Saccade kinematics modulate perisaccadic perception

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Around the time of execution of an eye movement, participants systematically misperceive the spatial location of briefly flashed visual stimuli. This phenomenon, known as perisaccadic mislocalization, is thought to involve an active process that takes into account the motor plan (efference copy) of the upcoming saccade. While it has been proposed that the motor system anticipates and informs the visual system about the upcoming eye movements, at present the type and detail of information carried by this motor signal remains unclear. Some authors have argued that the efference copy conveys only coarse information about the direction of the eye movement, while a second theoretical view proposes that it provides specific details about the direction, amplitude, and velocity of the saccade to come. To test between these alternatives, we investigated the influence of saccade parameters on a perisaccadic unmasking task in which performance in discriminating the identity of a target (face or house) followed by a trailing mask is dramatically improved around the time of saccade onset. We found that the amplitude and peak velocity of the upcoming saccade modulated target perception, even for stimuli presented well before saccadic onset. We developed a predictive model for the generation of the efference copy that incorporates both saccade amplitude and saccade velocity planning prior to saccade execution. Overall, these results suggest that the efference copy stores specific information about the parameters of upcoming eye movement and that these parameters influence perception even prior to saccade onset.

Introduction

Visual localization of briefly presented flashes is inaccurate around the onset of saccades; flashed targets are typically perceived as shifted in space toward the upcoming target of the saccade (Honda, 1995, 2006; Matin & Pearce, 1965; Ross, Morrone, Goldberg, & Burr, 2001). In line with Helmholtz's (1909) suggestion, the main, but not the only (Atsma, Maij, Corneil, & Medendorp, 2014), explanation for perisaccadic mislocalization is that the visual system makes use of the predictive efference copy of the eye movement (also known as corollary discharge; for review, see Wurtz, Joiner, & Berman, 2011). According to this hypothesis, the efference copy is used not only for accounting for the negative consequences of the saccadic eye movement on visual input, such as retinal smear, but also for actively preparing the visual system for the upcoming eye movement by changing its response properties.

An important question is what type of information the efference copy of the saccade conveys to the visual system. Some authors have argued for a relatively weak role of the efference copy, suggesting that it serves mainly as a warning of the impending saccade (Bridgeman, van der Heijden, & Velichkovsky, 1994). The visual system then assumes the prior hypothesis of a stable world across eye movement, ignoring saccade-induced retinal displacements. In line with this theory, studies have shown that postsaccadic visual references can serve as anchors to link pre- and postsaccadic coordinates (Lappe, Awater, & Krekelberg, 2000).

Other authors have argued for a strong role of the efference copy, suggesting that it provides specific details about direction, amplitude, and velocity of the programmed saccade (Dassonville, Schlag, & Schlag-Rey, 1992). Such information would seem to be critical, for example, for the predictive remapping of receptive fields (Cavanagh, Hunt, Afraz, & Rolfs, 2010; Melcher & Colby, 2008). Several previous studies have linked predictive remapping with perceptual effects of the anticipatory upcoming eye movement, including masking (De Pisapia, Kaunitz, & Melcher, 2010; Hunt & Cavanagh, 2011), adaptation aftereffects (Cha & Chong, 2014; Melcher, 2007; Zirnsak, Gerhards, Kiani, Lappe, & Hamker, 2011), and spatial updating of attention (Rolfs, Jonikaitis, Deubel, & Cavanagh, 2011). If a detailed efference copy plays a role in these perceptual effects, then it would be predicted that saccadic parameters could influence the magnitude of such effects.

In the case of perisaccadic mislocalization, previous studies have reported an effect of saccade amplitude on perisaccadic mislocalization (Kaiser & Lappe, 2004; Morrone, Ross, & Burr, 1997) as well as an effect of saccade velocity on perisaccadic compression (Ostendorf, Fischer, Finke, & Ploner, 2007).

These studies provide some preliminary evidence for an influence of saccade kinematics on subjective measures of perisaccadic perception. We tested the combined effect of saccade amplitude and saccade peak velocity on an objective measure of perception, the perisaccadic unmasking paradigm (De Pisapia et al., 2010). In this task, a briefly flashed target is followed by a backward mask. Around the time of saccade onset, participants become better at discriminating the identity of this brief target, which otherwise would have been rendered invisible by the trailing mask on no-saccade trials. If perisaccadic unmasking performance depends on an anticipatory motor signal that conveys information about saccade dynamics, then the occurrence of unmasking might depend on the kinematic parameters of the saccade on each trial. Consistent with this hypothesis, we found that saccade kinematics did modulate perisaccadic perception: Faster/larger saccades lead to a better performance than slower/smaller saccades. We propose a model that takes into account a combination of saccade kinematics to explain perisaccadic perception, supporting theories that posit an important role of efference copy in mediating visual stability.

