye-tracker data acquisition and analysis. The timing of the stimulus sequence on saccade trials was locked to the detection of the saccade initiation. We used an Eyelink 1000 plus to record participants' eye-movements throughout the runs. Calibration was conducted at the beginning of each run, and again during the runs if the Eyelink lost the ability to track the pupil. Participants' saccade onsets and offsets were extracted and combined with the EEG triggers for analysis of the EEG signal. We found a consistent delay of 4.28 ms between saccade onset and the EEG triggers for saccade onset embedded in the EEG signal.

EEG acquisition and preprocessing. EEG and EOG were recording using a Biosemi system, with 64 active electrodes and 3 ocular electrodes at 1024 Hz. The continuous EEG data was preprocessed

offline using MatLab and EEGLAB toolbox (Delorme & Makeig, 2004). First, the continuous data were notch filtered around 50 Hz to remove electrical artifacts, then band-pass filtered between 0.1 Hz and 80 Hz, and finally downsampled to 256 Hz. Saccade trials were analyzed in two epochs: the pre-saccade epoch was locked to the stimulus onset and covered 200 ms prior to stimulus onset until 300 ms after stimulus onset; the post-saccadic epoch was time locked to the saccade offset and covered 200 ms before saccade offset until 300 ms after saccade offset. Fixation trials were analyzed around stimulation onset, with 200 ms prior and 300 ms post onset. The data collected 200 to 100 ms prior to stimulus onset or saccade offset for each trial was used to baseline the remaining data in the trial. Individual electrodes with artifacts were interpolated by the mean of the adjacent electrodes, and manual rejection of epochs with artifacts was performed (average rejected epochs of saccade trials = 87.5 (SD = 14.5) out of 480 epochs; average rejected epochs of fixation trials = 32.4 (SD = 6.3) out of 400 epochs).

Multivariate Pattern Analysis. Multivariate pattern analysis (MVPA) distinguishes between electrophysiological signals associated with distinct brain states. Here, a linear classifier (see e.g. Crouzet et al., 2015) was used to distinguish between processing face and house stimuli in the peripheral or foveal region of the visual field at specific time-points. Importantly, we designed our experiment to ensure that the classifier decoded between only face and house information (present either peripherally or foveally in the visual field). The training conditions purposefully did not include any saccade, enabling our analysis to focus on contextual information transfer, rather than motor related discrepancies between conditions.

First, we tested the accuracy of the classifier on our two training sets (“central” or “peripheral” fixation trials) separately, at each time-point independently. The classifier performance was tested using a Monte-Carlo cross-validation procedure (n=50). On each cross-validation iteration, we randomly selected 90% of fixation trials to train the classifier and tested the classifier on the remaining 10% of fixation trials. There were always an equal number of face trials to house trials in

the training set. In order to increase signal-to-noise, we subaveraged every 3 trials in the training set and in the test set (Isik et al., 2014; Grootswager et al., 2017). Averaging across three trials was performed on each iteration after the trial order in each condition was randomized. We averaged at each time-point, essentially creating one time-course from three trials. On each cross-validation, the signal of each electrode was normalized across trials (z-score) at each time-point. Once the classifier was trained to distinguish between the electrophysiological signals elicited by face vs. house trials, a label was provided by the linear classifier at each time-point for each set of subaveraged trials in the test set. After 50 iterations, the percentage of correct labeling was calculated per participant. For group analysis, classifier performance was averaged at each time-point across participants and presented with non-parametric 95% confidence intervals. Classification accuracy was considered above chance (50%) by Bonferroni corrected p-values (Shaffer, 1995) from t-tests performed at each time-point.

