Visual sensitivity and bias oscillate phase-locked to saccadic eye movements

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Oscillations in perceptual performance have been observed before and after a voluntary action, like hand, finger, and eye movements. In particular, discrimination accuracy of suprathreshold contrast stimuli oscillates in the delta range (2–3 Hz) phase-locked to saccadic eye movements. Importantly, saccadic suppression is embedded in phase with these long-lasting perceptual oscillations. It is debated whether these rhythmic modulations affect only appearance of high-contrast stimuli or whether absolute detection threshold is also modulated rhythmically. Here we measured location discrimination of a brief Gabor patch presented randomly between 1 s before and after a voluntary saccade and demonstrated that absolute contrast thresholds oscillated at a similar frequency to suprathreshold contrast discrimination. Importantly, saccadic suppression is also embedded in phase with absolute threshold oscillations. Interestingly, response bias was also found to oscillate at the same frequency in both tasks. However, the frequency was in the alpha range for bias, while it was in the delta range for sensitivity. These results demonstrate the presence of perisaccadic delta oscillations in visual sensitivity phase-locked to saccadic onset, and independent from response bias alpha oscillations. Overall, the present findings reinforce the suggestion of a leading role of oscillations in the temporal binding between eye-movement and visual processing timing.

Introduction

Neural oscillations are ubiquitous in the brain and have been proposed to be causally linked to perception (Busch, Dubois, & VanRullen, 2009; de Lange, Rahnev, Donner, & Lau, 2013; Dugué, Marque, & VanRullen, 2011; Hanslmayr, Volberg, Wimber, Dalal, & Greenlee, 2013; Linkenkaer-Hansen, Nikulin, Palva, Ilmoniemi, & Palva, 2004; Romei, Gross, & Thut, 2012; VanRullen, 2016; VanRullen & Koch, 2003). The phase of these ongoing brain oscillations can be reset by salient attentional cues or sensory events (Fiebelkorn et al., 2011; Fiebelkorn, Saalmann, & Kastner, 2013; Ho, Leung, Burr, Alais, & Morrone, 2017; Huang, Chen, & Luo, 2015; Landau & Fries, 2012; Romei et al., 2012; Song, Meng, Chen, Zhou, & Luo, 2014), showing that perception is consistently modulated in a rhythmical fashion (VanRullen, 2016).

A growing body of scientific literature shows that perceptual rhythmic oscillations are also synchronized with voluntary actions, and this synchronization can modulate several visual functions including visual contrast discrimination of salient stimuli (Benedetto & Morrone, 2017; Benedetto, Morrone, & Tomassini, 2019; Benedetto, Spinelli, & Morrone, 2016; Tomassini, Spinelli, Jacono, Sandini, & Morrone, 2015), visual attention (Hogendoorn, 2016), feature binding (Nakayama & Motoyoshi, 2019), and temporal integration\segregation (Wutz, Muschter, van Koningsbruggen, Weisz, & Melcher, 2016). Consistent with the hypothesis of a strong link between sensori-motor integration and neural oscillations, it has been demonstrated that the phase of neural oscillations can predict reaction-time to perceptual events (Drewes & VanRullen, 2011; Lansing, 1957; Surwillo, 1961), and that a transient visual response can reset the phase of low-frequency tremor oscillations in peripheral muscles (Wood, Gu, Corneil, Gribble, & Goodale, 2015). This link between motor and visual rhythmic activity has been reinforced by Tomassini, Ambrogioni, Medendorp, and Maris (2017) who demonstrated that EEG theta-band oscillatory activity, measured seconds before the action onset, predicts visual performance in an

orientation discrimination task. Despite all this evidence connecting the intrinsic oscillatory nature of perception with action, there is no clear consensus about the basic mechanisms and functions of rhythmic modulation in early sensory process (Engel, Fries, & Singer, 2001; Fries, 2005; Klimesch, Sauseng, & Hanslmayr, 2007).

In our previous study (Benedetto & Morrone, 2017), we showed that suprathreshold contrast discrimination accuracy oscillated at delta frequencies (about 2–3 Hz), and this oscillation was synchronized with the execution of voluntary saccadic eye movements. Interestingly, the perceptual modulation emerged about one second before the saccade and continued for one second afterwards, similar to the perceptual oscillations measured before, during, and after arm movements (Benedetto, Burr, & Morrone, 2018; Benedetto et al., 2016; Tomassini et al., 2017; Tomassini et al., 2015). *Saccadic suppression*, the sharp decrease in sensitivity at saccadic onset that always accompanies saccades, was embedded in phase with the oscillation. Given that saccadic suppression takes place early in primary visual cortex, it suggests that perisaccadic delta oscillations might reflect the modulation of primary visual cortex. However, the general hypothesis that rhythmic fluctuations in perceptual accuracy emerge mainly from attentional or high-level mechanisms (Hogendoorn, 2016; Landau & Fries, 2012; VanRullen, 2016) cannot be dismissed.

The perceptual tasks adopted so far to investigate perisaccadic behavioral oscillations potentially mixed the effects of attention/decision with purely sensorial effects (Benedetto & Morrone, 2017; Hogendoorn, 2016; Wutz et al., 2016), since they all presented suprathreshold stimuli that are known to be strongly modulated by attention. Contrast increment thresholds and absolute contrast thresholds are limited by different mechanisms at different levels of visual processing, and the data are subject to different sources of external and internal noise (Dosher & Lu, 2000a, 2000b). Absolute contrast thresholds are known to be only slightly affected by attention (Dosher & Lu, 2000a, 2000b; Lee, Itti, Koch, & Braun, 1999; Morrone, Denti, & Spinelli, 2002), while the attention effect is strong at medium and high contrasts for contrast increment thresholds. To evaluate how attention affects the rhythmic modulation of vision, we measured the temporal dynamics of contrast increment thresholds (experiment 1) and absolute contrast thresholds (experiment 2). If sensitivity oscillations are driven by attentional or decisional processes, we might expect no fluctuations in absolute thresholds (experiment 2).