Materials and method

Participants

Seventeen participants took part in the present study. Participants were all students of the University of Trento (10 females; mean age = 23 years; age range = 20–32 years) and had normal or corrected-to-normal vision. The experiment was conducted in accordance with the ethical guidelines for psychophysical studies laid down by the University of Trento and the ethical standards laid down in the 1964 Declaration of Helsinki (most recently amended in 2008, Seoul). All participants were naive with regard to the main hypothesis of the experiment.

Apparatus and stimuli

Observers sat in a dimly lit room and viewed the computer screen at a distance of 57 cm with the head supported on a chin rest. Eye movements were measured using an EyeLink 1000 Desktop Mount (SR Research, Ontario, Canada) sampling at 1 kHz. Software implemented in MATLAB (MathWorks, Natick, MA) controlled stimulus display and response collection using the Psychophysics Toolbox (Brainard, 1997) and EyeLink Toolbox (Cornelissen, Peters, & Palmer, 2002). Stimuli sequences were presented on an Iiyama (Hoofddorp, the Netherlands) CRT 1900 monitor (1280 columns × 1024 lines; refresh rate = 100 Hz) on a uniformly gray background with an average luminance of 8.8 cd/m^2 (CIE coordinates: x = 0.28, y = 0.31).

Targets could be either grayscale male faces (randomly chosen among 20 images on each trial) or grayscale houses. Targets were presented on the uniform gray background and equated for root mean square (RMS) contrast (mean RMS for faces = 5.9, mean RMS for houses = 6.3; see Figure 1A). Targets size was 2.5° × 2.5° of visual angle. Masks were randomly generated on each trial and consisted of black (CIE coordinates: x = 0.35, y = 0.37; luminance = 0.25 cd/m^2) and white (CIE coordinates: x = 0.28, y = 0.30; luminance = 80 cd/m^2) squares (0.058°/visual angle each). Mask size was 3° × 3° of visual angle (see Figure 1A).

Procedure

Each trial began with a black fixation point presented at the center of the screen. Participants were instructed to fixate the point and press a button when ready to start. After a variable delay (extracted from a Gaussian distribution, 500 ± 350 ms), the fixation point disappeared from the center of the screen and a new (saccadic target) fixation point appeared that was shifted by 12° of visual angle to either the left or the right of the initial fixation point. Participants were instructed to perform a single saccadic eye movement toward the new fixation point. The target stimulus (face
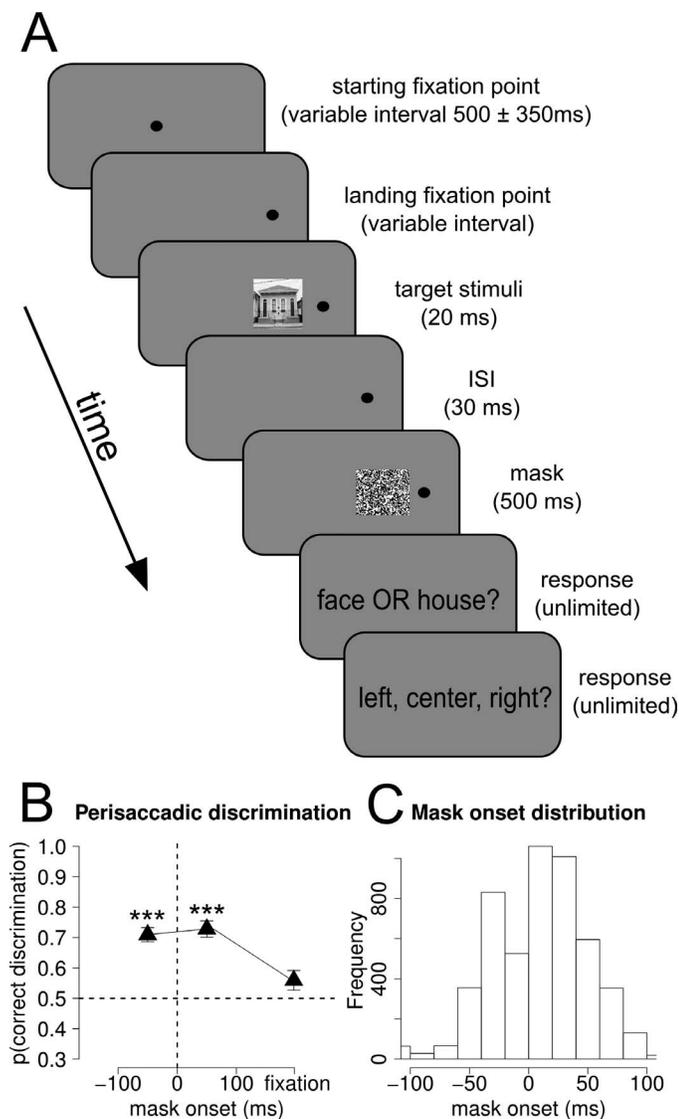
Figure 1. (A) Example trial sequence (rightward saccade; target stimuli: house). The central fixation point shifts 12° of visual angle right, signaling the participant to perform a saccadic eye movement. Then, after a variable delay (based on median saccade reaction time; see Procedure), a target stimulus (in this case a house) appeared for 20 ms, followed by a 30-ms blank ISI and then a noise mask for 500 ms. (B) Discrimination performance along the perisaccadic interval for the 17 participants for three intervals—presaccadic interval (−100,0], postsaccadic interval (0,100], and the fixation interval—when mask could be presented <150 ms before saccade onset or >150 ms after saccade onset. Error bars represents SEM (standard error of the mean). On the x-axis, 0 represents saccade onset time. Subjects were more accurate in the pre- and postsaccade intervals compared with fixation, consistent with a perisaccadic unmasking of the target stimulus. Dashed lines represent saccade onset time and baseline performance level of the two-alternative forced-choice task (0.5 on the y-axis). The asterisks represent Bonferroni-corrected significance