Next, we trained the classifier using the "peripheral" fixation trials, and test it with the first 300 ms of saccade trials, before any saccade (at the beginning of the saccade trials, subjects are attending to a face or house stimulus presented in the periphery, comparable to the stimulation in peripheral fixation trials). As described above, the classifier was trained on each time-point of the "peripheral" fixation trials, and tested at the corresponding time-point from stimulation onset of the saccade trials. The data was randomized and subaveraged across three trials within each trial type (as described above). Importantly, the z-score normalization was performed on the training and test data set separately. For each time-point within the first 300 ms of each saccade trial, the classifier would then label the trial as face or house according to the learnt patterns of the "peripheral" fixation trials (chance = 50%). Classification accuracy for each participant was determined from 10 iterations of randomizing and subaveraging the data in each trial type. Group analysis was performed as described in the above paragraph.

MVPA of the post-saccadic time-period was performed using the "central" fixation condition. The post-saccadic time-period was defined from saccade offset to 300 ms after saccade offset. This time-period is most similar to the "central" fixation condition, when processing is occurring at fixation. Importantly, here we used the classifier trained at the time-point of peak decoding accuracy for the central training set (at 140 ms) and then tested this classifier on every time-point of the saccade trials from saccade offset. This method was employed as we were uncertain of the "reference" time at which information would become available across saccade (and as the analysis revealed, this time could be different for the different saccade conditions: "same", "change" and "disappear"). The following multivariate analysis per subject and group analysis were performed as above. Latency of the post-saccadic decoding of the "same" and the "change" condition was quantified by selecting the peak of the classification performance for each condition in each participant after saccade offset. A t-test was performed to determine if there was a significant difference between processing latency for the "same" versus "change" condition.

The "disappear" condition was used to test for trans-saccadic information presence without post-saccadic stimulation and, as a comparison, we used the peripheral fixation condition as it was exactly the same as the "disappear" condition, but without saccade. Here, we trained the classifier at the time-point of peak decoding accuracy for the central training set (at 140 ms) and test this classifier on every time-point of the peripheral training trials from stimulation offset (plus 51 ms – to simulate the saccade latency in the "disappear" condition). This analysis enabled a direct comparison between information within the visual system with saccade ("disappear" condition), and information in the visual system without saccade (peripheral fixation condition).

The final MVPA analysis performed on the post-saccadic time-period examined how information generalized across time. The classifier was trained on every time-point of the "central" fixation conditions and tested at every time-point of the post-saccadic period of the saccade conditions. This

resulted in a matrix of decoding accuracy values, where the diagonal relates to corresponding time-points between training and test trials.

Criteria. Subjects were removed from analysis if the classifier trained on peripheral fixation trials was unable to decode between face and house stimuli (presented peripherally) prior to saccade. Specifically, the average classification performance was derived from 100 ms to 300 ms after stimulation onset, and if the 95% confidence interval included chance (50%), then the subject was removed from following analysis (3 participants were removed). Chance classification performance prior to saccade could have occurred for several reasons, including poor signal-to-noise ratio, or lack of proper attention to the peripheral stimuli. This rejection criterion was employed because our main question of interest (the potential transfer of stimulus information across the saccade) only makes sense when information is actually present and detectable before the saccade.

Results

Behavioral Data

Participants performed two tasks during the experiment. In the saccade task, the participants indicated if the stimulus prior to saccade was the same or different to the stimulus they perceived after saccade. In the fixation task, participants performed a 1-back task to indicate if the image presented in trial n was the same or different to the image presented in n-1, regardless of the spatial position of the image (central or peripheral).

All participants performed the matching task in the saccade conditions correctly above chance (above 50%, $p<0.0001$, 1-sample t-tests). In the group analysis, participants reported that the stimuli were the same in 95.1% (SEM = 2.4) of the “same” trials. They reported the change in 96% (SEM = 1.3) of the “change” trials. In the “disappear” condition, participants reported that they saw the same image in 95.7% (SEM = 2) of the trials when in fact there was no image present. There was no evidence for a difference in participants’ performance across conditions ($F(2,39)0.05$, $p=0.9482$,

ANOVA). However, the participants were not given an option to report 'neither' or 'nothing', so we cannot conclude that they actually perceived a post-saccadic persisting, spatiotopic image, nor can we rule it out. Reaction times (RT) were calculated from the beginning of the response period that followed the 300 ms no-response interval and did not differ across the conditions ($F(2,39)0.12$, $p=0.8843$, ANOVA), with participants performing the task with a mean RT of 191.2 ms (SEM = 16.5) for the "same" condition, 199.4 ms (SEM = 17.5) for the "change" condition, and 188 ms (SEM = 17.6) for the "disappear" condition. However, it is important to note that responses were recorded during a response period after the conclusion of the trial, and therefore do not reflect "true" reaction times.

