Title: Changes in neural activity around the time of saccades: Separate contributions of visual and non-visual signals on MEG alpha and theta band activity.

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Conflict of interest statement

The authors declare no competing financial interests.

Acknowledgments

We are grateful to Davide Tabarelli, Gianpiero Monitolla and Pietro Chiesa for technical support and advice, Giorgio Marinato, Poppy Sharp and Jeff Anesi for help with data collection, Kseniia Dmitrieva and Ceren Okatan for data preprocessing, and Daniel Baldauf for advice and comments on an earlier version of the manuscript.

This research was supported by a European Research Council grant “Construction of Perceptual Space-Time” (CoPeST; agreement 313658).

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Abstract

Visual processing mainly occurs during fixation, periods separated by saccadic eye movements, necessitating a close coordination between sensory and motor systems. It has been suggested that the intention to make a saccade can modulate neural activity, including predictive changes, suppression of peri-saccadic retinal input and trans-saccadic integration. Consistent with this idea, modulations of neural activity around the time of saccades have been reported in non-human species, showing non-visually mediated, extraretinal responses in specific brain regions. In humans, however, peri-saccadic whole-brain activity has mainly been studied in the context of a perceptual task, making it difficult to disentangle activity related to the task, visual transients from retinal stimulation and non-visual (saccade-related) responses. We measured magnetoencephalography (MEG) theta (3–7 Hz) and alpha (8–12 Hz) activity during voluntary horizontal saccade execution between two fixation points. To distinguish between visually and non-visually mediated activity, participants engaged in three tasks: voluntary saccades in near-darkness, fixation with visual input shifted to simulate the saccade, and volitional saccades in total darkness. Using correlational analyses, we found that patterns of neural activity are consistent with contributions of two separate mechanisms, one related to saccades (non-visual/extraretinal) and the other linked to the processing of visual input at the beginning of the new fixation (visual/retinal). Changes in occipital alpha power and instantaneous frequency showed a similar time course in near-dark and simulated saccade conditions, suggesting an effect of visually evoked responses. In contrast, alterations in parietal-occipital theta power and phase clustering were consistent with a non-visually-driven (extraretinal) mechanism, with similar multivariate patterns for near-dark and full-darkness conditions. Some effects, such as theta phase reset and alterations in alpha power, showed separable contributions of both the saccade and visual transient, with differing time courses. This combination of visual and non-visual mechanisms may support sensorimotor integration during active vision.

KEYWORDS (max 6)

MEG; saccades; alpha; theta; oscillations; active vision

HIGHLIGHTS (3 to 5 bullet points, 85 characters per point incl. spaces)

- We measured MEG θ - and α -band activity associated with saccades
- We compared saccades in near darkness, saccades in darkness and simulated saccades

- MVPA analyses revealed separable visual and non-visual contributions to the signal
- The results demonstrate how the sensory and motor systems align in active vision

1. INTRODUCTION

Humans typically make saccadic eye movements several times per second to scrutinize objects of interest in their environment. Saccadic eye movements are thus an essential feature of human visual processing (for review: Melcher and Colby, 2008; Schroeder et al., 2010). As most studies have focused on visually-mediated responses during artificially maintained fixation periods, much has been learned about evoked responses to suddenly appearing stimuli but less is known about how saccadic eye movements alter both background neural activity and also visual stimulus-induced brain responses (for review: Colby et al., 1993; Klier and Angelaki, 2008; Schroeder et al., 2010).

Intracranial electrophysiological recordings in animals around the time of saccades have yielded several main findings. First, some neurons change their spatial selectivity in the peri-saccadic time period, a phenomenon known as ‘remapping’ (Duhamel et al., 1992), observed in non-human primates (Duhamel et al., 1992; Nakamura and Colby, 2002; Umeno and Goldberg, 1997). Changes consistent with remapping have also been reported in human participants using EEG (Parks and Corballis, 2010, 2008) and fMRI (Merriam et al., 2007). Secondly, an enhancement of the visual response to stimuli has been observed in various visual areas following a saccade (Barczak et al., 2019; Ibbotson and Kregelberg, 2011; Ito et al., 2011; Kagan et al., 2008; MacEvoy et al., 2008; Reppas et al., 2002; Schroeder et al., 2010), whereas some neurons show a suppressed response to sensory input around the time of saccades (Chen and Hafed, 2017; Duffy and Burchfiel, 1975), which has also been reported in humans using steady-state visual evoked potentials (Chen et al., 2019) and is consistent with reduced perception of stimuli presented during saccades (Latour, 1962; Volkmann et al., 1968).

Moreover, a number of studies in non-human primates have reported changes in neural oscillations around saccades. Resets in theta oscillations have been observed in the hippocampus (Hoffman et al., 2013; Jutras et al., 2013; Ringo et al., 1994) as well as in visual areas (Bartlett et al., 2011; Ito et al., 2013; Rajkai et al., 2008). When making saccades in total darkness (Barczak et al., 2019; Rajkai et al.,

2008), neurons in primary visual cortex (V1) show an increase in post-saccadic theta power and phase clustering. On a theoretical level, such phase resets may reflect alignment of sensory and motor systems for the sensorimotor sampling process described across many different species (Schroeder et al., 2010). Indeed, eye-movement related top-down signals appear to affect both perception and the phase of neural oscillations (Veniero et al., 2021). Other studies have investigated the relationship between alpha oscillations and saccades (Drewes and VanRullen, 2011; Staudigl et al., 2017). Saccades are also linked to attention shifts (Deubel and Schneider, 1996; Hoffman and Subramaniam, 1995; Kowler et al., 1995; Nobre et al., 2000), for which alpha oscillations are thought to play inhibitory and selective roles (Klimesch, 2012). Thus, changes in both theta and alpha band activity have been linked to saccadic eye movements.

Previous neuroimaging studies of saccade-related changes in neural processing in humans have typically included a cognitive or perceptual task, while invasive electrophysiology in non-human subjects has been limited to a small group of neurons at a time. The goal of the present study is to examine changes in oscillatory activity around the time of saccades, measured at the whole-brain level, in human participants using magnetoencephalography (MEG). To disentangle neural activity that is non-visually mediated (related to oculomotor programming or action) from neural activity mediated by the visual transient caused by retinal input during the saccade, participants took part in three tasks: (1) perform self-paced voluntary horizontal saccades in near-darkness between two fixation points (near-darkness condition), (2) maintain fixation while visual input shifted to simulate a horizontal saccade (simulation condition), and (3) perform self-paced volitional horizontal saccades in the absence of visual input (total darkness condition). Based on previous non-human neurophysiology studies, and in particular the proposed role of low frequency oscillations in active sensing (Leszczynski and Schroeder, 2019), we focused on theta (3–7 Hz) and alpha (8–12 Hz) band signals, and studied them in terms of single-trial power, inter-trial phase coherence (ITPC), and instantaneous frequency (IF).

To understand the contribution of non-visual (related to motor action) and visual (related to retinal input) processes, we compared the three conditions using correlational analyses. Given the large differences between conditions (in saccade size and timing, visual input, potential active mechanisms of neural suppression or enhancement due to saccadic motor programming or efference copy, etc.), differences in

neural patterns between conditions are difficult to interpret. Our general approach was thus to look for *similarities* in neural patterns between conditions. We compared patterns in two complementary ways.

First, we looked at the time course of average occipital changes for each measure, asking the question of whether occipital neural activity shared features in time between conditions. Second, we compared the three conditions using time-generalized correlational analysis, across occipital and parietal sensors. This approach looks at whether, for each pair of time points, the pattern of activity across sensors between two conditions shares features. The use of the three conditions, combined with the correlational analyses, made it possible to characterize which activity patterns were likely due to retinal input (found only in the fixation condition or in both the fixation condition and the near-dark saccade conditions), in contrast to modulations that were likely non-visual/extraretinal (found for saccades in total darkness only or in both the total darkness and near darkness saccade conditions). Overall, the goal was to characterize the dynamics of theta and alpha band activity changes related to eye-movements and identify to what extent they were driven by visually and non-visually-mediated signals. Characterizing such changes in neural activity around the time of saccades is fundamental to understanding the contribution of sensorimotor integration in visual processing and, more generally, the nature of active sensing in humans (Leszczynski and Schroeder, 2019; Melcher and Colby, 2008; Schroeder et al., 2010).

2. MATERIALS AND METHODS

2.1. Participants

The participants were adults who reported normal or corrected-to-normal vision. Informed consent was obtained from all participants, who were given monetary compensation for their time. The experimental procedures were approved by the ethical committee of the University of Trento (Italy).

Data was collected from 26 participants. Participants' data were analyzed if, for each condition, at least 30 saccade epochs for each left/right direction remained after data epoching and cleaning. This resulted in data sets for 19 participants (14 female), for which the age range was 23–33 (mean 25.2; standard deviation 3.2).

2.2. Experimental Design

2.2.1. Participant preparation

Four electrooculography (EOG) and two electrocardiography (ECG) electrodes were prepared. Electrodes were placed above and below the left eye for measuring the vertical EOG, and on the outer canthi for measuring the horizontal EOG. ECG was recorded using Einthoven's lead II, which used the Left Leg and the Right Arm electrodes. Five head position indicator (HPI) coils were attached. Head coordinate frame, coil position and head shape were determined with a 3D digitization system (Fastrack, Polhemus, USA).

2.2.2. Experimental apparatus

Visual presentations were displayed using a PROPixx projector (VPixx Technologies Inc., Canada), with a screen resolution of 1440×1080 pixels and a refresh rate of 120 Hz. The visual distance of the participant from the screen was 100 cm. The size of the projection on the screen was 51 cm by 38 cm. Display and triggers were controlled using Matlab (Mathworks, Inc., USA) Psychtoolbox-3 (Brainard, 1997; Kleiner et al., 2007; <http://psychtoolbox.org>). In addition to triggers, visual display timing was measured using a photodiode.

An EyeLink 1000 Plus system (SR Research Ltd., Canada) controlled with the Eyelink extension of Psychtoolbox-3 was used to monitor the gaze position of the participants (except in total darkness), using the right eye. Sampling rate was 1 kHz. A nine-point calibration was performed at the beginning of each run. No drift correction was applied during runs.

MEG activity was recorded with an on-line sampling rate of 1 kHz using a whole-head MEG (Neuromag306 system; Elekta Instrument AB, Finland) in a magnetically shielded room. This system consists of 102 sensor locations each containing a triplet of one magnetometer and two orthogonally-oriented planar gradiometers. MEG, bipolar EOG and ECG channels, as well as gaze position coordinates, photodiode voltage and triggers were recorded and streamed into the same data set.

Participants' behavior and safety was monitored online using the EOG streams, the eye-tracking data and infrared camera (except during the full darkness condition), and the MEG room camera and intercom.

2.2.3. Procedure and tasks

Participants were asked to perform successively three tasks in separate blocks, which are considered here as three separate conditions. Each task was divided into 4 runs, between which the participant was allowed to rest. Run duration for each condition was 6 min in the near-darkness, 4 min in the total darkness, and 4 min in the simulation condition. The order of conditions was counter-balanced across participants.

At the beginning of each run, head position was recorded using the HPI coils. Each run (except in total darkness) was preceded by the eye-tracker calibration, followed by 5 s of a dark screen. In all conditions, online monitoring enabled the experimenter to instruct participants to adapt their behavior if the task was not performed properly, e.g. if the time between saccades was either overly long or short, if there were too many blinks, etc.