or house) was presented in the middle of the spatial trajectory (eccentricity of 5° of visual angle from initial fixation), jittered in time with respect to saccade target onset. The target was presented for 20 ms, and then after a constant ISI (inter-stimulus interval) of 30 ms the mask was presented for 500 ms (Figure 1A).

Saccade onset time was estimated online on each trial. Eye position was continuously monitored at 100 Hz with the aim of detecting a saccadic eye movement toward the new fixation point. The first derivative of the eye position signal was computed, and saccade onset was identified by using a speed criterion of 40°/s. In the first trial of the experiment, the target–mask sequence was presented at a time period 250 ms after the new (saccade target) fixation point appeared. For each subsequent trial, the participant-specific saccadic reaction time was estimated and the distribution of saccade onset times was updated such that the median saccade reaction time was computed from the distribution. On subsequent trials the target–mask sequence was presented at the estimated median saccadic reaction time. This method has been successfully adopted previously (Harrison et al., 2013; Hunt & Cavanagh, 2011). Figure 1C shows the distribution of mask onset with respect to saccade onset time (defined as 0 in the x-axis). The eye position signal was downsampled at 100 Hz only for the purposes of the online estimation of saccade onset for guiding stimulus presentation. The saccade onset estimates adopted in the final, offline analysis of the data are based on the eye signal acquired at 1 kHz.

After each trial, participants were required (a) to discriminate the category of the target (either a face or a house) in a two-alternative forced-choice procedure by pressing *1* or *2* on the keypad (1 = *face*, 2 = *house*) and (b) to report the perceived location of the target with respect to the mask by pressing *1*, *2*, or *3* on the keypad (1 = *left with respect to the mask*, 2 = *same location as the mask*, 3 = *right with respect to the mask*). Trials were categorized as mislocalized when participants reported the perceived location of the target as shifted toward the direction of the saccade. Trials were categorized as nonmislocalized when subjects reported the target in the same location as the mask. This subjective measure of mislocalization was useful to ensure that participants were paying attention to the target (house, face) and to ensure that there was a perisaccadic perceptual effect. Each participant performed a variable number of 50 trials blocks for a total number of trials that ranged from 450 to 500.

←

levels: ***p < 0.001 (one-sample t test against baseline performance, 0.5). (C) Distribution of mask onset times with respect to saccade onset for all trials across all participants.

Data analysis

Behavioral performance

For each participant we binned trials according to the mask onset times with respect to saccade onset time (defined as 0 ms in our analysis; see Figure 1B). We used this conservative measure to ensure that targets presented prior to the saccade (points to the left of the vertical dotted line in Figure 1B) appeared and disappeared before saccade onset. In particular, we were interested in targets presented shortly before (−100 to 0 ms] or after (0 to 100 ms] the saccade (bracket indicates included limit value, and parenthesis indicates excluded limit value). Trials in which the mask onset was presented <150 ms or >150 ms from saccade onset time were binned in the fixation condition (see Figure 1B). Before collapsing the two fixation time periods (<150 ms before saccade onset and >150 ms after saccade onset), we confirmed that there was no difference in performance in these two time periods using a paired two-sample t test, $t(16) = 0.68$, $p = 0.45$. We computed discrimination performance for each participant and each interval (Figure 1B). Data were analyzed using within-participant analysis of variance (ANOVA) and post hoc tests with Bonferroni correction.

Combined amplitude and peak velocity

The main objective of our study was to evaluate the influence of saccade amplitude and peak velocity on perisaccadic performance. Although saccade amplitude and saccade peak velocity are not independent with respect to each other, their relationship can be approximated by a linear function for a limited range of amplitude (Findlay & Gilchrist, 2003; see Figure 2A). In order to take into account the combined effect, we built a predictor based on this relationship. We split the data from each participant into two subgroups based on the specific saccade peak velocity × saccade amplitude (combined) relationship. For each participant, the linear coefficient (m) was computed and the line orthogonal to it was computed based on the inverse negative of the estimated linear coefficient ($m_{orthogonal}$):

$$m_{orthogonal} = \frac{-1}{m}. \tag{1}$$

Then the orthogonal to the linear regression was forced to pass through the point that represents saccade amplitude median and saccade peak velocity median to compute the orthogonal intercept ($q_{orthogonal}$) and obtain the line equation orthogonal to the regression line:

$$peakvelocity_{orthogonal} = m_{orthogonal} amplitude + q_{orthogonal}. \tag{2}$$

The Cartesian plane was then divided into two planes by the orthogonal regression line, giving the combined *amplitude × peak velocity*. All the trials falling on the subplane where

$$peakvelocity_{orthogonal} \geq m_{orthogonal} amplitude + q_{orthogonal} \tag{3}$$

were assigned to the faster/larger group, and all the remaining trials were assigned to the slower/smaller group (see Figure 2C).