All participants performed the 1-back fixation task significantly above chance (50%, $p<0.0001$, 1-sample t-tests). Across the group, participants performed the 1-back task correctly on 93.9% (SEM = 1.7) of trials, which was significantly above chance ($t(13)26.3667$, $p<0.0001$, 1-sample t-test).

EEG Data

Using electroencephalography (EEG) and multivariate pattern analysis (MVPA) we examined whether saccade target information affects post-saccadic target processing. If the saccade target changed during the saccade, we expected an alteration in processing latency and/ or processing performance of the new target after saccade. We further hypothesized that participants could perceive the saccade target momentarily after saccade landing, even when it was removed during saccade, and that we would find a reflection of this illusory percept in the EEG signal.

Classifier accuracy

First, we tested the accuracy of the classifier after being trained on the two separate sets of training trials, "peripheral" and "central". Using a leave 10% out Monte-Carlo cross-validation procedure (see methods section), we found that the classifier worked effectively at labelling the test set trials when it was trained using the "peripheral" trials and the "central" trials. When the classifier was trained on the "peripheral" fixation trials, the percentage performance showed two peaks at 179 ms and 246 ms

with a performance of 59.3% and 59% respectively (Figure 2a). This decoding accuracy on peripheral stimuli is similar to that found previously by Carlson et al. (2011), even though our peripheral stimuli were 3° further from fixation than in their study. The decoding topographies of the peripheral classifier suggest that frontal, central, and occipital electrodes contribute to both decoding performance peaks. The peak at 179 ms is slightly lateralized on the right, which is expected as the face and house stimuli were presented to the left of fixation. For the classifier trained on the "central" trials, classification performance peaked at 89.5% at 140 ms after stimulation onset (Figure 2b). This classifier was expected to perform considerably better than the classifier trained on peripheral stimuli.

Pre-saccadic decoding using fixation trial training

We trained the classifier at each time-point of the "peripheral" fixation conditions and tested the classifier using the corresponding time-point of the saccade conditions for the first 300 ms after stimulation onset (prior to saccade). We found that the classifier was able to distinguish between face and house processing activity in the periphery prior to saccade in all the saccade conditions (Figure 3). Note, three subjects were removed due to poor peripheral classification, therefore successful classification of the "peripheral" trials were expected. The "same" condition peaked at 164 ms with a classification performance of 59.5%, the "change" condition peaked at 156 ms at 58.3%, and the "disappear" condition peaked at 183 ms at 57.6%. According to the 95% confidence intervals, we were unable to differentiate between the three conditions, as expected since prior to the saccade, they are fully identical. These classification accuracies are quite similar to the training performance in the "peripheral" fixation condition.

Post-saccadic decoding using fixation trial training

The first classifier used to decode the post-saccadic time-period was trained at the time-point of best performance (at 140 ms; Figure 2) in the "central" fixation trials. The dotted vertical lines in Figure 4 show the 140 ms offset relative to the saccade landings. Figure 4 shows the performance of this