In addition to oscillations of visual sensitivity, it has been recently shown that visual response bias, or criterion, oscillates (Ho et al., 2017; Zhang, Morrone, & Alais, 2019) in agreement with a well-established result that spontaneous alpha oscillations modulate attention and predict decision bias (Benwell, Keitel, Harvey, Gross, & Thut, 2017; Busch et al., 2009; Haegens et al., 2014; Iemi, Chaumon, Crouzet, & Busch, 2017; Limbach & Corballis, 2016; Samaha, Iemi, & Postle, 2017; Sherman, Kanai, Seth, & VanRullen, 2016). Sensitivity and bias (or criterion) are two independent measures of perceptual performance: Sensitivity measures the ability of the subject to discriminate a stimulus; response bias is the tendency to favor one response amongst others (MacMillan & Creelman, 2005). Whereas both criterion and sensitivity are modulated by attention and context (Bashinski & Bacharach, 1980; Müller & Findlay, 1987; Wyart, Nobre, & Summerfield, 2012), their modulation can be uncoupled, suggesting that their underling neural mechanisms are different (Luo & Maunsell, 2015). Interestingly, both for auditory tone (Ho et al., 2017) and visual orientation (Zhang et al., 2019) discriminations, the frequency of the criterion oscillations is higher than that of sensitivity, falling within the alpha band. These results suggest the presence of independent oscillations modulating bias and sensitivity. In line with this finding, the point of subjective simultaneity (equivalent to bias) in audio-visual temporal order judgment is reported to fluctuate around the alpha range (Benedetto et al., 2018). To further investigate the relationship between oscillations in sensitivity and criterion, we extended our analysis to the perisaccadic fast dynamic of response bias for both tasks.

Methods

Participants

Thirteen volunteers (four women and nine men; mean age: 28 ± 4 years, including author AB) participated in the experiments, eight in experiment 1, and five in the experiment 2 (with four subjects performing both experiments). All had normal or corrected-to-normal vision. All participants provided informed consent. The experimental protocols were approved by the regional ethics committee (*Comitato Etico Pediatrico Regionale—Azienda Ospedaliero-Universitaria Meyer—Firenze*) and in adherence to the declaration of Helsinki.

Apparatus

The experiments were performed in a quiet, dark room. Subjects sat in front of a monitor (40 × 30 cm) at a distance of 57 cm, with their head stabilized by a chin rest. Stimuli were generated using the ViSaGe (Cam-
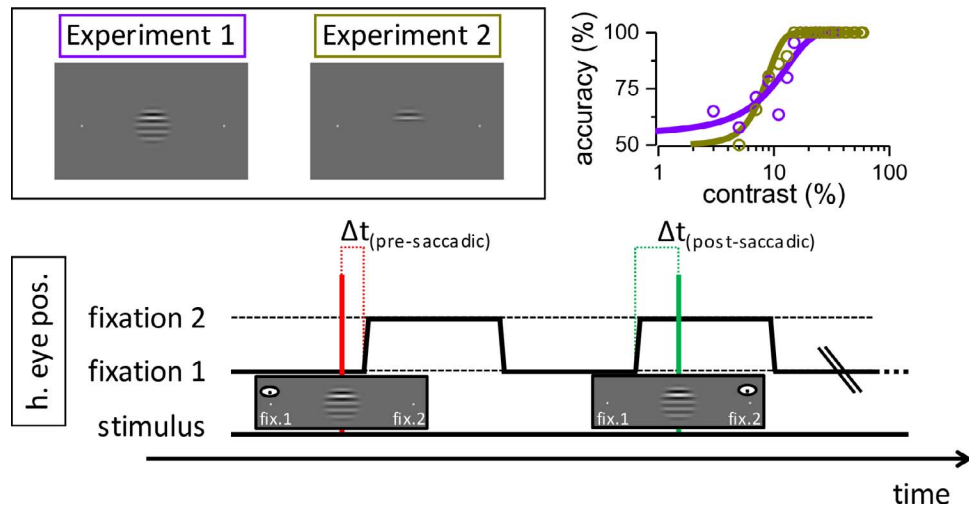
Figure 1. Experimental procedure. Participants performed, at their own pace, saccades to stationary saccadic targets (fixation 1 and fixation 2). At random times from the saccadic onset (Δt), a brief stimulus was presented, and participants reported its location. The stimulus (shown in the upper box) was a Gabor with a contrast increment presented at threshold over a pedestal (experiment 1, increment threshold) or over a gray background (experiment 2, absolute threshold). Data from a representative subject (that performed both experiments) show that experiment 1 (purple line) produces a shallower psychometric curve with respect to experiment 2 (yellow line).

bridge Research System) in MATLAB (MATLAB r2010a; MathWorks, Natick, MA) and presented on a CRT monitor (Barco Calibrator) with a resolution of 800 × 600 pixels and a refresh rate of 100 Hz. The two-dimensional position of the left eye was monitored at 1 kHz using an EyeLink 1000 system (SR Research) with an infrared camera mounted below the screen. Horizontal eye position recordings were linearized by means of a calibration performed at the beginning of each session.

Stimuli and procedure

The experimental procedure is shown in Figure 1. Two red square saccadic targets (0.25°), vertically aligned and horizontally separated by 20°, appeared at the beginning of the session and persisted until the end of the session. In experiment 1, the stimulus was a horizontal sinusoidal grating (1 cycle/°, pedestal contrast 10%) presented for 10 ms (1 monitor frame) in a 5° circular window with Gaussian smoothed edge at the center of the screen at 10° distance from both fixation points. The contrast was incremented in a Gaussian window in the upper or lower half of the circular stimulus. The luminance $l(x, y)$ was given by

$$l(x, y) = \sin(x\omega + \varphi)$$

$$\left(K + \Delta K \, e^{-\left[\left(\frac{x}{\sigma_x} \right)^2 + \left(\frac{y \pm \mu_y}{\sigma_y} \right)^2 \right]} \right) G(x, y) \quad (1)$$

where x and y and are the spatial coordinates; K is the pedestal contrast (10%), and ΔK is the contrast increment; $\sigma_x = 1.5°$ and $\sigma_y = 0.75°$ are the space constants and $\mu_y = 1.25°$ is the spatial vertical offset; $\omega = 1$ c/° is the spatial frequency, φ the random phase, and the function $G(x, y)$ is a circular step function of diameter 5° convolved with a Gaussian function of constant equal to 0.5° to smooth the stimulus-background edges. For experiment 2, the stimulus was identical with the exception that the pedestal contrast (K) was set to 0%. At the high spatial frequencies tested in our paradigm (i.e., 1 cycle/°), saccadic suppression is small (Burr, Morrone, & Ross, 1994), and for all participants the 10% contrast pedestal stimulus was always over threshold (for experiment 1). In the rare occasion in which subjects did not report seeing the pedestal, the trial was discarded. Given the high temporal uncertainty in experiment 2, a brief sound was generated in synchrony with the visual presentation (only for experiment 2).