Retinal distance computation

On some trials, the eye movement itself would displace the location of the target on the retina with respect to the mask. Target–mask retinal distance was computed on each trial to evaluate its possible influence on unmasking performance. We extracted single-trial eye traces. From these traces, we (a) computed the eye position at the time of target onset and (b) computed the median eye position during the time interval from mask onset time until mask onset time plus saccade duration. For example, in a trial in which saccade duration was 45 ms, we computed the median eye position from mask onset until 45 ms after mask onset. Then we subtracted eye position at target onset from this median eye position to obtain stimulus–mask retinal distance.

In this way, we took into account trials in which the mask was presented just prior to the saccade onset and thus shifted in retinal position due to the eye movement itself. These two values were subtracted, and we took the absolute value to obtain the distance between target stimuli and mask on the retina.

Results

Consistent with a previous study (De Pisapia et al., 2010), eye movements caused umasking of the target stimuli (Figure 1B). Target discrimination performance was modulated by the mask onset intervals, as confirmed by a within-participant ANOVA on mask onset interval level (see Data analysis) that revealed a significant main effect of interval level, $F(2, 32) = 12.56$, $p < 0.001$, $\eta_{partial}^2 = 0.44$. Performance was significantly above chance level for the (−100, 0] and (0, 100] intervals, Bonferroni-corrected one-sample paired t test, $t(16) = 9.49$, $p < 0.001$ and $t(16) = 8.48$, $p < 0.001$, respectively, but not for the fixation time interval, one-sample paired t test, $t(16) = 2.08$, $p = 0.18$ (see Figure 1B). These results replicated the basic finding reported
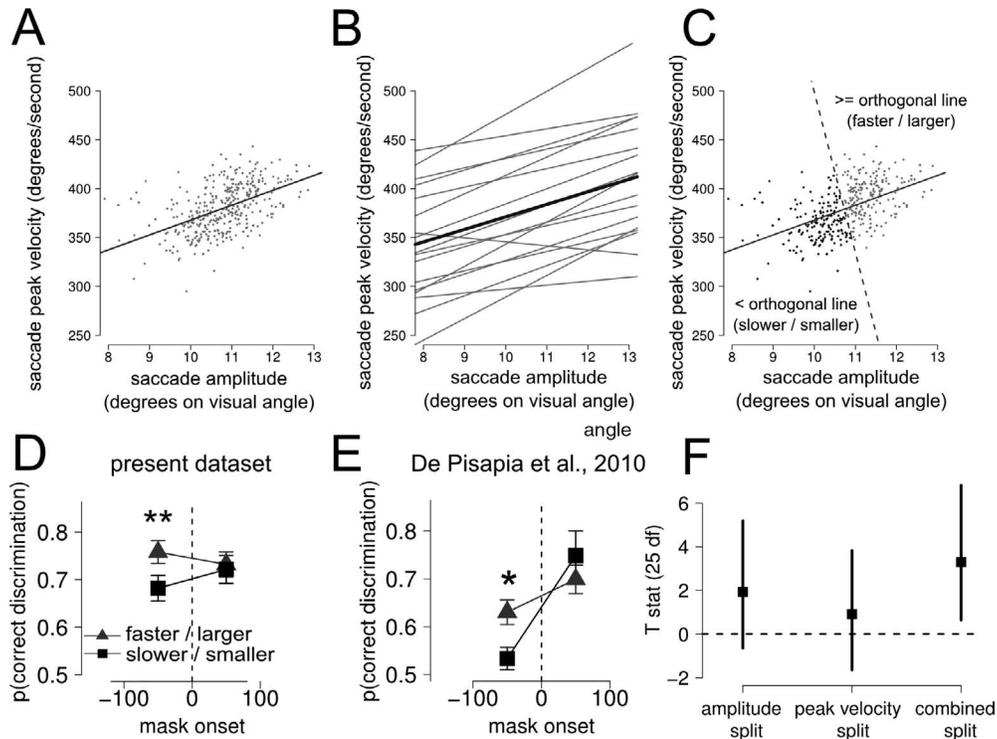
Figure 2. (A) Linear dependence between saccade peak velocity and saccade amplitude on a single participant; the regression line is superimposed to the data cloud. (B) Data are shown for single participants (gray lines) and average mean regression (black line). (C) Linear dependence between saccade peak velocity and saccade amplitude on a single representative participant. The gray continuous line represents the linear fit, whereas the gray dotted line represents the line orthogonal to the fit (see Equation 2). Gray points represent trials greater than or equal to the orthogonal line (assigned to the faster/larger group; see Equation 3), whereas black points represent trials less than the orthogonal line (assigned to the slower/smaller group; see Equation 3). (D) The perisaccadic discrimination performance as a function of mask onset time interval—presaccadic interval, (−100, 0] ms; postsaccadic interval, (0, 100] ms—and combined amplitude × peak velocity (faster/larger group and slower/smaller group) on the present data set (17 participants). (E) The same analysis was applied to an independent data set (De Pisapia et al., 2010; $n = 9$). Again, we observed a significant influence of combined amplitude × peak velocity only for the presaccadic interval. Asterisks represent intervals in which subjects' accuracy statistically differed from chance level: $*p < 0.05$, $**p < 0.01$, Bonferroni-corrected paired two-sample t test. Dashed lines represent saccade onset time (0 on the x-axis) and baseline performance level of the two-alternative forced-choice task (0.5 on the y-axis). Error bars represent 1 SEM. (F) The plot shows the bootstrapped one-sample t statistic for the faster/larger − slower/smaller difference in the presaccadic interval (−100, 0] across the two data sets (26 participants) with a 99% bootstrapped confidence interval (10,000 repetitions with resample). Three split criteria were tested: median amplitude, median peak velocity, and combined (amplitude × peak velocity) split. Only the test in the combined (amplitude × peak velocity) split condition was significantly different from the null distribution (horizontal line at $t = 0$).