classifier for each time-point of the post-saccadic time-period, from saccade offset up to 300 ms following saccade offset. The classifier for face versus house becomes significantly different between the “same” and “change” conditions at 92 ms after saccade ($t(13)2.628$, $p=0.0485$ Bonferroni corrected paired t-test). This is the earliest evidence for trans-saccadic transfer found using EEG. Classification between face and house stimuli then peaked in the “same” condition at 123 ms at 68.9% (Figure 4a). In contrast, classification in the “change” condition peaked 28 ms after the “same” condition at 151 ms at 72.6% (Figure 4b). The 28 ms time difference between the peak classification for the “same” and “change” conditions was consistent across subjects ($t(13)=6.8399$, $p<0.0001$, paired t-test). There was no overlap between the 95% confidence intervals around the times of the peak classification for the “same” and the “change” conditions (95% CI “same” (116.01, 131.95); “change” (138.44, 159.10)), further demonstrating a lag for peak classification in the “change” compared “same” conditions even when accounting for between subject variability. The increased latency found for the “change” condition suggests that there is a relative processing advantage for the “same” condition trials, reflecting information transfer across saccade (decoding after saccade in the “same” and “change” trials can only be distinguished by their pre-saccadic history). There was no difference in accuracy between the two conditions ($t(13)=1.6294$, $p=0.1272$, paired t-test).

The pattern for the “disappear” condition was less clear (Figure 4c - blue) but classification did rise above chance for several time-points, first reaching significance at 162 ms with 54.4% performance. The classifier performance was based on labelling each trial according to the stimulus, face or house, that was presented prior to saccade. Above chance classification therefore indicates that significant information about the stimulus presented prior to saccade was still available after the saccade, even though no stimulus was on the screen. Classification for the “disappear” condition was consistently later ($t(13)3.3676$, $p=0.0061$, paired t-test) and weaker ($t(13)8.2416$,$p<0.00001$, paired t-test) than for the “same” condition.

Importantly, we were able demonstrate that a saccade was necessary to retain decodable information in the visual system. We were unable to distinguish between face and house information in the EEG signal of the peripheral fixation condition when the stimulus was removed from the screen (plus 51.5 ms to simulate the saccade duration), and no saccade was performed (Figure 4c - grey). This peripheral fixation condition is identical to the "disappear" condition except for the saccade and the slightly different memory task (one-back instead of same vs different). Nevertheless, the decoding performance dropped in the absence of the saccade.

For completion, we next trained the classifier successively on all time-points of the "central" fixation trials, and tested at all time-points of that condition (central fixation), as well as during the post-saccadic time-period of the three saccade conditions. The diagonal in each panel of Figure 5 indicates when the time-point of the training trials matches the time-point of the test trials (e.g. train at 200 ms and test at 200 ms). Zero indicates the saccade offset in saccade conditions. This alignment is based on the assumption that saccade offset corresponds to stimulus onset in the fixation condition. Warmer colors off of the diagonal indicate that the training data from these time-points enables the classifier to generalize to other time-points within the test data. The horizontal line on each panel indicates the 140 ms peak performance chosen for the analysis presented in Figure 5. As expected, classification performance was strongest along the diagonal (with a peak at 140ms) for the Monte-Carlo procedure of the "central" fixation trials. The leftward shift of the strongest performance observed in the "same" condition suggests that the stimulus in the post-saccadic period of the "same" condition was more rapidly processed (Figure 5a and 5b). Similarly, the corresponding rightward shift of peak performance observed in the "change" trials indicates relatively delayed processing. Note that apparent latency differences relative to the "central fixation" condition may be contingent on our choice to use the saccade offset to mark the onset of post-saccadic processing. Post-saccadic processing may begin during saccade or even during saccade planning or during saccade, and this would effectively imply that processing latencies for both the "same" and "change" saccade conditions are underestimated in our analysis. Regardless, the relative rightward shift in the

389 performance pattern between the “same” and “change” conditions (Figure 5b and 5c; also visible as
390 a 28ms shift in peak classification latency when using only the 140ms classifier, Figure 4a, b) is
391 independent on the choice of post-saccadic time reference, since this choice affects all saccade
392 conditions equally. Finally, a rather different pattern was found in the “disappear” trials (Figure 5d).
393 In this case, the best classifier for each delay does not fall along the diagonal as it roughly does for
394 the other two saccade conditions. Instead, there are patches of significant classification performance
395 at later times, and mostly resulting from classifiers trained between 120 and 170 ms. The trans-
396 saccadic information thus seems to have a longer time-course with a lower signal strength when
397 there is no post-saccadic stimulus.