Individual thresholds for contrast were obtained during a training session, with a QUEST procedure (see Figure 1 for a representative subject). The contrast increment value that elicited about 75% correct responses was selected and kept constant within each block. In order to balance perceptual learning improvement, the contrast increment was adjusted slightly from block to block to maintain 75% correct response. For the whole duration of each session, participants made 20° horizontal saccades at will from one stationary saccadic target to the other. After each saccade, they were instructed to maintain fixation for at

least 3 s before performing a new saccade towards the opposite saccadic target. Participants performed a saccade about every 5.3 ± 0.9 s (mean and standard deviation), alternatively leftward and rightward. At a random interval, the stimulus was displayed with a probability of about 1 presentation every 2–3 saccades. This was established to avoid an automatic allocation of attention at the center of the screen for every saccade. The stimulus presentation was determined by the experimenter in order to maximize the amount of trials presented in the periods between 1.5 s before and 1.5 s after saccadic onset. The participants were unable to predict the ISI. Subjects were required to discriminate, in a 2AFC procedure, the location in either the upper or lower field of the pedestal stimulus plus the contrast increment (experiment 1, contrast increment thresholds) or of the Gabor stimulus presented over the gray background (experiment 2, absolute contrast thresholds), and verbally report the response to the experimenter after the execution of the impeding saccade. No feedback was given. Each session lasted for 5 minutes; single participants performed on average about 2.8 hours of eye movement recordings for each experiment over a number of days. Experiment 1 presents a new analysis of published data (Benedetto & Morrone, 2017), whereas experiment 2 contains original data.

Data analysis

The recorded eye-position traces were examined in an offline analysis, and individual saccades modeled with a trapezoidal function (Benedetto & Morrone, 2017). A positive/negative slope segment, with two abutting constant segments, was used to fit the saccade trace and derive the saccadic onset and offset. We included only saccades with intersaccadic separation greater than 3 s which were well fit by the trapezoidal model ($R^2 > 0.99$, ~80% of the saccades). To disentangle the contribution of saccadic preparation from the saccadic execution, we restricted the analysis only to a temporal window of ± 1.5 s from the saccadic onset and pooled together the data for the leftward and rightward saccades (416.5 ± 64.2 trials per participant, mean $\pm$ standard deviation).

To compare the sensitivity results obtained from the experiment 1 and experiment 2, we applied the fitting procedure adopted in Benedetto and Morrone (2017) to the temporal dynamic of percentage of correct response for experiment 2 on the aggregate observer obtained by pooling together all trials, and eliminating the subjects' tags (methodological details and results from experiment 1 have been published in Benedetto and Morrone, 2017). First, the data were binned in nonoverlapping bins of 80 ms with respect to saccade onset. The

presaccadic-onset (from -1.16 to 0.16 s) and postsaccadic-onset time series (from 0.16 to 1.16 s), hereafter simply referred as presaccadic and postsaccadic trials, were separately fitted with two independent sinusoidal functions (all free parameters), as:

$$f(x) = A \cos(2\pi f x + \varphi) + \mu \quad (2)$$

The best-fit statistical significance was evaluated using a permutation procedure on surrogate data obtained by randomly shuffling the single trial responses and then performing the standard binning procedure (1,000 simulations). The timestamps of the original data were maintained in the surrogate dataset, in order to prevent spurious effects caused by the temporal distribution of the trials. In order to correct for multiple comparison, the surrogate data were fit with a sinusoidal waveform with amplitude, phase, and frequency as free parameters. The statistical significance was assessed by evaluating the probability of the permuted R^2 distribution being higher than the R^2 obtained from the actual dataset ($\alpha = 0.05$). Additionally, for both experiments, we estimated the phase distribution of the best fits by adopting a bootstrap procedure for the real data. Separately for pre- and postsaccadic trials, we bootstrapped our dataset (1,000 repetitions, with replacement). For each simulation, the bin length was randomly selected between 0.06 and 0.09 s (with nonoverlapping bins) to increase the reliability of the bootstrap procedure. The phase of the best sinusoidal fit was estimated at lags between 0.25 and 1 s from saccadic onset, for both pre- and postsaccadic responses to avoid phase biases caused by saccadic suppression.

For both experiments, we ran a single-trial multivariable generalized linear model (GLM). We fitted a linear regression model including, as predictors, a sine and a cosine for a given frequency of interest f_t (between 2 and 15 Hz, resolution of 0.01 Hz). The probability model behind this analysis can be written as:

$$\hat{Y}_n = \beta_0 + \beta_1 \sin(\omega t_n) + \beta_2 \cos(\omega t_n) \quad (3)$$

where t is the time lag of the single trial n; β_0, β_1, and β_2 are the fixed-effect linear regression parameters; $\hat{Y}_n$ is the predicted behavioral performance (i.e., response "up"); ω is the angular frequency ($\omega = 2\pi f_i$). For each frequency, we restricted the analysis to those trials presented within ± 1.5 s from saccadic onset. The fixed-effect linear regression parameters were estimated using standard least square method (LSM) as

$$\begin{bmatrix} \beta_0 \\ \beta_1 \\ \beta_2 \end{bmatrix} = (X^t X)^{-1} X^t Y \quad (4)$$

where Y is the vector of the single trial responses (0 or

1, for "up" or "down" responses, respectively). The matrix X has the form:

$$X = \begin{bmatrix} 1 & \sin(\omega t_1) & \cos(\omega t_1) \\ \cdots & \cdots & \cdots \\ 1 & \sin(\omega t_n) & \cos(\omega t_n) \end{bmatrix} \quad (5)$$

Statistics were computed on the Euclidean length of the β_1 and β_2 coefficients with a permutation technique, shuffling the aggregate responses (10,000 simulations) to create the empirical noise distribution of the aggregate observer. As done in the fitting analysis, the timestamps of the original dataset were maintained in the surrogate dataset, in order to prevent spurious effects caused by the temporal distribution of the trials. Spectral power (P) was computed as the square of the Euclidean length of the β_1 and β_2 coefficients. P values were corrected for multiple comparison with FDR correction ($q = 0.05$; Benjamini & Hochberg, 1995).