by De Pisapia et al. (2010) but with complex images (face or houses) and noise masks rather than simple shapes with metacontrast masking. Discrimination performance increased during the perisaccadic interval with respect to baseline (chance level; see Figure 1B).

As expected, saccade peak velocity and saccade amplitude showed a statistically significant linear relation (Findlay & Gilchrist, 2003; see Figure 2A), with a mean linear coefficient of 14°/s × 1 amplitude degree, one-sample t test, $t(16) = 7.49$, $p < 0.001$ (see Figure 2B).

We computed the discrimination performance for each participant for the (−100, 0] and (0, 100] time intervals and combined amplitude × peak velocity level (larger/ faster and slower/smaller; see Data analysis). Average

performance can be seen in Figure 2D. We found that amplitude × peak velocity had a significant main effect on average discrimination performance (within-participant repeated measures ANOVA), main effect of amplitude × peak velocity level on average discrimination performance, $F(1, 16) = 12.72$, $p = 0.002$, $\eta_{partial}^2 = 0.44$, and a marginal interaction between combined amplitude × peak velocity and time interval, $F(1, 16) = 3.48$, $p = 0.08$, $\eta_{partial}^2 = 0.18$. Post hoc analysis revealed that there was a significant influence of amplitude × peak velocity level only on the presaccadic interval (−100, 0], two-sample paired t test, $t(16) = 2.97$, $p = 0.009$, Cohen's $d = 0.72$.

We replicated these results using a separate, previously published data set (see De Pisapia et al., 2010, for

the specific details). In brief, the authors employed a metacontrast masking sequence with targets presented for 12 ms and a mask presented for 188 ms with an ISI of 12 ms. Masking sequences were presented around the perisaccadic interval. In order to allow for a direct comparison with the present data, our reanalysis was limited to trials in which target–mask ISI was set to 12 ms (one frame in their experimental setup). Data from nine participants were collected in the original study.

We computed discrimination performance for each participant, each time interval, and combined amplitude × peak velocity level (faster/larger and slower/smaller); the average discrimination performance is reported in Figure 2E. Within-participant ANOVA revealed a significant effect of time interval on average discrimination performance, $F(1, 8) = 16.02$, $p = 0.003$, $\eta_{\text{partial}}^2 = 0.66$, and an interaction between combined amplitude × peak velocity and time interval variables, $F(1, 8) = 9.1$, $p = 0.01$, $\eta_{\text{partial}}^2 = 0.53$. Post hoc analysis revealed a significant influence of the combined split variable only for the presaccadic interval (−100, 0], two-sample paired t test, $t(8) = 2.44$, $p = 0.04$, Cohen's $d = 0.81$. Thus, the same pattern of results was found with the data from the present study and from the original saccadic unmasking study.

Saccade peak velocity and amplitude are tightly correlated. Thus, it is not possible to determine to what degree the advantage of faster/larger saccades over slower/smaller saccades depends on amplitude or peak velocity alone. We compared three split criteria—median amplitude, median peak velocity, and combined split (amplitude × peak velocity)—to test whether the advantage comes from a single predictor (either amplitude or peak velocity) or from the combination between predictors (amplitude and peak velocity). We bootstrapped the one-sample within-participant t statistic for the faster/larger − slower/smaller difference in the presaccadic interval, (−100, 0] ms, across the two pooled data sets (26 participants), thus deriving the median t statistic within a 99% bootstrapped confidence interval (10,000 repetitions; Figure 2F). Only the test in the combined (amplitude × peak velocity) split condition was significantly different from 0, showing that the combined peak velocity × amplitude predictor was the only one that modulated performance. Either amplitude or peak velocity alone were not sufficient to modulate accuracy (Figure 2F).