2.2.3.1. Saccades in near-darkness

The near-darkness condition was designed to provide some minimal visual input to participants to help maintain fixation and plan saccades, whilst minimizing clutter and the visual transient from the retinal input. Lights in the MEG chamber were turned completely off and the main visual display was black except for four horizontally-aligned green dots of 0.1° of diameter. The dots were dimly lit and of green colour (4% of maximum intensity of the green channel of the display) separated by a visual angle of 6° and placed approximately at the height of the participant's eyes. Mean luminance and chromaticity over four measurements with a CS-100A (Konica Minolta, Inc., Tokyo, Japan) at participant distance from display, using a larger dot covering the 1° of measurement area, yielded the following values: $Y=11.175$ cd/m^2 , chromaticity $x=0.1823$, $y=0.7062$. Screen background luminance yielded $Y=0.125$ cd/m^2 . Participants were instructed to perform fixation and saccades by looking alternatively at the two central dots, but never looking at the outer two dots. This was chosen so that at each of the two eye positions

(i.e. fixating the left or right central dot), there were two peripheral dots present at $\pm 6^\circ$ eccentricity, thus minimizing the pre-saccadic versus post-saccadic differences in visual input. Green, rather than grey, dots were chosen to avoid a potential color breakup artefact due to the sequential display rate of the PROPixx projector. In each run, participants were asked, in two different sections of the run, to maintain fixation to the left, or right central dot for 45 s each, or to perform saccades between the two central dots. In the present paper, we only report data from the saccade sections, for which participants were instructed to make saccades as cleanly as possible, and to leave a few seconds before and after the saccade without blinks or eye movements.

2.2.3.2. *Simulated saccades*

This condition was designed to simulate the retinotopic visual input occurring in the near-darkness condition, although participants maintained fixation during each trial. Participants were instructed to fixate the point displayed at the center of the screen. The four horizontally-aligned fixation points of the previous conditions were used, but they were shifted so that the left (or right) central dot was at the center of the screen. Saccade-related changes in the visual input were simulated by a short inter-stimulus interval (ISI) during which the dots were removed, and after which the fixation dots were shifted by $\pm 6^\circ$ (see Fig. 1a). The duration of the ISI was sampled using the distribution of saccade durations of a previous preliminary experiment in the same conditions, with mean (M) of 50.0 ms and standard deviation (SD) of 4.2 ms. Simulated fixation times were sampled randomly from a uniform distribution between 3 and 5 s. Each run contained 18 saccades in each direction. Simulated saccade and fixation onset times were determined using triggers and a photodiode. As for the near-darkness condition, each run contained two sections of 45 s during which the left, or right, central dot was fixated. We report only data related to the saccades.

The choice of modelling the saccade visual input by simply removing the dots for a short duration rather than including a whole motion of the dots offers the advantage of preventing the introduction of neural activity from visual input motion that would not be present during a saccade. Precise models of the actual motion of the eyes during saccades would be necessary, as well as a sufficiently correct restitution of the movement on a 120 Hz screen that covers only a $54.0^\circ \times 41.6^\circ$ portion of the visual field. In addition, modelling motion saccadic suppression may be more ecologically valid than a ‘raw’ motion with some

suppression modelled, since at least some of the suppression appears to occur as early as the retina (Idrees et al., 2020). However, many factors affect suppression, including low-level features (see e.g., Baumann et al., 2021) and high-level factors, including context (Zimmermann, 2020). Because we considered that any simulated motion may introduce some artefact, we decided to remove the motion altogether. This way the reappearance of the dots models the new fixation, whose evoked response is orders of magnitude stronger than the neural response to visual input during the saccade (for review: Huber-Huber et al., 2021).

2.2.3.3. Saccades in total darkness

In this condition, participants were put in total darkness. All sources of light inside the MEG room were shut down, including the display and the EyeLink infrared light, which emits also in visible frequencies. Light leaks from the outside of the room were covered as much as possible. Luminance measured toward the screen at 1 m distance was below the chromatometer sensitivity threshold of 0.01 cd/m². In addition, participants were wearing a pair of cardboard glasses to prevent any remaining light to be perceived. All participants reported the total absence of visual input under these conditions. During piloting, the experimenters and other lab members reported no visual input even after adaptation. Prior the start of the total-darkness condition, two dots separated by 6° were shown on the screen. Participants were asked to perform saccades of approximately this amplitude during the sessions in total darkness. Each run also included 30 s of fixation, during which participants were asked to look right ahead at the beginning or the end of each run. We report only data related to the time period surrounding the saccades.

As the eye-tracker was not usable in this condition, the participants' eye movements were measured using the EOG stream only. Details on the EOG data are given below, showing that the EOG provided similar information to the EyeLink.

a Simulation condition

b

c

d

e

Figure 1. Experimental paradigm and details of MEG and eye movement analyses. **(a)** The display in the simulation condition was designed to simulate visual input from the saccades and fixations in the near-dark condition. Four horizontally-aligned green dots separated by 6 degrees of visual angle were displayed on a black background. The left- and right-central dot were alternatively located on the vertical midline of the screen to simulate left- and right-fixation. The dots disappeared briefly between the changes to simulate the saccade itself. The display in the near-dark condition was identical, but centered with respect to the vertical midline. **(b)** Location of gradiometer sensors used for the analysis. For the univariate analyses, only the occipital sensors were used. Correlational analyses used both occipital and parietal sensors. Analyses to assess the influence of non-neural signal contamination during the saccade used the two frontal locations shown. **(c)** Saccade duration in the full-darkness and near-darkness conditions. Horizontal line: mean; dark box: $\pm$ standard error; light box: $\pm$ standard deviation; dots: individual participant values. **(d)** Example of the horizontal EOG time course from a single rightward saccade trial in the full-darkness condition. Time origin is set to saccade onset. **(e)** Example of the horizontal component of the eye position determined by the eyetracker, from a single rightward saccade in the near-darkness condition. Time origin is set to saccade onset.

2.3. Data Preprocessing

2.3.1. MEG data preparation

For each run, magnetometers and gradiometers were visually inspected, and noisy channels were identified for reconstruction. Using the head position measured at the start of every run, the reference head position for each participant was defined as the head position closest to the head position of the other runs. Temporal Source Space Separation (tSSS; Taulu and Hari, 2009) and head position alignment were then applied on the remaining channels using the Elekta MaxFilter implementation. The tSSS algorithm leverages the Maxwell equations to express the magnetic signal space into a sum of spherical harmonic functions, allowing its decomposition into two independent subspaces: one with the sources inside the helmet (containing the neural signals of interest) and the other one outside the helmet (containing only disturbance signals). This decomposition allows the subtraction of the latter. Default tSSS parameters were applied with a temporal buffering of 10 s. Noisy channels were reconstructed by the algorithm, and head position across runs was aligned for each participant to their reference head position, reducing within-participant between-runs variability.

All remaining analyses were performed in Matlab, using the Fieldtrip toolbox (www.fieldtriptoolbox.org; Oostenveld et al., 2011) and custom scripts, unless otherwise stated. To facilitate data storage and processing, the raw, Maxfiltered data was subsampled to 500 Hz. To remove heartbeat signals, the data was subjected to an independent component analysis (ICA) training procedure, and corresponding components were removed. First, gradiometers and magnetometers were separated and each subjected to the extended ‘runica’ algorithm as implemented in the Fieldtrip toolbox. Then, the coherence between the time course of each ICA component and the ECG channel was calculated between 1 and 45 Hz and the average coherence (thereafter ‘coherence score’) was then calculated. Components ranked 20th or higher in power, and whose coherence score was larger than 0.5 were removed. The time course of the chosen components was inspected. No more than 2 components were removed per run and sensor type. The continuous resulting signal was then visually inspected prior to commencing the subsequent steps.

Saccadic eye movements generate non-neural signals, recorded by the MEG mostly in frontal sensors (Gawne et al., 2017). While ICA is commonly used as a way to remove eye-movement artifacts, we chose to keep the signal as is, as removing ICA components related to eye movements may also remove temporally associated neural activity. As mentioned above, each of the 102 MEG sensor locations contains a pair of orthogonal planar gradiometers and a magnetometer. Magnetometers are a single loop that generates current when magnetic flux passes inside it, which makes them able to detect distant sources, including deep neural sources, but also distant non-neural signals. By contrast, gradiometers are 8-shaped sensors that measure the difference in magnetic flux between their two loops. This has the effect of cancelling out the flux generated by distant sources. For this reason, non-neural artifacts generated by the saccade differentially affect magnetometers and gradiometers. Saccadic artifacts more strongly affect and gradiometers closest to the sources (i.e. more frontal sensors) and magnetometers. We therefore only used data from the gradiometers for our analyses, as eye movement artifacts were more localised than for magnetometers.

Following the epoching procedures described below for each condition, MEG and eye-movement data were visually inspected, and trials with falsely detected saccades, additional eye movements (saccades or blinks) or noise were removed. The number of leftward and rightward saccades were then equalized within each condition and participant by randomly subsampling trials (without replacement) from the direction that had the most trials.

2.3.2. Saccade detection in near-darkness

The algorithm described in Nyström and Holmqvist (2010) was used for the detection of eye events, based on velocity and acceleration criteria. Saccades were kept if they started and landed at eccentricities 3° with a tolerance of 2° and were not preceded or followed by any eye event (other saccade, blinks) for a period of 1200 ms. Saccades of amplitude $< 1^\circ$ were ignored. Then 2400 ms-long epochs locked to saccade onset and fixation onset were generated. An illustration of the horizontal component of the eye-tracking signal for a trial in near-darkness is shown in Figure 1e.

2.3.3. Saccade detection in total darkness

In the total darkness condition, saccades were detected, and saccade/fixation onsets were determined on the basis of the EOG signal. The correspondence between the EOG signal and the eye-tracker position was reliable in the near-darkness trials (mean Pearson's correlation coefficient across participants: $r=.93$, minimum: $r=.80$), thus providing confidence that EOG changes in total darkness would also reflect eye-movements accurately. To detect saccades, the horizontal EOG stream was low-pass filtered using a zero-phase shift filter with a 40 Hz cut-off. The resulting signal was then differentiated using 50 ms as Δt . Local peaks corresponded to the occurrence of saccades. The portions of the continuous data stream corresponding to the saccade task were then epoched around the detected saccades.

To determine the onset and offset of each detected saccade, a piecewise linear function constituted of three lines (modelling respectively the pre-saccadic fixation, the saccade, and the post-saccadic fixation) was used to fit the original saccadic EOG signal. The onset and offset of the saccades were defined as the intersection between the fitted lines. The 2400 ms-long epochs locked to saccade onset and saccade offset were generated. An illustration of the horizontal EOG signal for a trial in full-darkness is shown in Figure 1d.

2.3.4. Simulated saccades

As for the near-darkness condition, the eye-tracking data was used to detect saccades, fixations and blinks. Trial periods of 2400 ms were extracted using the timing of the photodiode signal corresponding to the offset and onset of the fixation points, respectively indicating the onset and offset of the simulated saccade. Trials containing blinks, saccades of horizontal amplitude $> 1^\circ$, and with fixation beyond $\pm 2^\circ$ of eccentricity in the 1200 ms preceding or following the event were removed.

2.4. Measures

Trials were filtered in the theta and alpha bands using 3rd order Butterworth filters of cutoffs 3–7 Hz for theta and 8–12 Hz for alpha, passed forward and backward. Butterworth filters were chosen because their response is as flat as possible in the passband, which is a desirable property for the instantaneous

frequency measure (Cohen, 2014a). The temporal resolution of the power and ITPC analyses derived from these filtered signals are driven by the filter. When defining the temporal resolution (or smoothing) as the width of the interval containing 90% of the energy of the impulse response function, its values are 268 ms for theta and 260 ms for alpha. The procedures described below are applied to each participant, condition and frequency band. After calculation of the measures, epoch duration was reduced to the [–700, +800] ms interval for analysis. Unless indicated otherwise, the baseline corresponds to the 700–500 ms period preceding saccade onset. For completeness, event-related fields (ERFs) are shown in Figure S1.