We additionally ran a group-mean analysis on bias which combined the data from experiment 1 and 2. This analysis was conducted for the intervals between -1 and 1 s from action execution and pooling the single-subject data across both experiments (resulting in nine participants). We tested the group average of the participant-specific beta coefficients (expressed as vectorial length) against the distribution of the maximal vectorial lengths obtained—at any tested frequency—from a permuted dataset (1,000 simulations).

Furthermore, we posthoc selected the significant frequency with the higher spectral amplitude and estimated the t statistic (under the null hypothesis $H_0 = 0$) for that frequency as:

$$t = \frac{\left| \vec{\bar{V}} \right| - H_0}{\frac{\sigma}{\sqrt{N-1}}} \quad (6)$$

Where $\vec{V}$ is the complex number of the individual subject given by

$$\vec{V} = \beta_1 + \beta_2 i, \quad (7)$$

The mean vector ($\vec{\bar{V}}$) and standard deviation (σ) across subjects were computed, respectively, as

$$\vec{\bar{V}} = \frac{1}{N} \sum_{j=1}^{N} \vec{V}_j \quad (8)$$

and

$$\sigma = \sqrt{\frac{1}{N} \sum_{j=1}^{N} \left| \vec{V}_j - \vec{\bar{V}} \right|^2} \quad (9)$$

Where N is the number of subjects. The standard deviation, $SD(\hat{\varphi})$, of the phase ($\hat{\varphi}$) was estimated from propagation of errors formula as follows:

$$SD(\hat{\varphi}) = \frac{|\beta_1||\sigma \cos(\hat{\varphi})| + |\beta_2||\sigma \sin(\hat{\varphi})|}{|\beta_1 + \beta_2|^2} \quad (10)$$

where

$$\hat{\varphi} = \arctan\left(\vec{\bar{V}} \right) \quad (11)$$

Results

We investigated the temporal dynamics of visual performance around the time of a voluntary eye movement in the two different 2AFC localization tasks: In experiment 1 the subjects had to report the position (up/down) of a contrast increment presented over a 10% contrast pedestal grating (contrast increment threshold); in experiment 2 the contrast increment was presented over a gray background, measuring absolute contrast threshold (see Figure 1 and Methods for more details). In both experiments, subjects made saccades at their own pace between two very small stationary saccadic targets in an otherwise empty and large display. Our main interest is to measure how visual sensitivity and bias varies as a function of stimulus presentation time from saccadic onset. The rationale to compare the two tasks is that they are limited by different mechanisms at different levels of visual processing and are subject to different sources of external and internal noise (Dosher & Lu, 2000a, 2000b). Experiment 1 produces shallower psychometric curves (Figure 1, purple line) with respect to experiment 2 (Figure 1, yellow line), and as such contrast increment thresholds from experiment 1 are more susceptible to being modulated by the presence of a bias for a specific location and by attention or learning. The average just-noticeable-difference (JND) estimated from the psychometric function across subjects and stimulus-onset-asynchronies (SOAs) was 0.076 ± 0.07 (for experiment 1) and 0.02 ± 0.01 (for experiment 2), confirming that the effect was generalized across participants.

The sensitivity (% correct responses) was computed in 31 bins of 80 ms time-locked to saccade onset, from -1.5 s before and up to 1.5 s after the saccade, aggregating the trials of all subjects. Presaccadic and postsaccadic accuracy in experiment 1 oscillated at around 2.9 Hz (95% confidence bounds: [2.6 Hz, 3.2 Hz]; red curve in Figure 2A) and around 2.3 Hz (95% confidence bounds: [1.9 Hz, 2.5 Hz]; green curve in Figure 2A), respectively. Similar results emerged also for experiment 2 (Figure 2E), where pre-saccadic sensitivity oscillated at around 2.3 Hz (95% confidence bounds: [2 Hz, 2.6 Hz]; red curve in Figure 2E) and post-saccadic sensitivity at around 2.9 Hz (95% confidence bounds: [2.6 Hz, 3.2 Hz]; green curve in Figure 2E).
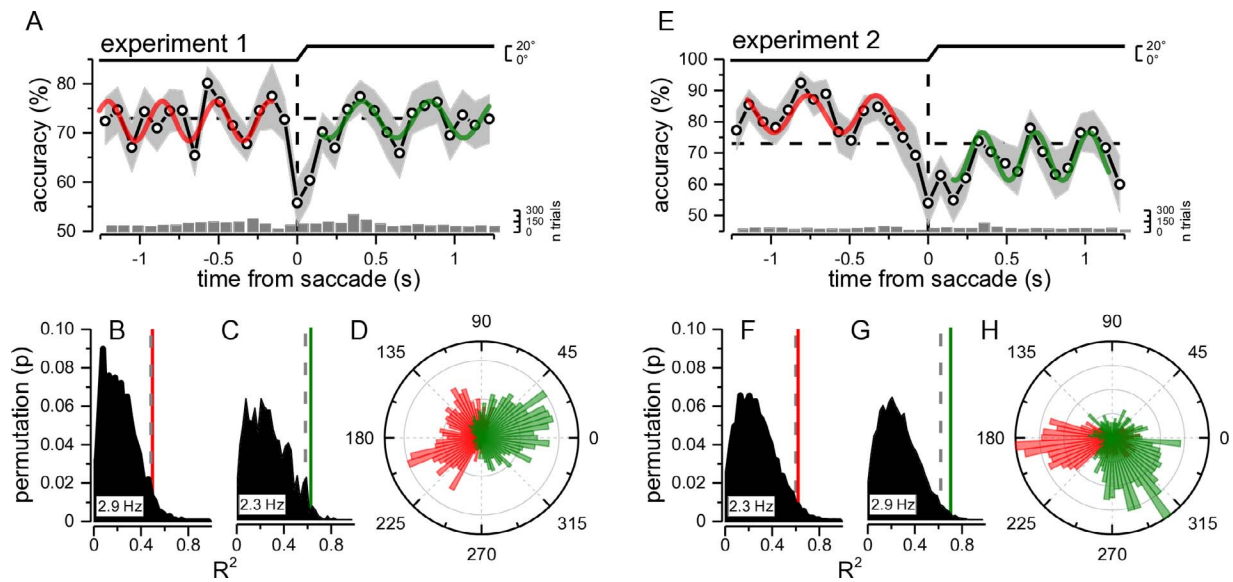
Figure 2. Accuracy results from aggregate observer for experiments 1 and 2. (A, E) presaccadic and postsaccadic contrast discrimination performance as a function of time from saccadic onset from experiment 1 ($n = 8$, A) and experiment 2 ($n = 5$, E). The bar plot shows the number of observations for each bin (80 ms). The gray area represents ± 1 *SEM* from bootstrapping; thick lines represent the best sinusoidal fit to the data for presaccadic responses (in red) and for postsaccadic responses (in green). Dashed vertical and horizontal lines report the time from saccadic onset and the median probability of correct response, respectively. Top trace shows the mean horizontal eye position. (B, F) black area marks the R^2 distribution obtained by permuting the responses from experiment 1 (B) and experiment 2 (F). Vertical red line shows the goodness of fit of the best sinusoidal fit for presaccadic oscillation; gray dashed line marks the 95th percentile of the permutation goodness of fit distribution. (C, G) same as in (B, F) for postsaccadic responses in experiment 1 (C) and experiment 2 (G). (D, H) phase estimation at saccadic onset (0 ms) for presaccadic (red) and postsaccadic (green) oscillations in experiment 1 (D) and experiment 2 (H), respectively. The phase of the presaccadic oscillation clustered for both experiments at around 180°, i.e., the trough of the oscillation period.