Model

We built a two-stage model to explain the effect of saccade kinematics on perisaccadic discrimination performance. The purpose was to investigate whether the influence of saccade kinematics on perisaccadic

unmasking performance could be predicted by explicitly incorporating saccade kinematics into an already existing model of perisaccadic perception (Dassonville et al., 1992). This model had an initial sensory stage followed by a decision stage.

At the sensory stage, we considered saccadic eye movements modeled as a minimum jerk movement (Flash & Hogan, 1985) with variable amplitude and duration. Experimental results show that, after learning, movements tend to be performed more smoothly (Georgopoulos, Kalaska, & Massey, 1981). This indicates that moving an effector from a starting point to an ending point relies on achieving the smoothest possible movement. Flash and Hogan (1985) showed that the best quantitative prediction for forearm movement is achieved by minimizing jerk (the third time derivative of location). The one-dimensional minimum jerk function has been shown to have the following analytical form (Shadmehr & Wise, 2005); we explicitly refer to eye movement trajectories, hence *eye(t)*:

$$eye(t) = eye_{start} + (eye_{end} - eye_{start})$$
$$\times \left(10(t/d)^3 - 15(t/d)^4 + 6(t/d)^5\right), \quad (4)$$

where d is saccade duration. Data were extracted from each single trial measured in our present data (17 participants) and the previously reported (De Pisapia et al., 2010) data (nine participants).

In the model proposed by Dassonville et al. (1992), localization errors arise because of a discrepancy between $eye(t)$ and the perceived eye displacement at time t, the efference $eye_{perceived}(t)$ copy. Following Dassonville et al. (1992), the first step of the sensory stage was to shift (by the amount Δt) and low-pass filter $eye(t)$ trajectory:

$$eye_{perceived}(t) = \int_{-\inf}^{t} eye(t + \Delta t) h(t) dt, \quad (5)$$

with $h(t)$ being the low-pass filter:

$$h(t) = \frac{t^{(n_s - 1)}}{n_s - 1!} e^{\frac{-t}{T_s}}, \quad (6)$$

with time constant T_s and order n_s. For our purposes, T_s was set to 20 and n_s was set to 2.

The second step at the sensory stage consisted of reading out the transformed target stimuli and mask positions on each trial based on the trial onset time and mask onset time with respect to saccade onset (see Figure 3A). From these two values, we computed the absolute transformed distance between target stimuli and mask and provided these values to the decision stage.

The decision stage consisted of a single step in which the absolute transformed distance (a continuous measure) was converted in the [0 1] range (single-trial
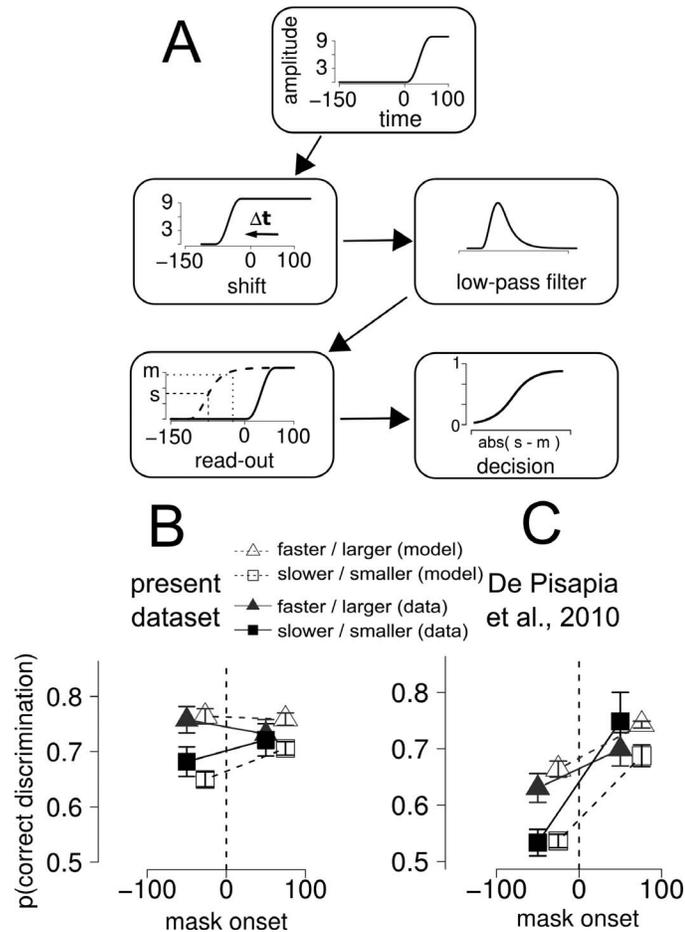
Figure 3. A model of the influence of saccade kinematics on perisaccadic perception. (A) To calculate perceived eye displacement, the eye movement trajectory is shifted by Δt and low-pass filtered. From this transformed trajectory, target stimuli position (dashed line, s) and mask position (dotted line, m) are then read out. The absolute distance between target stimuli position and mask position is computed and fed into the decision stage. (B) The results of the model superimposed on the observed data of the present data set (17 participants). The model captures the presaccadic advantage of trials in the faster/larger group with respect to the slower/smaller group as well as the lack of an effect of saccade kinematics during the postsaccadic period. (C) The results of the model superimposed on data from an earlier study (De Pisapia et al., 2010) with nine participants. Error bars represent 1 *SEM*.