2.4.1. Power

Power was calculated at each time point of each gradiometer as the squared amplitude of the analytic representation of the filtered signal (obtained by applying the Matlab function ‘hilbert’). This instantaneous power estimate is equivalent to the one obtained using Fourier or wavelet approaches (Bruns, 2004; Cohen, 2014b). For each condition, participant and sensor, the average power was calculated. For the univariate analyses and topographical maps, gradiometers within the same location were combined by summing power, before averaging across locations. For correlational analysis (a type of multivariate pattern analysis; MVPA), individual sensors were kept. Relative power change was then calculated relative to power in the baseline interval.

2.4.2. Inter-trial phase coherence (ITPC)

Inter-trial phase coherence measures the phase alignment of oscillations across trials. If, across trials, phases are aligned, then the ITPC value is close to 1, while if phases are randomly distributed, its value is close to 0. We measured phase at each time point and trial by taking the argument of the filtered signal’s analytic representation ($\text{phase} = \arg(\text{hilbert}(\text{filtered_signal}))$ in Matlab), and then calculated the ITPC at each time point of each condition using this estimation of instantaneous phase. A theoretical baseline was calculated for each participant and condition using the mean of 50,000 ITPC values calculated from N randomly-generated angles, N being the number of trials for the given participant and condition, as ITPC is a measure sensitive to the number of trials. This theoretical baseline was subtracted

from the ITPC values. For topographical visualization, gradiometers were combined at each location by averaging ITPC values.

2.4.3. Instantaneous frequency (IF)

IF is defined as the time derivative of the phase scaled by 2π , and can be understood intuitively as the speed of the oscillations in the frequency band of interest at each time point. IF was estimated from the instantaneous phase of the filtered signal's analytic representation, using previously applied methods (Cohen, 2014a; Samaha and Postle, 2015) and adapted scripts from *mikexcohen.com*. As the phase angle time series is prone to noise that can cause sharp, non-physiological responses in the IF, median filters were applied (10 equally spaced window sizes between 10 and 400 ms), and the median IF value across the different filters windows was calculated at taken for each time point. For faster computation, instantaneous frequency was evaluated every 10 ms. The IF time series were then averaged across trials for each sensor and the mean IF during baseline was subtracted. For topographical visualization, gradiometers were combined at each location by averaging IF values.

2.4.4. Correlation between power and instantaneous frequency changes

To investigate the statistical link between IF and power variations, the Pearson's correlation was calculated across trials, for each sensor and time point, between the time derivative of the IF and the time derivative of power. The power time course was subsampled to match the 100 Hz rate of the instantaneous frequency. No baseline was used for this measure.

2.5. Control analyses

The rotation of the eyeball and the contraction of the periocular muscles can be detected by the MEG sensors, contaminating the signal with non-neural sources (Carl et al., 2012; Gawne et al., 2017; Keren et al., 2010). In particular, the eye dipole rotation generates low frequency artifacts, strongest at sensors located fronto-laterally (Gawne et al., 2017). Inspection of the time course of the ERFs (Supplementary materials Fig. S1a and S1b) and measures at the occipital (Fig. 2, S2, 6, S3) and frontal (Fig. S1c, S1d

and 10) sites, as well as the topographical maps (Fig. 5 and 10) indicates that occipital sensors contain a signal locked to saccade/fixation onset which might reflect contamination by an eye-movement artifact during saccade execution, in particular in the theta band and the total darkness condition. Furthermore, the smoothing effects of the passband filters spread the artifact in time, potentially confounding the results we attributed to post-saccadic neural activity (see Results section). We therefore performed the following complementary analyses for power and ITPC, which were non-time resolved and excluded the portion of the signal that would be most contaminated by the eye movement (i.e. during saccade execution). First, for each trial, the 50–250 ms interval following fixation was extracted from the non-filtered signal, effectively excluding from analysis the data points occurring during saccade execution. This portion was then detrended to remove low-frequency drifts that may occur following the saccade due to the eye movement (Fig. S1c and S1d), and zero-padded to one second to increase the frequency resolution for the frequency decomposition. Power and phase were then calculated for this entire interval using multi-taper frequency transformation for each individual frequency between 3 and 7 Hz, with steps of 1 Hz. The same procedure was applied for the 700–500 ms interval prior saccade onset to calculate baseline power. After averaging power across trials, relative power change from baseline was calculated for each frequency, sensor, and condition, and then collapsed across frequencies. Similarly, ITPC was calculated for each frequency, sensor and condition, and then averaged across frequencies, before subtracting the ITPC baseline defined above. Inspection of the topographies from these control measures (Fig. 7c and f) indicates that this procedure successfully excluded eye movement-related artifacts previously observed at frontal locations (Fig. 10a and b), uncovering theta activity clearly localised at occipital sensors for the darkness and near-darkness conditions. These control power and ITPC measures were then subjected to the same univariate and multivariate analyses as the other measures, described below.

To further ensure that any significant effect in the total or near-darkness condition could not be explained by residual eye movement artifact signal contamination, we correlated, across participants, the power and ITPC baseline departures provided by these analyses with the magnitude at frontal sites (in the non-corrected analysis). Because frontal sites artifacts were stronger in the theta than the alpha band, we used frontal theta in addition to frontal alpha as an index of artifact magnitude when examining the alpha band.

2.6. Statistical Analyses

2.6.1. Occipital sites temporal pattern analyses

To study the time course of the measures at occipital sites, 48 gradiometers whose 24 locations are illustrated in Figure 1b, were used. For each participant and condition, measures were averaged across sensor locations and trials (except for ITPC which is by definition calculated across trials) before being subjected to statistical analysis. To evaluate the morphological similarity of the time course between conditions for each measure, we calculated, for each participant the Pearson's correlation coefficient of the time courses between the pairs of conditions. In addition, because of the potential contamination of the occipital sensor signal by eye movement artifacts, we also computed partial correlations controlling for the frontal sensor signal of the conditions of interest. T-tests were then performed to infer whether the correlations were significant. All correlation values and statistics are also reported in the Supplementary Materials.

To help the characterisation of the time course of the measures, we also tested for deviations from baseline. Two-tailed one-sample t-tests at each time point between -500 and +800 ms were applied. For the IF-power correlation measure, which was not baseline-corrected, F-tests were used to compare the different conditions. Like the t-tests, F-tests were applied at each time point between -500 and +800 ms. Tests were cluster-corrected for multiple comparisons across time (Maris and Oostenveld, 2007) using $p=0.025$ of significance at the data point level and $p=0.05$ for clusters. We report points belonging to significant clusters.

2.6.2. Parietal-occipital spatial pattern analyses

While the analyses described above allow a coarse comparison of the overall morphology of the univariate occipital signals across time, they do not allow to compare the similarity of neural patterns at each time point. For this purpose, we extended the analysis to 100 occipital and parietal individual gradiometers whose locations are illustrated in Figure 1b (temporal and frontal sensors were not included as they likely carried non-neural signals coming from the eye movement themselves). As conditions and neural signals were very different between conditions, we opted for correlational analyses, which find

similarity between patterns across sensors, using Pearson's correlation. Patterns for power, ITPC and IF were compared using this method. In addition, to account for differences in the time course of neural activity between conditions, we applied a time-generalization procedure. After applying a Fisher transformation to the correlation values, we applied two-tailed one-sample t-tests at each time×time location within the ± 200 ms diagonal, cluster corrected. These multivariate analyses were performed using the CoSMoMVPA Matlab toolbox (Oosterhof et al., 2016; <http://www.cosmomvpa.org/>). For each significant cluster, the pair of maps corresponding to the point of maximum correlation is shown. These maps show the signals from combined occipital and parietal gradiometers only (i.e. removing frontal and temporal ones), from which the mean was removed.

Finally, time-resolved partial correlations (without time generalization) were performed, to assess the independent contribution of total darkness and visual input to the changes in neural activity for saccades in near-darkness. The time courses generated correspond to the diagonal of the time-generalization maps, but controlled for the remaining condition.

It is to be noted that – with the exception of the IF–power time course correlation measure – we do not explicitly test for *differences* between conditions in time. Instead, our approach was focused on finding *similarities* between conditions, with the underlying idea that similar timecourse and topographical patterns may reflect common processes.

3. RESULTS AND DISCUSSION

3.1. Eye movement analyses

We first characterized the attributes of saccades made in the near-darkness and full-darkness conditions. Saccade duration in full-darkness was longer than in near-darkness, and with more variability (full-darkness duration: $M=169$ ms, $SD=55.2$ ms; near-darkness: $M=82$ ms, $SD=5.7$ ms; see Fig. 1c). Notable differences were expected, as eye movements are more difficult to plan and control in the absence of any visual input. Saccades in full-darkness were also larger: EOG amplitude in near-darkness was on average

18 % of the EOG amplitude in full-darkness. Mean saccade amplitude in near-darkness was 5.45° (SD=0.27°). Under the assumption of a linear relationship between EOG and saccade amplitude (see e.g. Jia and Tyler, 2019), saccade amplitude in full-darkness was approximately 34.8° (SD=11.0°). Across the 19 participants, the number of trials for each condition was: near-darkness M=144.4 (SD=67.8); darkness M=126.4 (SD=52.4); simulation M=112.0 (SD=42.0).

Saccade duration (defined as the duration between saccade onset to fixation onset) in near-darkness was longer than the simulated saccades (M=48.9 ms, SD=.6 ms), whose durations were set following a previous (unpublished) experiment with a similar task. In this past experiment, eye movements were recorded with EOG electrodes. The difference in duration likely due to the difference in the definition of fixation onset, which was previously defined as the point of maximum of the second-derivative of the EOG signal. In the current experiment, fixation onset was set as the end of the glissade following the saccade, defined in Nyström and Holmqvist (2010). Indeed, when excluding the glissade from the saccade in near-darkness, saccade in near-darkness and simulated saccades match more closely in durations (M=63.5 ms, SD=6.7 ms).

Due to the between- and within- condition variability in saccade duration, the MEG signal was analyzed in two ways, once with the time origin set at saccade onset and once with the zero point set at fixation onset. Aligning the data to each saccade and fixation onsets addresses latency mismatches between neural events that are time-locked to one of the two events.

3.2. Alpha frequency

We first report the changes in alpha frequency measures (power, ITPC, IF) around the time of the saccades for occipital sensors. We then report results from the time-generalized correlational analyses between conditions over a wider set of sensors (occipital and parietal) to evaluate the similarity of patterns between conditions. This is then followed with a discussion of the pattern of results, taking into account both the time course measures and the correlation analyses.

3.2.1. Occipital alpha temporal pattern analyses

As shown in Figure 2, there were variations in each of the alpha band activity measures from occipital sensors when time-locked to fixation onset, compared to baseline. Observations were unchanged according to whether saccade or fixation onset was used to temporally align the data (see Fig. S2 for time courses aligned to saccade onset).