To evaluate the significance of the models, we compared the R^2 values of these fits with the distribution of the R^2 obtained by fitting the best possible sinusoidal waveform to surrogate data. Figure 2B–C and 2F–G shows the results of this analysis for both the presaccadic and the postsaccadic model, in experiment 1 and 2. For both models and experiments, the goodness of fit was statistically higher than that expected from chance (experiment 1: presaccadic model: $R^2 = 0.49$, $p = 0.041$; postsaccadic model: $R^2 = 0.62$, $p = 0.019$. Experiment 2: presaccadic model: $R^2 = 0.61$, $p = 0.046$; postsaccadic model: $R^2 = 0.70$, $p = 0.016$. *P* values corrected for multiple comparison).

Presaccadic sensitivity in experiment 1 oscillated at 2.9 Hz versus 2.3 Hz from experiment 2; postsaccadic sensitivity oscillated at 2.3 Hz in experiment 1 and at 2.9 in experiment 2. Interestingly, within both experiments, the differences between pre- and postsaccadic frequencies were statistically significant. Despite the difference in frequencies, in both experiments the phase analysis (Figure 2D–2H) revealed that saccadic suppression was embedded in phase with presaccadic oscillation. The 2D plots of Figures 2D and 2H show the phase distributions of the best-sinusoidal fit estimated using random intervals between 0.25 and 1 s

from saccadic execution (for both pre- and postsaccadic responses), and random bin size between 0.06 and 0.09 s. The trough of the presaccadic oscillation occurred around the time of maximal perceptual suppression caused by the eye movement (mean phase $\pm$ standard deviation: 167.6° $\pm$ 51.8° in experiment 1 and 208.1° $\pm$ 63.3° in experiment 2). Similarly, the phase of the postsaccadic oscillation is consistent with a maximum accuracy of around 350–400 ms from saccadic onset, which corresponds to an average phase of 14.6° $\pm$ 56.9 in experiment 1 and of 310.5° $\pm$ 63° in experiment 2 at the respective frequencies. These results reinforce the finding that saccadic suppression is not contributing to the alignment of the phase with saccadic onset.

The histograms in Figures 2A and 2E show that the number of trials presented right before the saccadic onset (around 160 ms before saccadic execution) presented a small but statistically significant reduction ($t(8) = 3.5$, $p = 0.008$), preceded by an increase 320 ms before saccadic execution. Visual stimuli presented around the planning time of a saccade (presaccadically) are known to inhibit the generation of the saccades delaying it, a phenomenon known as saccadic inhibition (SI; Reingold & Stampe, 2000). This inhibition typically creates a characteristic dip in the saccadic
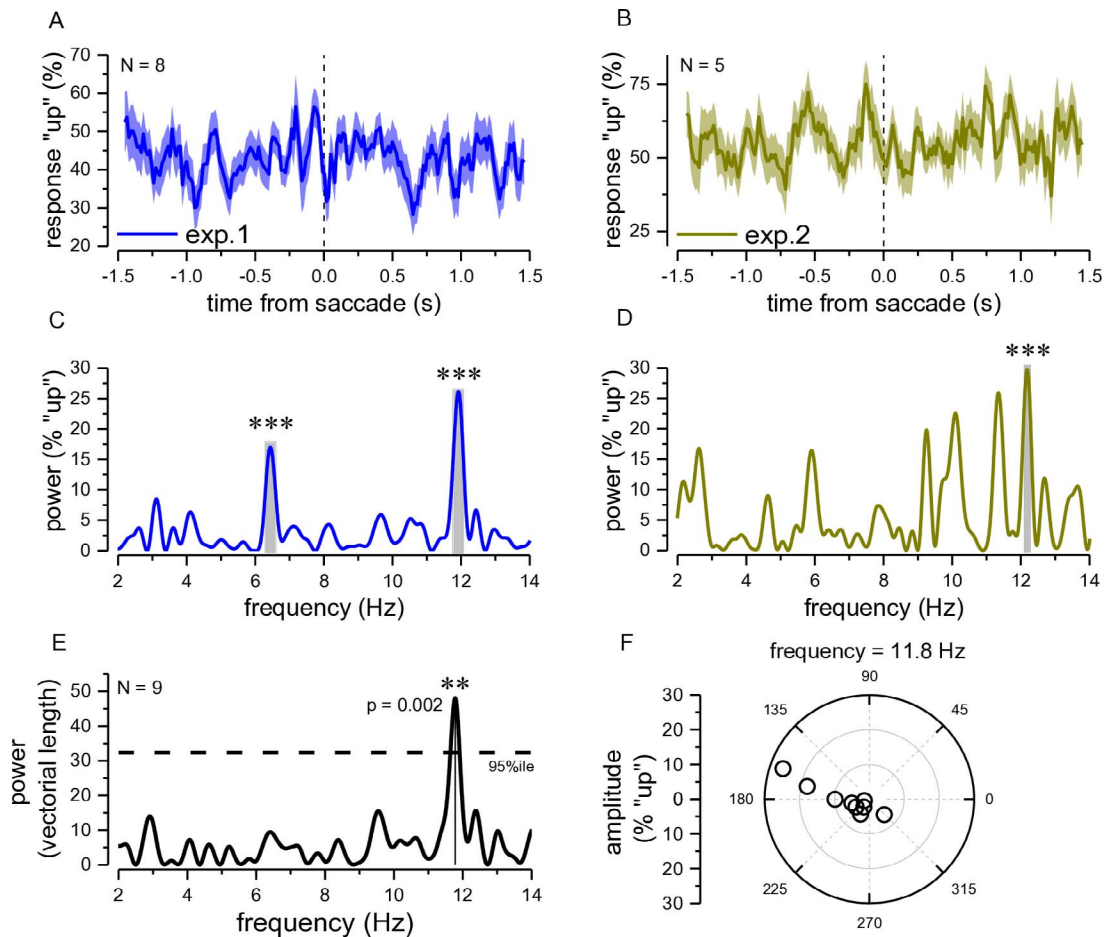
Figure 3. Response bias results from aggregate observer for experiments 1 and 2. (A, B) mean and *SEM* of the temporal dynamic of response bias as a function of time from saccadic onset for experiment 1 and 2, respectively. Data were binned—for representation only—in 75 ms bins (80% overlap). The vertical dashed line marks the time of saccadic execution. (C, D) power-spectrum obtained from single-trial GLM analysis of response bias for experiment 1 and 2, respectively. A strong oscillation at 12 Hz emerged from the spectrum for both experiments. Horizontal gray area reports the significant frequencies after FDR correction for multiple comparison ($p < 0.05$). (E) group-mean spectrum of response bias results for both experiment 1 and experiment 2. Horizontal dashed line indicates the 95% percentile of the maximal power distribution obtained from the permuted dataset. Only frequencies around 12 Hz results significantly higher than the estimated noise level ($p = 0.002$). (F) single-subject vectors obtained at 11.8 Hz, i.e., the significant peak in the power spectrum from panel E (vertical line). Black dots report single subjects ($N = 9$).