expected discrimination) by means of generalized linear model (GLM; R Development Core Team, 2013) fit with logit function as link (McCullagh & Nelder, 1989) with two parameters, representing the slope and the intercept of the GLM model:

$$X\beta = \ln\left(\frac{1}{1-a}\right), \tag{7}$$

where X is the $n_{\text{trials}} \times 2$ design matrix and β is the 2×1 coefficient vector for each participant, and a is the

absolute transformed distance. From this point on, we refer to the β vector elements as β_1 and β_2, respectively.

Overall, the model had three free parameters: the shift at the sensory stage Δt and the GLM parameters β_1 and β_2 of the decision stage. The first parameter Δt was optimized via an iterative procedure for each single participant. The parameters β_1 and β_2 were estimated via GLM fit to the observed discrimination accuracy at the decision step (see Equation 7). Then the goodness of fit of the result was tested using a standard linear model between the predicted discrimination accuracy values based on the fit and the observed values.

The model was tested via cross-validation, estimating the parameters on $n - 1$ participants and testing the model on the nth participant for each data set. A range of Δt parameters were tested on each iteration, spanning the range [–200 to 200] ms with a step of 1 ms, and the value of Δt parameter was selected based on the best goodness of fit obtained at cross-validation. Model results and comparison with empirical results are reported in Figure 3.

The model captures the main pattern of results, in particular the influence of saccade kinematics on performance during the presaccadic time period. For the current data set, a significant difference was found between the presaccadic (−100, 0] faster/larger group with respect to the slower/smaller group, $t(1, 16) = 7.94$, $p < 0.001$. This was replicated for the De Pisapia et al. (2010) data set, $t(1, 8) = 4.01$, $p = 0.003$. The estimated parameters on the two data sets are the following: present data set (17 participants): $\Delta t = -111.64 \pm 25.94$, $\beta_1 = -0.12 \pm 0.12$, $\beta_2 = 0.64 \pm 0.09$, variance explained by the model = 35%; De Pisapia et al. (2010) data set (nine participants): $= \Delta t = -93.8 \pm 16.99$, $\beta_1 = -0.38 \pm 0.12$, $\beta_2 = 0.82 \pm 0.07$, variance explained by the model = 27%.