Power—Mean occipital alpha power in the near-darkness and simulation showed a similar behavior [mean $r=0.667$, $t(18)=9.544$, $p=10^{-8}$] including when controlling for the near-darkness frontal site time courses [mean partial $r=0.586$, $t(18)=7.234$, $p=10^{-6}$], with a large and long-lasting depression following the saccade (Fig. 2a). Power dropped by up to 30% relative to baseline, and did not recover by 800 ms after fixation onset. The largest t-score in absolute value was reached at time=544 ms [$t(18)=-6.53$, $p=4\times 10^{-6}$] in the near-darkness condition, and time=380 ms [$t(18)=-6.06$, $p=10^{-5}$] in the simulation condition. Average occipital power in total darkness followed a drastically different time course [non-significant correlations with near-darkness: mean $r=0.226$, $t(18)=1.967$, $p=0.065$; and simulation: mean $r=0.202$, $t(18)=1.723$, $p=0.102$], with a rapid increase following the saccade and peaking at around 200 ms following fixation onset (maximum t-score $t(18)=4.23$, $p=5\times 10^{-4}$ at time=18ms). By 800 ms post-saccade, the alpha power in this condition returned to baseline. To further ensure that the significant alpha power increase in the total darkness condition was not due to eye movement artifacts, the complementary analyses in the 50–250 ms interval (excluding time points during saccade; see Section 2.5) were applied (Suppl. Fig. S3c). We found that the occipital alpha power increase remained significant [$t(18)=3.67$, $p=0.0034$] and that it was not correlated with power changes at the frontal sites in the alpha [$r=0.27$, $p=0.26$] or theta [$r=0.042$, $p=0.86$] bands across participants, when using frontal data points during saccades (-0.05–0 to fixation onset) from the main analysis. Overall, these analyses support the neural origin of post-saccadic alpha power increase we observe in full darkness. As described above, based on the previous literature our hypotheses-driven analyses focused on theta and alpha bands, but it is worth noting that we occipital beta power followed the same patterns as alpha in all conditions: an increase in total darkness and a decrease in near-darkness and simulation conditions (Suppl. Fig. S8).

ITPC—Mean occipital phase clustering also behaved in a similar manner in the near-darkness and simulation conditions [mean $r=0.336$, $t(18)=4.105$, $p=7\times 10^{-4}$] including when controlling for the near-darkness frontal site time courses [mean partial $r=0.273$, $t(18)=3.287$, $p=4\times 10^{-3}$], with a transient departure from baseline, peaking at around 100–200 ms post-saccade (Fig. 2b). The maximum t-score was reached at 88 ms [$t(18)=6.65$, $p=3.08\times 10^{-6}$] in the near-darkness condition and 174 ms [$t(18)=4.84$, $p=1.33\times 10^{-4}$] in the simulation condition. These effects also remained in both conditions when applying the complementary analyses (Suppl. Fig. S3f) [near-darkness: $t(18)=10.48$, $p=4\times 10^{-9}$; simulation: $t(18)=5.14$, $p=7.4\times 10^{-5}$]. In addition, the occipital ITPC increase in near-darkness was not correlated with the ITPC increase observed at frontal in the alpha [$r=0.07$, $p=0.75$] and theta bands [$r=0.36$, $p=0.12$] during saccade (-0.05–0 to fixation onset). No significant ITPC departure from baseline was observed in the total darkness condition in the time-resolved analysis (Fig. 2b). However, the control analysis, which collapses the measure across the 50–250 ms interval (Suppl. Fig. S3f) yielded a significant phase clustering effect [$t(18)=2.26$, $p=0.036$] which did correlate with the signal at frontal sites in the alpha [$r=0.83$, $p=9\times 10^{-6}$] but not theta [$r=0.18$, $p=0.46$] bands.

Two observations suggest that the increase observed in the near-darkness condition was locked to the saccade onset event, rather than the fixation onset. First, the ITPC peaks occur simultaneously for the near-darkness and simulation conditions when signals are locked to saccade onset. However, when signals are locked to saccade offset, then the peak in near-darkness occurs first, before the peak in the simulation condition (Fig. 2b vs S2b). This difference is consistent with the mismatch in saccade duration between the two conditions. The second observation is that when considering the near-darkness condition, the peak is larger when signal is locked to saccade onset (Fig. S2b) versus fixation onset (Fig. 2b). This pattern is to be expected if phases are time-locked to the saccade onset event: when the signal is locked to fixation onset, the inter-trial variability in saccade durations in near-darkness will reduce the ITPC amplitude for events locked to saccade onset, as the ITPC is a measure sensitive to jitter. Finally, the total darkness time courses did not significantly correlate with neither the near-darkness [mean $r=0.189$, $t(18)=1.952$, $p=0.067$] nor the simulation [mean $r=0.164$, $t(18)=1.680$, $p=0.11$]. Overall, results indicate a clear and similar post-saccadic phase clustering in the alpha band for the near-darkness and simulation conditions, as well as a possible clustering for the total darkness condition. Occipital ITPC in beta appeared to follow a similar pattern with a post-saccadic increase in all conditions (Suppl. Fig. S8).

Instantaneous frequency—Mean occipital alpha IF in total darkness showed a significant increase (+0.1 Hz, most reliable at 320 ms following saccade with $t(18)=3.63$, $p=1.9\times 10^{-3}$; Fig. 2c). Neither alpha IF time courses in the near-dark and simulation conditions significantly departed from baseline. In addition, none of the time courses correlated significantly on average [near-darkness–simulation: mean $r=0.129$, $t(18)=1.270$, $p=0.221$; near-darkness–total darkness: mean $r=-0.029$, $t(18)=-0.275$, $p=0.787$; total darkness–simulation: mean $r=0.090$, $t(18)=-0.640$, $p=0.530$].

Power–IF correlation—A transient increase in correlation following saccade can be observed in the near-dark and simulation conditions (Fig. 2d). This portion was however not statistically different from zero, but a cluster-corrected F-test revealed a difference between the three conditions in this time period, most reliable at 120 ms [$F(2,36)=13.05$, $p=6.5\times 10^{-11}$]. By contrast, no clear deviation was observed in the total darkness condition. None of the pairwise timecourse correlations between conditions reached significance [near-darkness–simulation: mean $r=0.061$, $t(18)=1.247$, $p=0.228$; near-darkness–total darkness: mean $r=0.115$, $t(18)=1.610$, $p=0.125$; total darkness–simulation: mean $r=-0.081$, $t(18)=-1.265$, $p=0.222$].

We observed that occipital alpha band time courses in near-darkness behaved in a very similar manner to alpha following a visual input, showing in particular a decrease in power and an increase in ITPC. By contrast, in the saccade-in-darkness condition, alpha showed an increase in power, no or little phase clustering, and an increase in IF.

Figure 2. Occipital alpha band activity. Mean of measure locked to fixation onset for each condition: saccades in total darkness (blue), saccades in near-darkness (orange), visual changes simulating saccades in near-darkness (purple). Shaded areas indicate ± 1 standard error. Colored horizontal lines indicate significant departure from baseline, cluster-corrected. **(a)** Power: relative change from baseline (mean across [-700,-500] ms interval prior saccade onset). **(b)** Inter-trial phase coherence: departure from theoretical baseline. **(c)** Instantaneous frequency: departure from baseline (mean across [-700,-500] ms interval prior saccade onset). **(d)** Correlation between power changes and instantaneous frequency changes. The black horizontal line indicates significant difference between conditions with a cluster-corrected F-test.

3.2.2. Occipital-parietal alpha spatial pattern analyses

Figure 3 summarizes the results of the time-generalized correlational analyses of occipital-parietal patterns in the alpha band, locked to fixation onset. Figure 4 shows time-resolved partial correlations between the near-darkness condition and each of the two other conditions, with signals locked to fixation onset. Figure 5 shows the evolution in time of the whole-scalp topographies (Suppl. Fig. S4 shows the

non-normalised topographies). The equivalent figures with saccade onset as time origin are not shown, as the results are largely unchanged.

Power—Occipital-parietal correlational analysis (Fig. 3a–c) found that pre- and early post-fixation power patterns in near-darkness significantly resembled those of total darkness [peak t-score at time pair -180 ms (darkness) and 0 ms (near-darkness) from fixation onset, $t(18)=4.42$, $p=3.3\times 10^{-4}$], while later patterns resembled those of the simulation condition [peak t-score at time pair 340 ms (simulation) and 440 ms (near-darkness), $t(18)=2.98$, $p=0.008$]. No significant cluster was found in the comparison between simulation and total darkness (Fig. 3c), suggesting that the correlations with near-darkness come from independent contributions. This was also supported by the partial correlation analyses finding that these two early and late correlations remained even when regressing out respectively the simulation and total darkness conditions (see Fig. 4a, b), with the early partial correlation between the darkness and near-darkness conditions most reliable at 200 ms with $t(18)=3.5$, $p=0.0025$ and the late significant correlation between simulation and near-darkness most reliable at 380 ms with $t(18)=2.84$, $p=0.011$. To check whether the significant peri-saccadic correlation between the total and near-darkness conditions could be due to eye movement artefacts, we performed the complementary analyses (which exclude datapoints during saccade before the frequency decomposition) in two intervals: one presaccadic (-250 to -50 ms preceding saccade onset), one post-saccadic (50 to 150 ms post-fixation onset). The former led to non-significant correlations: $M=0.034$, $SD=0.17$, $t(18)=0.86$, $p=0.40$, suggesting that the presaccadic part of the correlation between these conditions may be due to the eye movement artefacts. By contrast, the correlation remained in the latter analysis ($M=0.276$, $SD=0.28$, $t(18)=4.29$, $p=4.44\times 10^{-4}$), suggesting that the early post-saccadic correlation between the near-darkness and total darkness conditions reflects similar alpha power patterns.

ITPC—A significant late cluster was found in the correlation between the near-darkness and total darkness conditions. This cluster was present in the time generalisation representation (Fig. 3d), with the most reliable time pair point at 400 ms (darkness) and 520 ms (near-darkness) with $t(18)=5.72$, $p=2.0\times 10^{-5}$ and also in the partial correlation analysis (Fig. 4c), with the most reliable significant correlation at 520 ms with $t(18)=3.24$, $p=4.6\times 10^{-3}$. However, it was not significant when the signals were locked to saccade onset.

676

677 *Instantaneous frequency*—A significant cluster was observed between the near-dark and simulation
678 conditions (Fig. 3h and 4f), with the most reliable time pair point at 200 ms (near-darkness) and 400 ms
679 (simulation), $t(18)=3.91$, $p=0.001$ for the time generalisation analysis, and 220 ms with $t(18)=2.85$,
680 $p=0.01$ for the partial correlation analysis.

681

682 Occipital-parietal alpha power patterns were in contrast with mean occipital power: while mean occipital
683 power time course in the near-darkness and simulation conditions were morphologically similar,
684 occipital-parietal power patterns in near-darkness resembled those of total darkness in earlier latencies,
685 and those of simulation at later latencies. Alpha IF spatial patterns appeared to behave similarly between
686 the near-darkness and simulation conditions. This suggests that post-saccadic alpha IF changes in near-
687 darkness were driven by visually-mediated processes. By contrast, alpha power changes appeared to be
688 driven by both visually and non-visually-mediated processes.

689

Figure 3. Time-generalized correlational analysis on alpha activity. **(a,b,c)** Power; **(d,e,f)** Inter-trial phase coherence; **(g,h,i)** Instantaneous frequency. Heat maps indicate Fisher-transformed correlation values between the conditions under consideration, as a function of time for each condition. Statistical analyses were run on the ± 200 ms strip, indicated by the two parallel oblique lines. Significant clusters are outlined. For each significant cluster, the point of maximum correlation is indicated by a red dot, and the corresponding pair of topographies shown below the heat map. Time origin corresponds to fixation onset.

Figure 4. Partial correlation analysis on alpha band activity. **(a,b)** Power; **(c,d)** Inter-trial phase coherence; **(e,f)** Instantaneous frequency. The first column **(a,c,e)** shows the partial correlation between the near-darkness and the full-darkness conditions, regressing out the simulation condition. The second column **(b,d,f)** shows the partial correlation between the near-darkness and the simulation conditions, regressing out the full-darkness condition. Time origin corresponds to fixation onset. Correlation values are Fisher-transformed. Time points belonging to significant clusters are indicated by dots.