398 **Using post-saccadic signals to train the classifier**

399 We also performed an alternative analysis where we trained the classifier to discriminate “same” vs
400 “change” trials based on post-saccadic EEG signals instead of our fixation trial training of house vs
401 face applied to “same” and “change” trials individually. This additional analysis answered a number
402 of critical questions: 1) why did we find evidence for trans-saccadic transfer at early time points and
403 others did not; 2) could the change of the stimulus pattern (house to face or vice versa) have
404 generated any EEG consequences, either from the change itself or the effect it would have on
405 corrective saccades; 3) can the pre-saccadic stimulus be classified based on training with post-
406 saccadic traces.

407 1) Why do we find evidence for early transfer whereas others did not? Ours is not the first study to
408 examine the transfer of information across saccades using neuroimaging (for example: Dimigen et al.,
409 2012; Kaunitz et al., 2014; Dunkley et al., 2016; Fairhall et al., 2016; Zimmermann et al., 2016; Niefind
410 & Dimigen, 2016; Kornrumpf et al., 2017), however this is the first neuroimaging study to find
411 evidence for early information transfer which correlates with findings in psychophysical experiments
412 (Fracasso et al., 2010; Vetter et al., 2012; Wittenberg et al., 2008). Our classifier, built on steady
413 fixation stimuli, gave the advantage of pin-pointing early post-saccadic information which may have

been hidden under saccade-related noise in previous neuroimaging studies. To demonstrate the improvement offered by our training on fixation trials, we replicated the leave-10%-out analysis performed by Kaunitz et al., 2014. To do this, we use only post-saccadic signals to train the classifier to distinguish between "same" and "change" trials after saccade offset. Here, we find evidence for only a late information transfer across the saccade: significant discrimination between "same" and "change" trials occurred at 248 ms rather than the 92 ms for our original analysis using the fixation trial classifier to analyze these same post-saccadic EEG signals (Figure 6a). We assume that the extra saccade-related information incorporated into this alternative classifier masks the detection of the emerging difference between "same" and "change". With regard to the fMRI studies on trans-saccadic integration (Fairhall et al., 2016; Dunkley et al., 2016; Zimmerman et al., 2016), we note that fMRI does not have the temporal sampling advantage of EEG, which may have resulted in the inability to locate the rapid trans-saccadic signal found in the present study.

2) Could the differences in the stimulus sequence between "same" and "change" generate the delayed classification in the "change" trials? In the "change" trials, the initial stimulus is switched with the alternative stimulus during the saccade. This could have two consequences that may delay the classification on "change" trials relative to "same" trials. First, the stimulus exchange on "change" trials may trigger a transient signal that could mask the processing of the post-saccadic stimulus; second, the change of stimulus might drive different pattern of corrective saccades once the saccade lands. We again used the results of the leave-10%-out analysis of purely post-saccadic EEG signals (the replication of Kaunitz et al., 2014) to rule out an influence from either of these two factors. This analysis showed that there is no extra transient-related signal in the "change" condition compared to the "same" condition as the presence of this signal would have supported classification at the delays where transients are typically picked up in EEG signals. The EEG response to a transient would become evident at around 100ms in the n1-p1 complex (Naatanen & Picton, 1987) in the "change" trials and if present, this would have contributed to a significant classification accuracy at that time delay. However, the "same" and "change" conditions do not differ significantly until *248 ms* after the

stimulus change (Figure 6a; Bonferroni Corrected). This indicates that the significant difference between the "same" and "change" conditions found in our original analysis reflects the post-saccadic processing of an expected target versus an unexpected target and not a non-specific disruption or extra noise effect from the change transient. The same logic also rules out any impact of differences in corrective saccades on the EEG signals in the time frame where the house and face are classified. It is also a clear demonstration of how our classifier trained on face-versus-house at fixation and applied separately to "same" and "change" trials is able to robustly analyze post-saccadic processing.