frequencies peaking around 100 ms from saccadic onset, preceded by a rebound phase where the delayed saccades are executed (Dombrowe, 2018; Reingold & Stampe, 2000, 2002). Both experiment 1 and experiment 2 show the saccadic inhibition phenomenon, given that in both experiments the targets were associated with a salient (high contrast pedestal or sound) stimulus which can divert attention from saccadic preparation. Interestingly, the detection performance of the targets does not correlate with the dynamics of the saccadic inhibition modulation: In experiment 1, participants showed a higher accuracy for trials presented in the dip of SI whereas, for experiment 2, accuracy was higher for trials presented in the rebound of SI (see Figures 2A and 2B). Overall, these results indicate that SI may be not driven by the

correct detection of the target and that delayed saccades do not have higher probability of correctly detecting the target. Instead it is likely that the cue presented together with the target is generating the SI (Pannasch, Dornhoefer, Unema, & Velichkovsky, 2001).

Panels A and B of Figure 3 show the probability of responding "up" as a function of time from saccadic execution for experiment 1 and 2 respectively, obtained by pooling together the data from all subjects (*aggregate observer*), and averaging in bin of 75 ms (80% overlap). The performance was not constant over time, exhibiting fluctuations clearly visible well before and after the execution of the saccade. Data-binning presents a trade-off between the amount of data within each bin (and hence the reliability of the estimation

obtained) and the sampling rate of the signal (and hence the resolution of the frequency analysis). For our dataset, the large bin was adequate for the analysis of slow oscillations in sensitivity (Benedetto & Morrone, 2017; Hogendoorn, 2016; Wutz et al., 2016), but problematic for faster oscillations typically observed for oscillations in response bias (around 7 to 14 Hz) (Benedetto et al., 2018; Ho et al., 2017; Zhang et al., 2019). To obtain a robust estimation of alpha fluctuations in response bias, we ran a single-trial multivariable generalized linear model (GLM) analysis (Benedetto et al., 2018; Tomassini et al., 2017) on the aggregate observer. The GLM analysis is a measure of how well the single trial (1 for an up response and 0 for a down response) predicts the amplitude and the phase of an oscillation at the frequency tested, given by the beta estimates of equation 3. Figure 3C–D shows the power spectrum of the GLM analysis (square of the amplitude), which has a strong peak in the high-alpha range (at around 12 Hz). For experiment 1, the permutation test revealed a significant power component at around 12 Hz (FDR corrected $p < 0.001$) and one at around 6.5 Hz (FDR corrected $p < 0.001$). Only a peak at around 12 Hz was significant for experiment 2 (FDR corrected $p < 0.001$).

Given the similarities between the oscillations in response bias, we combined the results from the two experiments (see Methods for more details), performing a group mean analysis where the data for each subject for the two experiments were aggregated (resulting in nine participants; Figure 3E). Participants revealed a consistent oscillation in the high-alpha range, with a strong phase coherence at around 12 Hz ($p = 0.002$, corrected for multiple comparison). Figure 3F shows the beta values of the single subjects at 11.8 Hz (i.e., the point of maximal group-mean amplitude). At this frequency, individual subject phase lay in the semiplane (mean phase and standard deviation: 182° ± 7°). The t test and Rayleight test at 11.8 Hz confirmed, respectively, that the amplitude distribution was significantly different from zero, $t(8) = 2.08$; $p = 0.03$, and that the phases (mean phase and standard deviation: 182° ± 7°) were not uniformly distributed around the circle, $z(8) = 5.06$, $p = 0.003$.

For the significant oscillation at 11.8 Hz, we additionally controlled for possible phase differences in bias across different eye-positions. We ran a phase analysis separately for trials presented when the eye was fixating on the point on the left or right side of the screen. The mean phases and standard deviations were 193° ± 9° for left fixations, and 179° ± 8° for right fixations (as compared to 182° ± 7° when pooling together the position of the eyes). The V test for nonuniformity of circular data revealed that—for both eye positions—the phases of the 11.8 Hz oscillation were not distributed uniformly around the circle, and

the mean direction was not different from the mean phase obtained pooling together both eye positions (left eye position: $V_8 = 5.52$, $p = 0.004$; right eye position: $V_8 = 4.13$, $p = 0.025$). This indicates that phase of the oscillation at 11.8 Hz for criterium is independent from the position of the eye.