Figure 5. Topographical maps for measures in the alpha band. **(a)** Power; **(b)** Inter-trial phase coherence; **(c)** Instantaneous frequency. In each panel, each row corresponds to a condition and each column a time interval, from -500 to $+700$ ms from fixation onset, by steps of 200 ms. Each map shows all combined gradiometer values, and is scaled between $\pm \text{abs}(\text{max})$.

3.2.3. Discussion on alpha frequency results

In the absence of visual input, occipital alpha IF increased around the time of the saccade, with this boost independent from changes in alpha power. Such an effect is a novel result, as it was not reported in previous studies of saccades and visual processing areas (Bartlett et al., 2011; Ito et al., 2013; Rajkai et al., 2008). This increase was not observed in the other two conditions. In addition, there was no significant correlation in parietal-occipital alpha IF patterns between the total darkness and the near-darkness conditions, indicating that the non-visually mediated changes in alpha IF are overridden when saccades are performed with visual input. However our data indicate that changes in alpha IF measured

in parietal-occipital sensors follow similar patterns after simulated and near-darkness saccades, indicating that alpha IF is differentially affected by visual and non-visual events. In addition, the visually-driven changes in IF appeared correlated with power changes and thus may be related to alpha desynchronization. This difference between conditions with respect to coupling of IF with power suggests that the mechanisms driving alpha IF in each case are distinct: one is related to the saccade plan or execution (increase in occipital alpha IF) and one related to visual transient or post-saccadic visual reafference (change in parietal-occipital alpha IF pattern).

Alpha oscillations have been suggested to play a key role in selective attention (for review, see Jensen et al., 2012) and in the temporal resolution of visual processing (Kristofferson, 1967; Samaha and Postle, 2015; VanRullen, 2016). Alpha phase has been linked to visual sampling via saccades (Barczak et al., 2019; Bartlett et al., 2011; Drewes and VanRullen, 2011). We did not find any evidence for an alignment of occipital alpha phase to the saccade onset before the saccade, in the absence of visual input. The strong occipital alpha phase clustering in near-darkness following the saccade we observe is likely mainly driven by the response evoked from the visual transient due to the saccade. We however did find in our complementary analysis some (equivocal) evidence for alpha phase clustering following saccades in total darkness. Such alpha phase clustering following saccades in full darkness has been reported in the supragranular V1 layers of monkeys, using intracranial recording (Barczak et al. 2019). As Rajkai et al. (2008) did not find such effect under the same conditions, it may be that the effect is very localized, both in terms of frequency range and spatially, and of relatively weaker magnitude (as our data suggest), making it difficult to be reliably measured.

The loss in occipital alpha power in the near-darkness and simulation conditions, possibly reflecting desynchronization of neural ensembles, is typical of the response to stimulus onset (e.g., Nogawa et al., 1976; Pfurtscheller et al., 1994) and consistent with the electrophysiology literature in visual areas (Deneux et al., 2017). Interestingly, and in contrast to the desynchronization effect, we found that average occipital alpha power increased following a saccade in full-darkness. We observed that this increase was also apparent in the beta band (Suppl. Fig. S8). While the occipital alpha power increase appeared overridden for saccades with visual input, parietal-occipital pattern analyses revealed that alpha power patterns in near-darkness, in particular in early latencies, did actually resemble those of total darkness.

This indicates that alpha power measures following a saccade contain both visually and non-visually mediated signals.

3.3. Theta frequency

As we did for the alpha band, we first report results pertaining to the time course of each measure in the signal from occipital sensors. We then report results from the time-generalized correlational analyses between conditions over a wider set of sensors (occipital and parietal) to evaluate the similarity of patterns between conditions. We then discuss the results from both analyses.

3.3.1. Occipital theta temporal pattern analyses

An overview of the main effects across the different conditions can be found in Figure 6 and S5, showing the time course of the mean theta band measures from occipital sensors, with signals locked to fixation and saccade onset respectively. As can be seen in the figure, there were again large modulations over the time course around the saccade, with the patterns in the theta band differing in interesting ways from the effects in alpha discussed above.

Power—Mean occipital theta power (Fig. 6a) showed a transient increase following saccade. This increase was largest for the near-darkness condition with a 40% increase, and significant only for the near-darkness [maximum t-score at 42 ms: $t(18)=6.91$, $p=1.8\times 10^{-6}$] and total darkness conditions [maximum t-score at 24 ms: $t(18)=5.34$, $p=4.5\times 10^{-5}$], and was followed by a depression in the near-darkness and simulation conditions [maximum t-scores at 750 ms, $t(18)=-2.74$, $p=0.013$ and 800 ms, $t(18)=-3.30$, $p=0.004$, respectively]. This common pattern across conditions was reflected in significant correlations between all pairs of conditions [near-darkness–simulation: mean $r=0.687$, $t(18)=12.746$, $p=2\times 10^{-10}$; near-darkness–total darkness: mean $r=0.604$, $t(18)=13.31$, $p=9\times 10^{-11}$; total darkness–simulation: mean $r=0.437$, $t(18)=6.314$, $p=6\times 10^{-6}$]. Partial correlations regressing out frontal sensors for the near-darkness and total darkness conditions also yielded significant pairwise correlations [near-darkness–simulation: mean $r=0.658$, $t(18)=12.338$, $p=3\times 10^{-10}$; near-darkness–total darkness: mean

$r=0.574$, $t(18)=8.929$, $p=5\times 10^{-8}$; total darkness–simulation: mean $r=0.398$, $t(18)=5.018$, $p=9\times 10^{-5}$]. In total darkness, the peak was attained around the time of saccade (about -50 ms before fixation onset), suggesting that this part of the signal is contributed to, at least in part, by sources of non-neural origin, potentially reflecting eye rotation artefacts (Gawne et al., 2017). This is qualitatively confirmed by studying the power signal from lateral-frontal sensors during saccade (see topographies in Fig. 10a and time course comparing occipital sensors with frontal sensors in Fig. 7a, b). The later part of the signal (from 0.15 s post-fixation) is most likely largely of neural origin, as suggested by the time course and topographies (Fig. 10a). To ensure that it is indeed the case, the complementary analyses described in the Materials and Methods subsection 2.5 were performed. The results, shown in Figure 7c, confirm the neural origin of the occipital increase in power in the total and near-darkness following saccade as the effects remained [darkness: $t(18)=3.94$, $p=9.5e-4$, $M=.33$, $SD=.37$; near-darkness: $t(18)=3.24$, $p=.005$, $M=.40$, $SD=.54$]. In addition, to ensure that these effects were not linked to potential residual eye movement artifacts, we correlated the occipital power changes after correction to the magnitude of the power measured during saccade (-0.05–0 to fixation onset) at frontal sites before correction, across participants. We did not find significant correlations, further supporting the fact that the reported increases in occipital theta power are genuine and not due to saccade artifacts [Pearson correlations: total darkness $r=0.087$, $p=0.72$; near-darkness: $r=-0.01$, $p=0.95$]. Finally, the occipital power increase in the complementary analysis was significant for the simulation condition as well [$t(18)=2.62$, $p=.018$, $M=.18$, $SD=.30$].

ITPC—Mean occipital inter-trial theta phase coherence increased around the time of the saccade (Fig. 6b). It was significant in all conditions and most reliable for the near-darkness condition (maximum t -score for darkness at -118 ms, $t(18)=7.27$, $p=9.31\times 10^{-7}$; near-darkness at 52 ms, $t(18)=18.35$, $p=4.24\times 10^{-13}$; simulation at 254 ms, $t(18)=8.58$, $p=8.92\times 10^{-8}$). All three conditions significantly correlated with one another across participants [near-darkness–simulation: mean $r=0.735$, $t(18)=12.558$, $p=2\times 10^{-10}$; near-darkness–total darkness: mean $r=0.487$, $t(18)=6.445$, $p=5\times 10^{-6}$; total darkness–simulation: mean $r=0.374$, $t(18)=4.810$, $p=10^{-4}$], including using the partial correlations regressing out frontal sensors [near-darkness–simulation: mean $r=0.674$, $t(18)=9.610$, $p=2\times 10^{-8}$; near-darkness–total darkness: mean $r=0.486$, $t(18)=5.738$, $p=2\times 10^{-5}$; total darkness–simulation: mean $r=0.371$, $t(18)=4.312$, $p=4\times 10^{-4}$]. As for power, *ITPC* around the time of saccade appeared contaminated by non-neural eye movement noise

for the total darkness condition (see topographies in Fig. 10b and time course in Fig. 7d). However, inspection of the signal locked to saccade onset (Suppl. Fig. 5) shows points belonging to significant clusters from prior saccade onset in total and near darkness respectively. To verify whether these ITPC increases could be attributed to neural activity or artefacts, we performed the control analyses in the -250,-50 ms interval prior to saccade onset in the three conditions. Results are shown in Supplementary Figure S6. We found no significant occipital ITPC increase in this time range [darkness: $t(18)=1.18$, $p=0.25$; near-darkness: $t(18)=-1.36$, $p=0.19$; simulation: $t(18)=-1.08$, $p=0.29$]. This suggests that the occipital theta phase clustering we observed prior to saccade onset is artefactual, likely the product of the combination of eye-movement artefact and temporal leakage due to filtering and cluster-based statistics.

By contrast, complementary analyses confirmed the significant increase in post-saccadic ITPC in all conditions [darkness: $t(18)=2.86$; $p=.01$; $M=.073$; $SD=.11$; near-darkness: $t(18)=12.2$; $p=3.94\times 10^{-10}$; $M=.33$; $SD=.12$; simulation $t(18)=6.06$; $p=1\times 10^{-5}$; $M=.18$; $SD=.13$; see Fig. 7f]. The occipital ITPC changes following saccades in total and near-darkness from the complementary analyses were not significantly correlated with frontal ITPC changes during saccade (-0.05 – 0 before saccade onset) before correction across participants [darkness: $r=0.25$, $p=0.31$; near-darkness: $r=0.12$, $p=0.64$], further supporting their neural origin.

Instantaneous frequency—There was a significant decrease in mean occipital theta IF in the near-darkness condition during and after saccade (Fig. 6c), most reliable at 240 ms [$t(18)=-7.53$, $p=5.74\times 10^{-7}$]. A later non-significant decrease can be observed in the simulation condition, although the two time courses did not significantly correlate [mean $r=0.124$, $t(18)=1.321$, $p=0.203$]. The total darkness condition did not follow the same pattern [correlation with near-darkness: mean $r=0.161$, $t(18)=1.521$, $p=0.146$; correlation with simulation: mean $r=0.074$, $t(18)=0.664$, $p=0.515$].

IF-power correlations—The correlation between theta power and instantaneous frequency changes was positive in all conditions. A significant difference between the three conditions was observed during a transient increase in the total darkness and near-dark during and after saccade respectively (Fig. 6d). This difference was most reliable at 170 ms [$F(2,36)=17.32$, $p=5.68\times 10^{-13}$]. The total darkness timecourses significantly correlated with the near-dark time course [mean $r=0.198$, $t(18)=5.135$, $p=10^{-4}$] and

simulation to a lesser extent [mean $r=0.129$, $t(18)=2.768$, $p=0.013$], including when regressing out frontal sensors from the conditions with real saccades [with near-darkness: mean partial $r=0.196$, $t(18)=4.916$, $p=10^{-4}$; with simulation: mean partial $r=0.125$, $t(18)=2.678$, $p=0.015$]. The correlation between the near-darkness and simulation conditions was not significant [mean $r=0.106$, $t(18)=2.035$, $p=0.057$].

Overall, mean occipital theta power and ITPC followed a similar pattern across all three conditions, with an increase in power and ITPC, followed by a small power depression. Mean occipital IF time courses did not significantly correlate between conditions. It showed a significant increase in full darkness, but not in the other two. However, the theta IF–power correlation time course was similar between total darkness and the near-darkness and simulation conditions.