3) Can the pre-saccadic stimulus be classified based on training with post-saccadic traces? As a further assurance that the information in the post-saccadic EEG signals corresponds to the pre-saccadic stimulus, we trained the classifier at the peak decoding time-point in the post-saccadic time period for each condition separately ("same": 123 ms, "change": 151ms, "disappear": 162 ms), and then tested the classifier at each time-point in the pre-saccadic period from stimuli onset to 300 ms in the corresponding condition. We found similar results to those we reported when using the classifier trained on fixation trials: all conditions classify significantly above chance with "same" peaking at 164 ms (58.25%), "change" peaking at 156 ms (59.67%), and "disappear" peaking at 187 ms (54.86%; Figure 6b). The peak for the classifier trained on the "disappear" condition was delayed and weaker. This is not unexpected as the "disappear" classifier is trained on a time-period when no sensory stimulation is present, whereas the "same" and "change" classifiers are trained on EEG signal during stimulus processing.

Discussion

We found that pre-saccadic stimulation affects early post-saccadic processing, indicating that information transfers across saccade and interacts with initial stimulus processing at the new fixation. We provide two examples of information transfer across saccade: 1) The identity of the pre-saccadic stimulus modulated the latency at which we could decode the identity of the post-saccadic

464 stimulus, 2) A post-saccadic neural marker was found for a saccade target stimulus that had been
465 removed during saccade.

466 The decreased post-saccadic processing latency of the "same" condition in comparison to the
467 "change" condition demonstrates that post-saccadic processing does not start anew from saccade
468 offset; some internal information is retained and influences the processing speed of the post-
469 saccadic stimulus. Furthermore, we were able to find evidence for post-saccadic processing of a face
470 or house when the stimulus was no longer present. The only explanation is that information
471 pertaining to the pre-saccadic stimulus remains available within the visual system; this could reflect a
472 potential mechanism intended to aid with post-saccadic processing (since in ecological conditions,
473 the pre-saccadic target tends to remain present throughout and after the saccade).

474 We were able to find this evidence of early transfer of information across the saccade because of
475 changes to the classification procedure we used compared to that used in earlier studies (e.g.,
476 Kaunitz et al., 2014). Specifically, the classification was performed separately on "same" and
477 "change" trials using non-saccade, fixation trials for training. This ensured that saccade-related
478 signals that differed in "change" and "same" trials could not directly drive any classification
479 performance – "same" and "change" trials were never compared for classification. The earlier
480 demonstration of trans-saccadic transfer had used a classifier trained on post-saccadic traces and the
481 extra, saccade-related signals may have masked the evidence for early transfer.

482 The processing advantage of the "same" stimulus in our primary finding is consistent with the
483 preview facilitation (Boucart et al., 2016) and trans-saccadic memory research (Higgins & Rayner,
484 2015). Despite the low spatial resolution of information in the periphery, saccade target preview
485 benefits object identification (Henderson & Agnes, 1994; Schotter et al., 2013), face identification
486 (Crouzet et al., 2010; Boucart et al., 2016), and increases reading speed (Rayner et al., 2011). Within
487 the preview facilitation research, trans-saccadic information is related to visual short-term memory

(Higgins & Rayner, 2015). Visual short-term memory can last for a few seconds, therefore may also contribute to information transfer across saccade (Hollingworth et al., 2008).

However, it is also possible that the mid-saccade stimulus change resulted in a cost to the visual system that could explain the processing latency effect between the "same" and the "change" condition. We tested and rejected this alternative by showing that there was no discrimination between "same" and "change" trials until 248 ms when using a classifier trained on the post-saccadic EEG signals. This argues against any signals in the earlier post-saccadic trace that could interfere with the house-vs-face classification differently in "same" and "change" trials. If they could, they would also have supported a "same" vs "change" discrimination at the earlier time period.