Discussion

Visual perception has been hypothesized to be a cyclic process (Harter, 1967; VanRullen, 2016; VanRullen & Koch, 2003; Varela, Toro, Roy John, & Schwartz, 1981), whose rhythm can be influenced by several factors, including stimulus properties (Benedetto, Lozano-Soldevilla, & VanRullen, 2017; Benedetto et al., 2016; Benedetto & Morrone, 2017; Drewes, Zhu, Wutz, & Melcher, 2015; Hogendoorn, 2016; Holcombe & Chen, 2013), the difficulty of the task (Chen, Wang, Wang, Tang, & Zhang, 2017), and subject-by-subject variability (Benedetto et al., 2018, Benedetto et al., 2016; Fiebelkorn et al., 2013; Ho et al., 2017; Tomassini et al., 2015).

Recent research has demonstrated the presence of visual oscillations synchronized with action onset (Benedetto et al., 2018; Benedetto et al., 2019; Benedetto & Morrone, 2017; Hogendoorn, 2016; Tomassini et al., 2017; Tomassini et al., 2015; Wutz et al., 2016; Zhang et al., 2019). In particular, delta oscillations in visual sensitivity have been shown in contrast discrimination between highly salient stimuli (Benedetto & Morrone, 2017; Hogendoorn, 2016), phase-locked to saccadic events, likely reflecting a synchronization between endogenous visual neuronal rhythms and the oculomotor system. An open and crucial question is which are the mechanisms generating this rhythmic modulation?

One of the main hypotheses is that perceptual oscillations are mediated by top-down modulation of spatial attention. Attention can induce changes in visual sensitivity in several ways: by enhancing the response to the attended visual signal, by enhancing the selectivity of the neuronal spatial filter—for instance increasing visual resolution in discrimination tasks (Cameron, Tai, & Carrasco, 2002; Yeshurun & Carrasco, 1998), and by suppressing response in unattended locations or the response to external or internal noise. Attention can also be directed very efficiently in time, operating on endogenous rhythms. For instance, it has been suggested that brain oscillations might adjust to align in time the high (low) excitability states with the expected events, leading to sensory enhancement (suppression) of relevant (irrelevant) predictable stimuli and consequent behavioral benefits (Bonnefond & Jensen, 2012; Cravo, Rohen-

kohl, Wyart, & Nobre, 2011; Lakatos et al., 2009; Morillon, Hackett, Kajikawa, & Schroeder, 2015; Samaha, Bauer, Cimaroli, & Postle, 2015; Schroeder & Lakatos, 2009; Stefanics et al., 2010).

For efficient interaction with the physical world, it would be important that the temporal series of the inputs arriving at our sensory organs is shaped by our own movements:

We actively, rather than passively, collect sensory information, and we do so by constantly moving our receptors (Gibson, 1962). Eye-movements of any kind have proper rhythms and saccadic eye movements are naturally performed by humans at a rate of ~2–3 Hz (Rucci, Ahissar, & Burr, 2018). The similarity between behavioral motor rhythmicity and the perceptual oscillation has led some authors to suggested that they may rely on similar neuronal mechanisms (Benedetto et al., 2016; Helfrich et al., 2018; Schroeder, Wilson, Radman, Scharfman, & Lakatos, 2010). Motor-related signals (like anticipatory intention-to-move signals or corollary discharge) are available before the actual execution of a movement and may thus serve as endogenous predictive cues, to inform the sensory systems about the upcoming inputs. Traditionally, these anticipatory signals have been conceived to counteract the disruptive side-effects of movement on perception by selective sensory suppression, and may participate in the mechanism mediating perceptual stability by updating and remapping spatial information across movements (Benedetto & Binda, 2016; Binda & Morrone, 2018; Burr & Morrone, 2011; Crapse & Sommer, 2008; Diamond, Ross, & Morrone, 2000; Duhamel, Colby, & Goldberg, 1992; Medendorp, 2011; Ross, Morrone, Goldberg, & Burr, 2001). A corollary discharge signal may also operate as a momentary boost of perceptual sensitivity to optimize processing of the new sensory inflow brought about by the movement itself (Binda & Morrone, 2018; Knöll, Binda, Morrone, & Bremmer, 2011; Melloni, Schwiedrzik, Rodriguez, & Singer, 2009). This perceptual enhancement/suppression might be achieved through the active modulation of neuronal oscillations. Recent monkey (Fiebelkorn, Pinsk, & Kastner, 2018) and human intracranial (Helfrich et al., 2018) data provided converging evidence that the rhythmic sampling of visual spatial locations is shaped by multiplexed oscillations across the fronto-parietal network. Altogether, this evidence points back to the long-debated link between attention and eye movements (Rizzolatti, Riggio, Dascola, & Umiltá, 1987; Smith & Schenk, 2012) and raises the question of whether the saccadic initiation might actually be dictated by a covert attentional rhythm (Helfrich, 2018; Helfrich et al., 2018). Fiebelkorn and Kastner (2019) have proposed a model that aims at reconciling attention-based sensory sampling and eye movements control

within a unified view. According to their proposal, two opposite states would alternate at a theta rhythm (Fiebelkorn & Kastner, 2019). A given phase of this theta rhythm would be associated with increased perceptual sensitivity (at the attended location) and concomitant motor suppression. Within this model, sensory (sampling) and motor (exploratory eye movements) processes would be boosted at opposite phases of a common theta rhythm.

Although attention is effective in modulating increment contrast thresholds (such as in many discrimination tasks), it facilitates little absolute thresholds (Dosher & Lu, 2000b, 2000a; Lee et al., 1999; Morrone et al., 2002). Therefore, if the behavioral fluctuations represent an expression of attentional mechanisms, we should expect no or much weaker oscillations in sensitivity when measuring absolute contrast thresholds. However, the comparison between the perisaccadic temporal dynamics of accuracy from experiment 1 (contrast increment thresholds) and experiment 2 (absolute contrast thresholds) disproved this hypothesis: We observed similar oscillations in sensitivity in the two different tasks. The strong similarities in the results between the two experiments support the hypothesis of an independence between attention and peri-saccadic sensitivity oscillations and suggest the presence of an attentional-independent mechanism mediating their emergence. It has been proposed that perceptual oscillations may also arise from a rhythmic sampling orthogonal to the deployment of attention, but dependent on intrinsic neuronal properties, such as local neuronal interactions (Landau, 2018). This hypothesis, corroborated by recent neurophysiological findings (Kienitz et al., 2018) and consistent with our results, suggests that rhythmic sampling can indeed emerge as a general property of early visuo-motor processing, and that not only attention (VanRullen & Koch, 2003) but also sensation may present an intrinsic degree of rhythmical sampling.