Figure 6. Occipital theta band activity. Mean of measure locked to fixation onset for each condition: saccades in total darkness (blue), saccades in near-darkness (orange), visual changes simulating saccades in near-darkness (purple). Shaded areas indicate ± 1 standard error. Colored horizontal lines indicate significant departure from baseline, cluster-corrected. **(a)** Power: relative change from baseline (mean across $[-700, -500]$ ms interval prior saccade onset). **(b)** Inter-trial phase coherence: departure from theoretical baseline. **(c)** Instantaneous frequency: departure from baseline (mean across $[-700, -500]$ ms interval prior saccade onset). **(d)**

Correlation between power changes and instantaneous frequency changes. Black horizontal line indicates significant difference between conditions with F test, cluster-corrected.

Figure 7. Control analyses for potential eye-movement artifacts in the theta power and ITPC measures. Time course of frontal sensors, where the artifacts are likely to be strongest for power (a, b) and ITPC (d, e), indicating that the full-darkness condition is particularly contaminated by eye-movement artifacts. Colored horizontal lines indicate significant departure from zero for the frontal signals, cluster-corrected, and time origin is fixation onset. To address this issue, control analyses were performed on the interval 50–250 ms following fixation (c,f). Topographies for each condition show that the eye-movement artifacts were

successfully removed. Bar plots show mean occipital value of the measure for each condition (dark horizontal line), $\pm$ standard error (darker box), $\pm$ standard deviation (lighter box), and individual values (scatter plots). Asterisks indicate statistically significant departure from zero, showing that the effects are not due to eye-movement artifacts.

3.3.2. Parietal-occipital theta spatial pattern analyses

As performed above for the alpha band activity, we again looked at the similarity of parietal-occipital patterns between conditions at each time point to clarify the nature of the MEG signal in terms of likely visual/retinal or non-visual/extraretinal origins. Figure 8 summarizes the results of the time generalized correlational analyses of occipital-parietal patterns in the theta band, locked to fixation onset. Figure 9 shows time-resolved partial correlations between the near-darkness condition and each of the two other conditions, with signals locked to fixation onset. Figure 10 shows the evolution in time of the whole-scalp topographies (and Suppl. Fig. S7 shows the time course of topographies without normalizing the scales). The equivalent figures with saccade onset as time origin are not shown, as the results are largely unchanged.

Power—The time generalization uncovered that early latency post-saccadic theta power patterns in near-darkness resembled those of total darkness (Fig. 8a), with maximum t-score $t(18)=5.23$, $p=5.7\times 10^{-5}$ at time pair 140 ms (near-darkness) and 240 ms (total darkness) post-fixation onset. This was confirmed using partial correlation (Fig. 9a) with the most reliable effect at 220 ms [$t(18)=4.18$, $p=5.6\times 10^{-4}$], and the control analysis to ensure that this correlation was not driven by eye movement artifacts [correlation: $t(18)=2.90$; $p=.009$; $M=.20$; $SD=.3$; partial correlation: $t(18)=3.03$; $p=.007$; $M=.20$; $SD=.28$]. Late positive correlations between near-darkness and simulation were also observed (Fig. 8b and 9b), but did not reach significance. No significant similarity was observed between the darkness and simulation conditions.

ITPC—Significant similarity clusters were observed in the early latencies following the saccade between the total and near-darkness conditions (Fig. 8d and 9c) [peak t-value $t(18)=5.89$, $p=1.4\times 10^{-5}$ at 220 ms (near-darkness) and 240 ms (darkness) for the time generalisation analysis; $t(18)=5.48$, $p=3.3\times 10^{-5}$ at 240 ms for the partial correlation]. We also observed early similar patterns between the near-darkness

and simulation conditions (Fig. 8e and 9d) [peak $t(18)=6.01$, $p=1.1\times 10^{-5}$ at 160 ms (near-dark) and 220 ms (simulation) for the time generalisation; $t(18)=5.67$, $p=2.24\times 10^{-5}$ at 220 ms for the partial correlation]. No significant cluster was found in the comparison between total darkness and simulation (Fig. 8f). Finally, the control analysis confirmed the neural origin of these patterns in the 50–250 ms interval [near-darkness–darkness correlation: $t(18)=3.01$; $p=.0075$; $M=.13$; $SD=.19$; near-darkness–simulation correlation: $t(18)=8.18$; $p=1.8\times 10^{-7}$; $M=.19$; $SD=.10$; near-darkness–darkness partial correlation: $t(18)=2.97$; $p=.008$; $M=.12$; $SD=.18$; near-darkness–simulation partial correlation: $t(18)=7.63$; $p=4.7\times 10^{-7}$; $M=.18$; $SD=.10$], but not in the -250–50 ms interval prior saccade onset (all $p>0.05$), suggesting that pre-saccading correlations are of non-neural origin.

Instantaneous frequency—No significant correlation was found (Fig. 8g–i and 9e–f).

While average occipital time courses of theta power and ITPC showed a transient increase in all conditions, occipital-parietal patterns generated by a visual transient as in the simulation condition and by a pure eye movement as in the total darkness condition both appeared to contribute to post-saccadic patterns in saccades with visual input. Parietal-occipital power patterns in near-darkness resembled those in total darkness in earlier post-saccadic latencies (< 400 ms). ITPC patterns in near-darkness showed more simultaneous resemblance to the other two conditions, before 400 ms after the saccade.

Figure 8. Time-generalized correlational analysis on theta activity. **(a,b,c)** Power; **(d,e,f)** Inter-trial phase coherence; **(g,h,i)** Instantaneous frequency. Heat maps indicate Fisher-transformed correlation values between the conditions under consideration, as a function of time for each condition. Statistical analyses were run on the ± 200 ms strip, indicated by the two parallel oblique lines. Significant clusters are outlined. For each significant cluster, the point of maximum correlation is indicated by a red dot, and the corresponding pair of topographies shown below the heat map. Time origin corresponds to fixation onset.

Figure 9. Partial correlation analysis on theta band signal. **(a,b)** Power; **(c,d)** Inter-trial phase coherence; **(e,f)** Instantaneous frequency. The first column **(a,c,e)** shows the partial correlation between the near-darkness and the full-darkness conditions, regressing out the simulation condition. The second column **(b,d,f)** shows the partial correlation between the near-darkness and the simulation conditions, regressing out the full-darkness condition. Time origin corresponds to fixation onset. Correlation values are Fisher-transformed. Time points belonging to significant clusters are indicated by dots.

Figure 10. Topographical maps for measures in the theta band. **(a)** Power; **(b)** Inter-trial phase coherence; **(c)** Instantaneous frequency. In each panel, each row corresponds to a condition and each column a time interval, from -500 to $+700$ ms from fixation onset, by steps of 200 ms. Each map shows all combined gradiometer values, and is scaled between $\pm \text{abs}(\text{max})$.

3.3.3. Discussion on theta frequency results

In terms of theta band activity, our data yielded two main findings: (1) an increase in phase clustering and power following saccade execution in all three conditions, and (2) as for alpha, a separable contribution from both visually-driven and non-visually-driven processes in terms of power and phase clustering patterns.

While visual input generated increased phase clustering (phase reset) in the theta band, likely due to the visually-evoked signal, it appears that a theta phase reset also occurred following a saccade in the absence

of visual input. This observation is consistent with previous studies in non-human animals showing theta phase resets in temporal cortex and in occipital regions following a saccade (Bartlett et al., 2011; Ito et al., 2013; Rajkai et al., 2008). Our correlational analyses indicate that the pattern of non-visually mediated theta reset (as measured in total darkness) is distinct from the visually-driven pattern, suggesting that different (although potentially overlapping) neural assemblies are reset in both conditions. In addition, in near-darkness, both patterns were present, indicating that visual input does not override the saccade-related reset patterns.

We found evidence for an occipital theta power increase following the saccade even in the absence of visual input. This appears consistent with electrophysiological recordings in non-human primates (Barczak et al., 2019; Rajkai et al., 2008). More generally, modulations in neural responses have repeatedly been reported in total darkness in various visual areas and mammal species (Corazza and Lombroso, 1971; Nakamura and Colby, 2000; Noda et al., 1972; Sobotka and Ringo, 1997). The role of this endogenous activity may be to optimize the processing of the upcoming visual information following saccade offset, or, as it has been recently proposed, to shorten the duration of saccadic suppression (Idrees et al., 2020). Stronger response, in terms of theta power increase and both theta and alpha phase locking for saccades with visual input, compared to simulated saccades, may thus be related to such an enhancement of the visual response. There is indeed evidence for a stronger and faster neural response to visual input following a saccade, as observed in various parts of the visual pathway by intracortical recordings in the monkey and fMRI in humans (Ibbotson and Krekelberg, 2011). However, the difference we observed between our two conditions could also be due to the fact that the screen could not cover the whole visual field, so that the visual differences generated by a real saccade were larger than for the simulated condition.

4. GENERAL DISCUSSION AND CONCLUSION

In this study, we provided an extensive characterization of theta and alpha band signals around the time of horizontal volitional saccades, in the absence of any other task. By including trials with saccades in total darkness and also trials with no saccade but a visual transient, focusing on the correlations

(similarities) between the different conditions, we found that a portion of the changes in these frequency bands under near-darkness condition were likely driven by the new visual input, while others appeared to be linked to saccade execution.

It is to be noted that we found strong similarities in neural activity between conditions despite them being notably different in several respects. In particular, saccades in total darkness were significantly larger than those in near darkness, and simulated saccades were shorter than in the other two conditions. These differences may have prevented us to detect more subtle similarities, but also an indication that the similarity of patterns that we found are very robust effects since they remained in spite of these differences.

One cause of concern is that signals in the total and near-darkness conditions might be contaminated by eye movement artifacts. We applied several methods to minimise potential confounds due to the eye movements. First, only parietal and occipital sensors were used for our analyses. These sensors are relatively distant from the eyes and the periocular muscles, therefore the signal coming from these sources will be weaker than for more anterior sensors. In addition, we only included gradiometers for our analyses. Gradiometers, unlike magnetometers, cancel out more distant sources from the sensors by design. Secondly, in our occipital analyses, we checked whether the time courses in occipital sensors correlated significantly with frontal sensor signals, which contained strong eye movement artifacts. Importantly, we ran complementary analyses with separate frequency decompositions that excluded time points during which the eye movement occurred. Indeed, the time resolved analyses are subject to temporal smearing by the filter, therefore perisaccadic signals may have been contaminated by artefactual events occurring during the saccade. Using these methods, we found in particular that presaccadic effects observed in the time-resolved analyses were likely caused by temporal smearing artifacts.

Despite all these precautions, there is still the possibility that some of the reported effects are due to eye movement-related artefacts. For instance, our design could not account for potential systematic head movements accompanying the saccades. These may have introduced head motion signals, in particular in the total darkness condition whose saccade amplitudes were larger.

Despite these limitations, our observations generally confirm and extend previous findings with non-human primates in visual processing areas (Barczak et al., 2019; Bartlett et al., 2011; Ito et al., 2013; Rajkai et al., 2008) and the hippocampus (Doucet et al., 2020; Hoffman et al., 2013; Jutras et al., 2013; Ringo et al., 1994), and are largely consistent with previous reports on a variety of motor tasks such as whisking or reaching, that demonstrate an active alignment of sensory and motor processing (Schroeder et al., 2010). However, the specific functions of patterns observed are unclear, in particular regarding the non-visually mediated ones. In addition to the frequency-specific discussion sections above, we provide below some additional suggestions for potential interpretations that could guide future research.