Memory transfer across saccades may be aided by predictive remapping of attended objects (Melcher & Colby, 2008; Melcher, 2009; Cavanagh et al., 2010; Howe et al., 2011; Jonikaitis et al., 2013; Rolfs et al., 2011; Zimmermann et al., 2013, Harrison & Bex, 2014; Ganmor, Landy, & Simoncelli, 2015; Wolf & Schütz, 2015; Wolfe & Whitney, 2015; Paeye, Collins, & Cavanagh, 2017). With each eye-movement, attention remains on objects of interest within the visual field. In order to retain attention at the appropriate spatial location after the saccade, receptive fields at the remapped location are activated in preparation for the arrival of the expected, attended stimulus (Gottlieb et al., 1998; Melcher & Colby, 2008). Schneider & Deubel (1995) found that visual discrimination was most accurate when the discrimination stimulus was also the saccade target, demonstrating attention allocation to new saccade targets. Melcher (2009) further demonstrated active remapping of attended objects with evidence that the processing of a pre-saccadic grating influenced the perception of a post-saccadic grating presented at the same spatiotopic position. Within our study, the receptive fields processing the fixation marker prior to saccade should be activated to receive the peripheral face or house stimulus after saccade. The increased processing latency found between "same" and "change" conditions indicates an expectation of the original

512 stimulus after the saccade. The remnant post-saccadic information in the “disappear” condition also
513 supports this notion.

514 Evidence of receptive field remapping has been found within saccade centers, such as the frontal eye
515 fields, intraparietal sulcus and superior colliculus (Duhamel et al., 1992; Goldberg & Bruce, 1990;
516 Umeno & Goldberg, 1997). fMRI studies have also demonstrated that the intraparietal sulcus (IPS)
517 and the frontal eye-fields (FEF) have retinotopic representations of visual attention and saccade
518 targets (Sereno et al., 2001; Kastner et al., 2007; Hagler et al., 2007).

519 Predictive coding may also contribute to information conservation and transfer across saccades
520 (Vetter et al., 2012). Predictive coding models propose that our perception is built from feedforward
521 sensory information and cortical predictions fed back from higher cortical areas (Rao & Ballard,
522 1999). Cortical predictions are internal models of our expected stimulation from our environment.
523 Recent studies have demonstrated that predictive codes can transfer across saccade and effect post-
524 saccadic processing, evidenced both behaviorally (Vetter et al., 2012) and in neuroimaging (Fairhall
525 et al., 2017). Vetter et al. (2012) found detection benefits for post-saccadic targets that were
526 predictable by their relationship with the pre-saccadic stimulus. In neuroimaging, predictable post-
527 saccadic stimulation resulted in a decrease in BOLD activity in the early visual cortex (Fairhall et al.,
528 2017), commonly accepted as a marker for predictive processes (Alink et al., 2010; Kok et al., 2012).

529 Interestingly, evidence for information transfer is present in the latency of pattern classification,
530 rather than in the classification performance, as seen in previous studies (Kok et al., 2012).
531 Decreased stimulus processing latency using internal predictive codes seems logical, yet others have
532 been unable to relate processing latency and stimulus predictability (Todorovic et al., 2011). We did
533 not find a significant difference in reaction times between our conditions but this is principally due to
534 our use of a response window 300ms after stimulus offset.

535 Notably, we may have found a possible neural correlate of the illusory “ghost” phenomenon
536 reported by Wolf et al. (1980). Wolf et al. found that a target removed during saccade was still

perceived on saccade landing. Jonides et al. (1982) replicated this illusion, but later found that phosphor persistence of CRT monitors could explain the percept (Jonides et al., 1983). Phosphor persistence was measured at 11 ms in our study, 40.5 ms shorter than the average saccade duration for our participants. Yet we were still able to decode between the perceptions of face and house after saccade on the "disappear" condition. However, the difference in the post-saccadic decoding ability of face and house percepts between "same" and "disappear" conditions is significant (both in terms of accuracy and latency). The late classification may indicate that the illusory percept has a long time-course with lower signal strength. It is also possible we are not exploiting the optimal processing strategy for illusory percepts: the classifier is trained with feedforward sensory stimulation, yet illusory percepts may be created from internal templates of sensory information which do not result in the same patterns of activity. For example, imagining a sound results in a correlated but significantly reduced classification performance in comparison to listening to that sound (Vetter et al., 2014).