Sensitivity is not the only perceptual dimension describing our perceptual systems; bias is also an important aspect of them. We show that bias was also rhythmically modulated in synchrony with saccadic onset, not in the delta range as sensitivity is, but in the alpha range. Whereas the majority of studies have focused on sensitivity indexes (for a review, see VanRullen 2016), converging evidence from recent studies has demonstrated that response bias oscillates in the alpha range (Ho et al., 2017), synchronized with a voluntary action (Benedetto et al., 2018; Zhang et al., 2019). For instance, Zhang and collaborators (2019) investigated the dynamics of bias and sensitivity for orientation discrimination around the time of a voluntary action. They demonstrated the presence of alpha oscillations in criterion (~10 Hz), synchronized with a voluntary button-press. The authors suggested a

possible link between behavioral alpha oscillation in criterion and neural alpha oscillation, with the latter proposed as an important mechanism for top-down (feedback) control of neuronal activity (Bastos et al., 2015; van Kerkoerle et al., 2014) generating the observed fluctuation in response bias. Interestingly, the same authors reported oscillations in sensitivity for similar stimuli at a lower frequency (at around 8 Hz), confirming the presence of two independent rhythmic mechanisms regulating bias and sensitivity (Benedetto et al., 2018; Ho et al., 2017; Zhang et al., 2019). Some electrophysiological data also support this dissociation having recently revealed that bias, but not sensitivity, can be predicted by the power and phase of prestimulus EEG alpha endogenous rhythms (Benwell et al., 2017; Iemi et al., 2017; Limbach & Corballis, 2016; Samaha et al., 2017; Sherman et al., 2016). Interestingly, single neuron electrophysiological studies in monkeys show that sensitivity and criterion are modulated by (at least) partially independent brain structures and rely on different brain mechanisms (Luo & Maunsell, 2015, 2018; Van Vugt et al., 2018).

Although the 2AFC tasks adopted here are known to minimize the effect of decision bias on the performance (MacMillan & Creelman, 2005), we cannot exclude a decisional component from the observed rhythmic oscillation (Morgan, Hole, & Glennerster, 1990; Witt, Taylor, Sugovic, & Wixted, 2015). A shift in criterion can also be achieved by biasing the sensory evidence accumulation process towards a certain choice and generating perceptual asymmetries. Coherent perceptual asymmetries have been reported for both spatial and temporal tasks (Cameron et al., 2002; Lundh, Lennerstrand, & Derefeldt, 1983; Rijsdijk, Kroon, & van der Wildt, 1980). A leftward spatial attentional bias has been commonly observed in a variety of tasks and a similar asymmetrical bias also applies for upper and lower visual fields (Previc, 1990; Thomas & Elias, 2011), with a lower visual field bias emerging in many instances (Carrasco, Williams, & Yeshurun, 2002; Lundh et al., 1983; Rijsdijk et al., 1980). The different tasks did not affect either the frequency or the phase of the main alpha oscillation, suggesting that the result may reflect a generalized bias mechanism, likely driven by perceptual expectations or by top-down influences rather than sensory asymmetries. Electrophysiological evidence indicates that alpha rhythms are crucial in conveying top-down information in the brain (Andreou et al., 2017; Bastos et al., 2015; Engel et al., 2001; Jensen, Bonnefond, Marshall, & Tiesinga, 2015; Michalareas et al., 2016; van Kerkoerle et al., 2014; Wang et al., 2014) and the phase of the prestimulus alpha activity has been demonstrated to shape the weighting of perceptual expectations (de Lange et al., 2013; Sherman et al., 2016). Crucially, prestimulus alpha activity over motor

cortex was found to reflect perceptual expectation (de Lange et al., 2013), indicating a privileged link between action and perceptual predictions. The results from experiment 1 and 2 revealed a similar and long-lasting cyclic modulation of response bias (at around 12 Hz) synchronized with the execution of the saccadic eye movement, and irrespective of the position of the eye.

The probability of performing a saccade at a given time from stimulus presentation is known to be modulated by a phenomenon known as saccadic inhibition (SI). After the visual stimulus presentation, saccades are inhibited (about 100 ms from stimulus onset) and delayed, resulting in a characteristic shape (Reingold & Stampe, 2000). Although SI has been mostly investigated for stimulus driven saccades (Bompas & Sumner, 2011; Buonocore & McIntosh, 2012; Reingold & Stampe, 2000, 2002), it is interesting that a similar effect affects also self-paced saccades where no measurements of saccadic reaction time is possible, as we also observed here in both experiments. This visuomotor synchronization might potentially contribute to the presaccadic oscillations with the correct detection of the stimulus, inducing a delay in the saccade and hence an increase in the accuracy during programming phase. However, the increase in accuracy corresponded at the time of the delayed saccade in experiment 2, but not in experiment 1, confuting, at least partially, this explanation. In addition, we did not observe a rhythmic modulation of trial frequency for the time preceding saccadic pro-gramming (< 250 ms), again confuting the idea that early oscillation reflects rhythmicity of the saccadic inhibition phenomenon. Despite the strong synchroni-zation demonstrated between the visual and the motor system, we could not find a clear influence of SI on visual rhythms, suggesting that presaccadic perceptual oscillations are likely genuine modulations of visual sensitivity and bias. Although we cannot dismiss completely that SI is not contributing to the behavioral oscillations, we would like to point out that a rhythmicity of the saccadic inhibition phenomenon well before the saccadic onset is consistent with the presence of a central clock synchronizing both vision and action, as we proposed in earlier work (Benedetto et al., 2019).

In conclusion, our results demonstrate that visual sensitivity and response bias oscillates over time— synchronized with saccadic execution—within the delta and alpha-range frequency, respectively. These modu-lations are likely caused by an interaction between ongoing brain oscillations and the actual sensory input and are synchronized with the planning of a voluntary eye movement, starting a second before its execution and lasting for up to one second thereafter. Although the mechanisms of these oscillations are still not clear, the current results suggest the presence of independent oscillations in visual sensitivity and response bias. In

addition, they suggest a dissociation between sensitivity oscillations and attentional deployment, indicating that oscillations in visual sensitivity likely reflect intrinsic and preattentive properties of the visuo-motor system.

Keywords: visual sensitivity, response bias, behavioral oscillations, saccades, eye movements

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