Endogenous alpha IF changes have been linked to visual task demands (Sharp, 2019; Wutz et al., 2018), with an increase in frequency corresponding to a demand in segregating visual information in time (versus integrating). We can therefore speculate that following a saccade, the non-visually mediated increase in alpha IF may reflect an increase in the temporal resolution of the visual system, facilitating the detection of visual changes in order to accelerate the processing of the incoming visual information. This effect would be masked for saccades in more natural condition by the strong alpha band power suppression driven by the new visual input.

A noteworthy finding is that alpha power changes following saccades with visual input contained patterns elicited by both visually and non-visually mediated processes. It is possible that endogenously driven alpha power changes are linked with saccadic remapping. Neural responses in monkey V4 suggest that alpha phase coherence following a saccade may mediate saccadic remapping (Neupane et al., 2017). As increased coherence between nearby neural ensembles translates, at the MEG sensor level, into increased power, we can speculate that the nonvisually-mediated alpha power changes observed correspond to processes supporting saccade-related changes in neural processing such as saccadic remapping.

As discussed above, visually and non-visually mediated increases in theta power, paired with phase alignment may reflect visual enhancement following the saccade, possibly to shorten saccadic suppression. The observation that theta phase aligns across trials in all three conditions can be linked to recent work uncovering perceptual fluctuations in the lower frequency bands (including theta). These perceptual fluctuations can time-locked to events that are (i) purely visual such as a flashes or visual

entrainment (Drewes et al., 2015; Ronconi and Melcher, 2017); (ii) both visual and endogenous such as saccades with visual input (Benedetto and Morrone, 2017; Hogendoorn, 2016); (iii) purely non-visual such as a motor action (e.g., Tomassini et al., 2015). This may be indicative of mechanisms tuned to facilitate and optimize the processing of incoming visual information by endogenously aligning the phase of the background activity to the phase of the visually elicited activity, effectively aligning the motor and sensory systems for active sampling (Schroeder et al., 2010).

The present study aimed at better understanding saccadic-related alpha and theta band activity in humans, using MEG. We were in particular interested in understanding to what extent the activity measured around saccades in relatively normal viewing conditions, which likely contains both visually and non-visually mediated processes, resembled purely visually mediated (visual changes simulating visual input during a saccade) and purely non-visually mediated (saccades performed in total darkness) activity. In addition to providing an extensive characterisation of alpha and theta band signals in the three conditions, we found that portions of the patterns could be attributed to visually-mediated processes, and others to non-visually-mediated processes. In addition, our study provides an indication of their temporal unfolding. While the exact functional significance of the patterns observed is still unclear, they likely reflect aspects of the necessary alignment of the motor and sensory systems for effective active sampling.

References

- Barczak, A., Haegens, S., Ross, D.A., McGinnis, T., Lakatos, P., Schroeder, C.E., 2019. Dynamic Modulation of Cortical Excitability during Visual Active Sensing. *Cell Reports* 27, 3447-3459.e3. <https://doi.org/10.1016/j.celrep.2019.05.072>
- Bartlett, A.M., Ovaysikia, S., Logothetis, N.K., Hoffman, K.L., 2011. Saccades during Object Viewing Modulate Oscillatory Phase in the Superior Temporal Sulcus. *Journal of Neuroscience* 31, 18423–18432. <https://doi.org/10.1523/JNEUROSCI.4102-11.2011>
- Baumann, M.P., Idrees, S., Münch, T.A., Hafed, Z.M., 2021. Dependence of perceptual saccadic suppression on peri-saccadic image flow properties and luminance contrast polarity. *Journal of Vision* 21, 15. <https://doi.org/10.1167/jov.21.5.15>
- Benedetto, A., Morrone, M.C., 2017. Saccadic Suppression Is Embedded Within Extended Oscillatory Modulation of Sensitivity. *Journal of Neuroscience* 37, 3661–3670. <https://doi.org/10.1523/JNEUROSCI.2390-16.2016>
- Brainard, D.H., 1997. The Psychophysics Toolbox. *Spat Vis* 10, 433–436.
- Bruns, A., 2004. Fourier-, Hilbert- and wavelet-based signal analysis: are they really different approaches? *Journal of Neuroscience Methods* 137, 321–332. <https://doi.org/10.1016/j.jneumeth.2004.03.002>
- Carl, C., Açık, A., König, P., Engel, A.K., Hipp, J.F., 2012. The saccadic spike artifact in MEG. *NeuroImage* 59, 1657–1667. <https://doi.org/10.1016/j.neuroimage.2011.09.020>
- Chen, C.-Y., Hafed, Z.M., 2017. A neural locus for spatial-frequency specific saccadic suppression in visual-motor neurons of the primate superior colliculus. *Journal of Neurophysiology* 117, 1657–1673. <https://doi.org/10.1152/jn.00911.2016>
- Chen, J., Valsecchi, M., Gegenfurtner, K.R., 2019. Saccadic suppression measured by steady-state visual evoked potentials. *Journal of Neurophysiology* 122, 251–258. <https://doi.org/10.1152/jn.00712.2018>
- Cohen, M.X., 2014a. Fluctuations in Oscillation Frequency Control Spike Timing and Coordinate Neural Networks. *Journal of Neuroscience* 34, 8988–8998. <https://doi.org/10.1523/JNEUROSCI.0261-14.2014>

1081 Cohen, M.X., 2014b. Analyzing neural time series data: theory and practice, Issues in clinical and
1082 cognitive neuropsychology. The MIT Press, Cambridge, Massachusetts.

1083 Colby, C.L., Duhamel, J.-R., Goldberg, M.E., 1993. The analysis of visual space by the lateral
1084 intraparietal area of the monkey: the role of extraretinal signals, in: Hicks, T.P.,
1085 Molotchnikoff, S., Ono, T. (Eds.), Progress in Brain Research. Elsevier, pp. 307–316.
1086 [https://doi.org/10.1016/S0079-6123\(08\)60378-7](https://doi.org/10.1016/S0079-6123(08)60378-7)

1087 Corazza, R., Lombroso, A.T., 1971. The neuronal dark discharge during eye movements in awake
1088 “encéphale isolé” cats. Brain Research 15.

1089 Deneux, T., Masquelier, T., Bermudez, M.A., Masson, G.S., Deco, G., Vanzetta, I., 2017. Visual
1090 stimulation quenches global alpha range activity in awake primate V4: a case study.
1091 Neurophotonics 4, 031222. <https://doi.org/10.1117/1.NPh.4.3.031222>

1092 Deubel, H., Schneider, W.X., 1996. Saccade target selection and object recognition: Evidence for a
1093 common attentional mechanism. Vision Research 36, 1827–1837.
1094 [https://doi.org/10.1016/0042-6989\(95\)00294-4](https://doi.org/10.1016/0042-6989(95)00294-4)

1095 Doucet, G., Gulli, R.A., Corrigan, B.W., Duong, L.R., Martinez-Trujillo, J.C., 2020. Modulation of
1096 local field potentials and neuronal activity in primate hippocampus during saccades.
1097 Hippocampus 30, 192–209. <https://doi.org/10.1002/hipo.23140>

1098 Drewes, J., VanRullen, R., 2011. This Is the Rhythm of Your Eyes: The Phase of Ongoing
1099 Electroencephalogram Oscillations Modulates Saccadic Reaction Time. Journal of
1100 Neuroscience 31, 4698–4708. <https://doi.org/10.1523/JNEUROSCI.4795-10.2011>

1101 Drewes, J., Zhu, W., Wutz, A., Melcher, D., 2015. Dense sampling reveals behavioral oscillations in
1102 rapid visual categorization. Sci Rep 5, 16290. <https://doi.org/10.1038/srep16290>

1103 Duffy, F.H., Burchfiel, J.L., 1975. Eye movement-related inhibition of primate visual neurons. Brain
1104 Research 89, 121–132. [https://doi.org/10.1016/0006-8993\(75\)90139-0](https://doi.org/10.1016/0006-8993(75)90139-0)

1105 Duhamel, Colby, C., Goldberg, M., 1992. The updating of the representation of visual space in parietal
1106 cortex by intended eye movements. Science 255, 90–92.
1107 <https://doi.org/10.1126/science.1553535>

1108 Gawne, T.J., Killen, J.F., Tracy, J.M., Lahti, A.C., 2017. The effect of saccadic eye movements on the
1109 sensor-level magnetoencephalogram. Clinical Neurophysiology 128, 397–407.
1110 <https://doi.org/10.1016/j.clinph.2016.12.013>

1111 Hoffman, J.E., Subramaniam, B., 1995. The role of visual attention in saccadic eye movements.
 1112 Perception & Psychophysics 57, 787–795. <https://doi.org/10.3758/BF03206794>
 1113 Hoffman, K.L., Dragan, M.C., Leonard, T.K., Micheli, C., Montefusco-Siegmund, R., Valiante, T.A.,
 1114 2013. Saccades during visual exploration align hippocampal 3–8 Hz rhythms in human and
 1115 non-human primates. Frontiers in Systems Neuroscience 7.
 1116 <https://doi.org/10.3389/fnsys.2013.00043>
 1117 Hogendoorn, H., 2016. Voluntary Saccadic Eye Movements Ride the Attentional Rhythm. Journal of
 1118 Cognitive Neuroscience 28, 1625–1635. https://doi.org/10.1162/jocn_a_00986
 1119 Huber-Huber, C., Buonocore, A., Melcher, D., 2021. The extrafoveal preview paradigm as a measure
 1120 of predictive, active sampling in visual perception. Journal of Vision 21, 12.
 1121 <https://doi.org/10.1167/jov.21.7.12>
 1122 Ibbotson, M., Krekelberg, B., 2011. Visual perception and saccadic eye movements. Current Opinion
 1123 in Neurobiology 21, 553–558. <https://doi.org/10.1016/j.conb.2011.05.012>
 1124 Idrees, S., Baumann, M.P., Franke, F., Münch, T.A., Hafed, Z.M., 2020. Perceptual saccadic
 1125 suppression starts in the retina. Nature Communications 11. [https://doi.org/10.1038/s41467-](https://doi.org/10.1038/s41467-020-15890-w)
 1126 [020-15890-w](https://doi.org/10.1038/s41467-020-15890-w)
 1127 Ito, J., Maldonado, P., Grün, S., 2013. Cross-frequency interaction of the eye-movement related LFP
 1128 signals in V1 of freely viewing monkeys. Frontiers in Systems Neuroscience 7.
 1129 <https://doi.org/10.3389/fnsys.2013.00001>
 1130 Ito, J., Maldonado, P., Singer, W., Grün, S., 2011. Saccade-Related Modulations of Neuronal
 1131 Excitability Support Synchrony of Visually Elicited Spikes. Cerebral Cortex 21, 2482–2497.
 1132 <https://doi.org/10.1093/cercor/bhr020>
 1133 Jensen, O., Bonnefond, M., VanRullen, R., 2012. An oscillatory mechanism for prioritizing salient
 1134 unattended stimuli. Trends in Cognitive Sciences 16, 200–206.
 1135 <https://doi.org/10.1016/j.tics.2012.03.002>
 1136 Jia, Y., Tyler, C.W., 2019. Measurement of saccadic eye movements by electrooculography for
 1137 simultaneous EEG recording. Behavior Research Methods 51, 2139–2151.
 1138 <https://doi.org/10.3758/s13428-019-01280-8>

1139 Jutras, M.J., Fries, P., Buffalo, E.A., 2013. Oscillatory activity in the monkey hippocampus during
1140 visual exploration and memory formation. *Proceedings of the National Academy of Sciences*
1141 110, 13144–13149. <https://doi.org/10.1073/pnas.1302351110>

1142 Kagan, I., Gur, M., Snodderly, D.M., 2008. Saccades and drifts differentially modulate neuronal
1143 activity in V1: Effects of retinal image motion, position, and extraretinal influences. *Journal of*
1144 *Vision* 8, 19–19. <https://doi.org/10.1167/8.14.19>

1145 Keren, A.S., Yuval-Greenberg, S., Deouell, L.Y., 2010. Saccadic spike potentials in gamma-band
1146 EEG: Characterization, detection and suppression. *NeuroImage* 49, 2248–2263.
1147 <https://doi.org/10.1016/j.neuroimage.2009.10.057>

1148 Kleiner, M., Brainard, D.H., Pelli, D., 2007. What’s new in Psychtoolbox-3? Presented at the 30th
1149 European Conference on Visual Perception, Arezzo, Italy.