Conclusion

Information about the peripheral pre-saccadic stimulus is transferred across the saccade so that it becomes available and influences processing at a new retinal position (the fovea) when the saccade has landed. Pre-saccadic information was found to interact with post-saccadic stimulus processing, and remain available when no stimulus was present after saccade.

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696

697 **Figure Legends**

698 **Figure 1: Saccade and fixation task stimulus. 1a) Fixation conditions.** In both conditions, subjects

699 fixate between the two dashed lines for 200 ms. An image (a house or a face) was then presented

either centrally or 10° to the left of fixation for 500 ms. The black bar across eyes of the face is for publishing purposes only, bar not present in experimental stimuli. Participants are required to keep their fixation regardless of the position of the stimuli and report whether the image in trial n is the same or different to the image in trial n-1. In this example only the face stimulus is shown, however there was equal likelihood of the presentation of the house stimulus. **1b) Saccade conditions.** In all conditions, participants fixate on empty space between the two dashes. After 200 ms, an image was presented 10° to the left of the fixation point. The image could be a house or a face. Participants remain fixated on the fixation point whilst attending to the image for 500 ms until the fixation point disappears, which cued subjects to saccade to the image. In the "same" condition, participants' saccade would land on the same stimulus, whereas in the "change" condition, participants' saccade would land on a different image. These images would be presented for 45 ms after saccade offset. In the "disappear" condition, the image would disappear as soon as the saccade was detected, so that the saccade would land on an empty space. Subjects were instructed to respond 'same' if they landed on the same image, or 'different' if they landed on the changed image.

Figure 2: 2a) Peripheral training stimuli: Classifier trained on 90% of peripheral fixation trials at each time-point individually, and tested at each corresponding time-point with the remaining 10% the trials. **2b) Central training stimuli:** Classifier trained on 90% of central fixation trials at each time-point individually, and tested at each corresponding time-point with the remaining 10% the trials. **Note:** the classification scales change from panel a) to panel b).

Figure 3: Classification of pre-saccadic time-period of saccade trials. Classifier trained on peripheral fixation conditions at each time-point and tested on the corresponding time-point within the pre-saccadic time-period, from stimulation onset to 300 ms. Solid horizontal line indicates chance level (50%), 95% confidence intervals and Bonferroni corrected p-values depicted.

Figure 4: Classification of post-saccadic time-period from saccade offset. The classifier was trained on the "fixation" condition trials with central stimuli. 4a) Classification performance between face and house for "same" saccade condition. **4b)** Classification performance between face and house for "change" condition. **4c)** Classification performance between face and house for "disappear" condition and "peripheral fixation" condition after stimulus offset (plus 51.5 ms to simulate saccade). Solid horizontal line indicates chance level (50%), vertical dotted line is the peak performance time-point of the fixation trials (140 ms), used to train the classifier. 95% confidence intervals and Bonferroni corrected p-values depicted. Note the classification performance scale is different for **4a/4b** and **4c**.

Figure 5: 5a) Train classifier on each time-point of 90% of central fixation trials and test on every time-point of the remaining 10% of central fixation trials. **5b) – d)** Train classifier on each time-point of central fixation trials and test on every time-point after saccade offset of: **b)** "same" trials, **c)** "change" trials, & **d)** "disappear" trials. Note that the range of classification performance changes in each panel.

Figure 6: Using post-saccadic signals to train the classifier. 6a: Classification between "same" and "change" in post-saccadic time-period from time-point corresponding to mid-saccade transient in "change" condition. Train classifier on each time-point of 90% of "same" and "change" trials and test classifier on the corresponding time-point of the remaining 10% of "same" and "change" trials. **6b: Classify pre-saccadic EEG signal using post-saccadic traces.** Classifier trained on peak decoding time-point in the post-saccadic time-period for each condition separately and then tested using the pre-saccadic time-period of corresponding condition. Solid horizontal line indicates chance level (50%). 95% confidence intervals and Bonferroni corrected p-values depicted.