1150 Klier, E.M., Angelaki, D.E., 2008. Spatial updating and the maintenance of visual constancy.
1151 *Neuroscience* 156, 801–818. <https://doi.org/10.1016/j.neuroscience.2008.07.079>

1152 Klimesch, W., 2012. Alpha-band oscillations, attention, and controlled access to stored information.
1153 *Trends in Cognitive Sciences* 16, 606–617. <https://doi.org/10.1016/j.tics.2012.10.007>

1154 Kowler, E., Anderson, E., Doshier, B., Blaser, E., 1995. The role of attention in the programming of
1155 saccades. *Vision Research* 35, 1897–1916. [https://doi.org/10.1016/0042-6989\(94\)00279-U](https://doi.org/10.1016/0042-6989(94)00279-U)

1156 Kristofferson, A.B., 1967. Successiveness Discrimination as a Two-State, Quantal Process. *Science*
1157 158, 1337–1339. <https://doi.org/10.1126/science.158.3806.1337>

1158 Latour, P.L., 1962. Visual threshold during eye movements. *Vision Research* 2, 261–262.
1159 [https://doi.org/10.1016/0042-6989\(62\)90031-7](https://doi.org/10.1016/0042-6989(62)90031-7)

1160 Leszczynski, M., Schroeder, C.E., 2019. The Role of Neuronal Oscillations in Visual Active Sensing.
1161 *Frontiers in Integrative Neuroscience* 13. <https://doi.org/10.3389/fnint.2019.00032>

1162 MacEvoy, S.P., Hanks, T.D., Paradiso, M.A., 2008. Macaque V1 Activity During Natural Vision:
1163 Effects of Natural Scenes and Saccades. *Journal of Neurophysiology* 99, 460–472.
1164 <https://doi.org/10.1152/jn.00612.2007>

1165 Maris, E., Oostenveld, R., 2007. Nonparametric statistical testing of EEG- and MEG-data. *Journal of*
1166 *Neuroscience Methods* 164, 177–190. <https://doi.org/10.1016/j.jneumeth.2007.03.024>

1167 Melcher, D., Colby, C.L., 2008. Trans-saccadic perception. *Trends in Cognitive Sciences* 12, 466–473.
1168 <https://doi.org/10.1016/j.tics.2008.09.003>

1169 Merriam, E.P., Genovese, C.R., Colby, C.L., 2007. Remapping in Human Visual Cortex. *Journal of*
1170 *Neurophysiology* 97, 1738–1755. <https://doi.org/10.1152/jn.00189.2006>

1171 Nakamura, K., Colby, C.L., 2002. Updating of the visual representation in monkey striate and
1172 extrastriate cortex during saccades. *Proceedings of the National Academy of Sciences* 99,
1173 4026–4031. <https://doi.org/10.1073/pnas.052379899>

1174 Nakamura, K., Colby, C.L., 2000. Visual, Saccade-Related, and Cognitive Activation of Single
1175 Neurons in Monkey Extrastriate Area V3A. *Journal of Neurophysiology* 84, 677–692.
1176 <https://doi.org/10.1152/jn.2000.84.2.677>

1177 Neupane, S., Guitton, D., Pack, C.C., 2017. Coherent alpha oscillations link current and future
1178 receptive fields during saccades. *Proceedings of the National Academy of Sciences* 114,
1179 E5979–E5985. <https://doi.org/10.1073/pnas.1701672114>

1180 Nobre, A.C., Gitelman, D.R., Dias, E.C., Mesulam, M.M., 2000. Covert Visual Spatial Orienting and
1181 Saccades: Overlapping Neural Systems. *NeuroImage* 11, 210–216.
1182 <https://doi.org/10.1006/nimg.2000.0539>

1183 Noda, H., Freeman, R.B., Creutzfeldt, O.D., 1972. Neuronal Correlates of Eye Movements in the
1184 Visual Cortex of the Cat. *Science* 175, 661–664. <https://doi.org/10.1126/science.175.4022.661>

1185 Nogawa, T., Katayama, K., Tabata, Y., Ohshio, T., Kawahara, T., 1976. Changes in amplitude of the
1186 EEG induced by a photic stimulus. *Electroencephalography and Clinical Neurophysiology* 40,
1187 78–88. [https://doi.org/10.1016/0013-4694\(76\)90181-4](https://doi.org/10.1016/0013-4694(76)90181-4)

1188 Nyström, M., Holmqvist, K., 2010. An adaptive algorithm for fixation, saccade, and glissade detection
1189 in eyetracking data. *Behavior Research Methods* 42, 188–204.
1190 <https://doi.org/10.3758/BRM.42.1.188>

1191 Oostenveld, R., Fries, P., Maris, E., Schoffelen, J.-M., 2011. FieldTrip: Open Source Software for
1192 Advanced Analysis of MEG, EEG, and Invasive Electrophysiological Data. *Computational*
1193 *Intelligence and Neuroscience* 2011, 1–9. <https://doi.org/10.1155/2011/156869>

1194 Oosterhof, N.N., Connolly, A.C., Haxby, J.V., 2016. CoSMoMVPA: Multi-Modal Multivariate Pattern
1195 Analysis of Neuroimaging Data in Matlab/GNU Octave. *Frontiers in Neuroinformatics* 10.
1196 <https://doi.org/10.3389/fninf.2016.00027>

1197 Parks, N.A., Corballis, P.M., 2010. Human transsaccadic visual processing: Presaccadic remapping and
1198 postsaccadic updating. *Neuropsychologia* 48, 3451–3458.
1199 <https://doi.org/10.1016/j.neuropsychologia.2010.07.028>

1200 Parks, N.A., Corballis, P.M., 2008. Electrophysiological correlates of presaccadic remapping in
1201 humans. *Psychophysiology* 45, 776–783. <https://doi.org/10.1111/j.1469-8986.2008.00669.x>

1202 Pfurtscheller, G., Neuper, C., Mohl, W., 1994. Event-related desynchronization (ERD) during visual
1203 processing. *International Journal of Psychophysiology* 16, 147–153.
1204 [https://doi.org/10.1016/0167-8760\(89\)90041-X](https://doi.org/10.1016/0167-8760(89)90041-X)

1205 Rajkai, C., Lakatos, P., Chen, C.-M., Pincze, Z., Karmos, G., Schroeder, C.E., 2008. Transient Cortical
1206 Excitation at the Onset of Visual Fixation. *Cerebral Cortex* 18, 200–209.
1207 <https://doi.org/10.1093/cercor/bhm046>

1208 Reppas, J.B., Usrey, W.M., Reid, R.C., 2002. Saccadic Eye Movements Modulate Visual Responses in
1209 the Lateral Geniculate Nucleus. *Neuron* 35, 961–974. [https://doi.org/10.1016/S0896-](https://doi.org/10.1016/S0896-6273(02)00823-1)
1210 [6273\(02\)00823-1](https://doi.org/10.1016/S0896-6273(02)00823-1)

1211 Ringo, J.L., Sobotka, S., Diltz, M.D., Bunce, C.M., 1994. Eye movements modulate activity in
1212 hippocampal, parahippocampal, and inferotemporal neurons. *Journal of Neurophysiology* 71,
1213 1285–1288. <https://doi.org/10.1152/jn.1994.71.3.1285>

1214 Ronconi, L., Melcher, D., 2017. Alpha oscillation phase determines the timing of perception: evidence
1215 from sensory entrainment. *Journal of Vision* 17, 726. <https://doi.org/10.1167/17.10.726>

1216 Samaha, J., Postle, B.R., 2015. The Speed of Alpha-Band Oscillations Predicts the Temporal
1217 Resolution of Visual Perception. *Current Biology* 25, 2985–2990.
1218 <https://doi.org/10.1016/j.cub.2015.10.007>

1219 Schroeder, C.E., Wilson, D.A., Radman, T., Scharfman, H., Lakatos, P., 2010. Dynamics of Active
1220 Sensing and perceptual selection. *Current Opinion in Neurobiology* 20, 172–176.
1221 <https://doi.org/10.1016/j.conb.2010.02.010>

1222 Sharp, P., 2019. Selective attention modulates temporal processing (Doctoral Thesis). University of
1223 Trento, Rovereto, Italy.

1224 Sobotka, S., Ringo, J.L., 1997. Saccadic eye movements, even in darkness, generate event-related
1225 potentials recorded in medial septum and medial temporal cortex. *Brain Research* 756, 168–
1226 173. [https://doi.org/10.1016/S0006-8993\(97\)00145-5](https://doi.org/10.1016/S0006-8993(97)00145-5)

1227 Staudigl, T., Hartl, E., Noachtar, S., Doeller, C.F., Jensen, O., 2017. Saccades are phase-locked to
 1228 alpha oscillations in the occipital and medial temporal lobe during successful memory
 1229 encoding. *PLOS Biology* 15, e2003404. <https://doi.org/10.1371/journal.pbio.2003404>
 1230 Taulu, S., Hari, R., 2009. Removal of magnetoencephalographic artifacts with temporal signal-space
 1231 separation: Demonstration with single-trial auditory-evoked responses. *Human Brain Mapping*
 1232 30, 1524–1534. <https://doi.org/10.1002/hbm.20627>
 1233 Tomassini, A., Spinelli, D., Jacono, M., Sandini, G., Morrone, M.C., 2015. Rhythmic Oscillations of
 1234 Visual Contrast Sensitivity Synchronized with Action. *Journal of Neuroscience* 35, 7019–
 1235 7029. <https://doi.org/10.1523/JNEUROSCI.4568-14.2015>
 1236 Umeno, M.M., Goldberg, M.E., 1997. Spatial Processing in the Monkey Frontal Eye Field. I.
 1237 Predictive Visual Responses. *Journal of Neurophysiology* 78, 1373–1383.
 1238 <https://doi.org/10.1152/jn.1997.78.3.1373>
 1239 VanRullen, R., 2016. Perceptual Cycles. *Trends in Cognitive Sciences* 20, 723–735.
 1240 <https://doi.org/10.1016/j.tics.2016.07.006>
 1241 Veniero, D., Gross, J., Morand, S., Duecker, F., Sack, A.T., Thut, G., 2021. Top-down control of visual
 1242 cortex by the frontal eye fields through oscillatory realignment. *Nat Commun* 12, 1757.
 1243 <https://doi.org/10.1038/s41467-021-21979-7>
 1244 Volkman, F.C., Schick, A.M.L., Riggs, L.A., 1968. Time Course of Visual Inhibition during
 1245 Voluntary Saccades. *Journal of the Optical Society of America* 58, 562–569.
 1246 Wutz, A., Melcher, D., Samaha, J., 2018. Frequency modulation of neural oscillations according to
 1247 visual task demands. *Proceedings of the National Academy of Sciences* 115, 1346–1351.
 1248 <https://doi.org/10.1073/pnas.1713318115>
 1249 Zimmermann, E., 2020. Saccade suppression depends on context. *eLife* 9, e49700.
 1250 <https://doi.org/10.7554/eLife.49700>
 1251