When the eyes are in motion toward the saccade landing position, the target and mask are presented in different portions of the retina. It could be argued that this favors target unmasking. We performed a further analysis to ensure that the advantage for faster/larger saccades compared with slower/smaller saccades in our paradigm was not simply due to the eye movements per se. The retinal distance analysis revealed a significant influence of combined amplitude × peak velocity variable for the postsaccadic interval (0, 100], Bonferroni-corrected two-sample paired t test, $t(16) = -4.45$, $p < 0.001$, but not for the presaccadic interval (−100, 0], Bonferroni-corrected two-sample paired t test, $t(16) = -1.12$, $p = 0.27$ (see Figure 4A). Thus, the retinal distance between target and mask could not explain the main effect that the combined amplitude × peak velocity had on perisaccadic discrimination of targets during the presaccadic interval (−100, 0]. The main effect of time interval on retinal distance is expected due to the ongoing eye movement in the first few
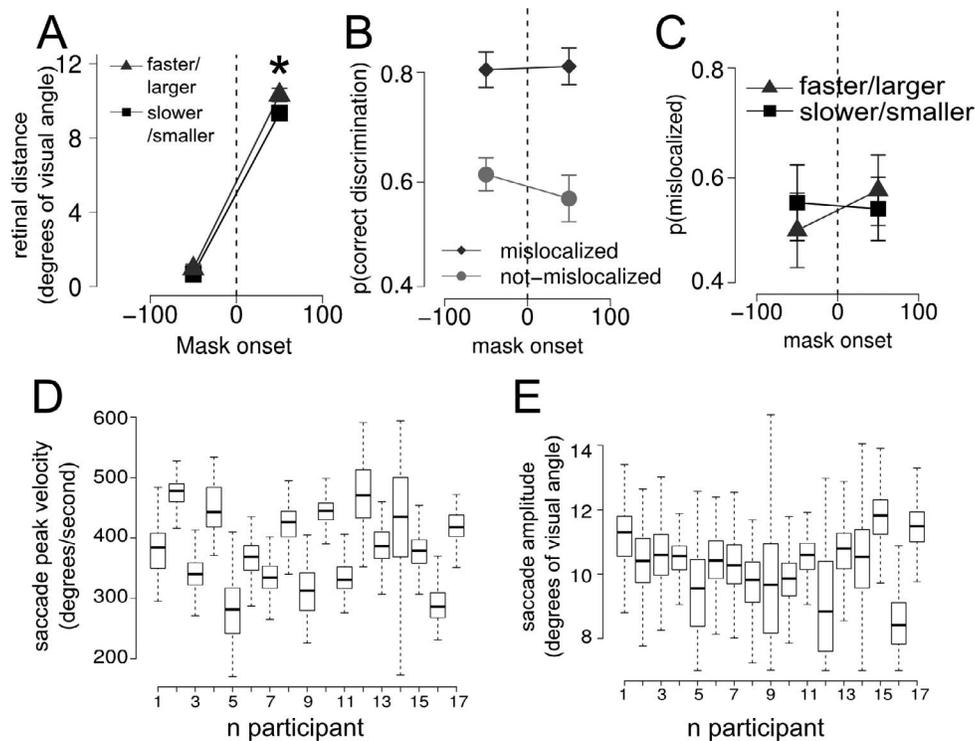
Figure 4. Further analyses of the influence of saccades on mislocalization and perceptual discrimination judgments. (A) Retinal distance between target stimuli and mask is shown as a function of mask onset time interval—presaccadic interval [−100, 0] ms, postsaccadic interval (0, 100] ms—and the combined amplitude × peak velocity predictor (faster/larger and slower/smaller) for the main data set (17 participants). For each trial we extracted the eye trace and read the eye position at the target stimulus onset and the mask onset. From these two values we computed the retinal distance between target stimuli and mask in degrees of visual angle. There was a significant influence of combined amplitude × peak velocity only for the postsaccadic interval (Bonferroni corrected significance levels: *$p < 0.05$, with a paired two-sample *t* test). (B) The effect of reported target mislocalization on participant performance. We observed a significant influence of mislocalization along the perisaccadic interval, $F(1, 16) = 24.4$, $p < 0.001$. (C) Saccade kinematics (combined amplitude × peak velocity predictor) did not have a consistent effect on mislocalization reports. (D, E) Single participant box plots of saccade peak velocity and saccade amplitude for trials included in the analysis: presaccadic interval [−100, 0) ms, postsaccadic interval (0, 100] ms. Overall, participants tended to undershoot the requested 12° of visual angle eye movement (E), as is commonly reported in similar studies (Findlay & Gilchrist, 2003).

samples of the postsaccadic interval. The influence of combined amplitude × peak velocity on the post-saccadic time interval (0, 100] is expected given the larger amplitude and faster peak velocity of saccades in the faster/larger group and the larger retinal distance between target stimuli and mask in the postsaccadic interval, (0,100] ms, while the eyes fly toward the saccade target position (Figure 4A).

Previously, it has been shown that perisaccadic unmasking performance peaks near saccade onset and decays as the target is presented farther away from saccade onset (De Pisapia et al., 2010). Differences in the distribution of mask onset times with respect to saccade onset might have given subjects an advantage to report targets in the presaccadic interval for faster/larger saccades over slower/smaller saccades. To rule out this possibility we ran a within-participant AN-OVA with mask onset time level and combined amplitude × peak velocity as factors. There was no

significant effect of the combination of amplitude × peak velocity on discrimination performance, $F(1, 16) = 0.59$, $p = 0.45$, and the interaction parameter was not significant, $F(1, 16) = 1.079$, $p = 0.31$. These results indicate that the influence of saccadic kinematics on perceptual discrimination was not dependent on the exact mask onset time.

Consistent with De Pisapia et al. (2010), we found an effect of mislocalization on perisaccadic unmasking performance. Participants showed increased discrimination accuracy on trials in which the target was reported as being mislocalized with respect to the mask. We tested the effect of mask onset time and reported mislocalization on discrimination performance with a 2 × 2 within-participant ANOVA. The analysis did not yield a main effect of time interval, $F(1, 16) = 0.58$, $p = 0.45$, but there was a significant effect of reported mislocalization, $F(1, 16) = 24.4$, $p < 0.001$, $\eta_{partial}^2 = 0.60$ (Figure 4B). In other words, when the target was

mislocalized it was also reported more accurately in terms of its identity.

On the other hand, the proportion of mislocalized trials was not influenced by the combination of amplitude and peak velocity during the perisaccadic interval (Figure 4C). We tested the effect of mask onset time level and combined amplitude × peak velocity on reported mislocalization. The analysis did not yield a main effect of time interval, $F(1, 16) = 0.39$, $p = 0.53$, or effect of combined amplitude × peak velocity, $F(1, 16) = 0.077$, $p = 0.78$. This overall pattern of results suggests that perisaccadic discrimination and reported mislocalization measures are related (as shown in Figure 4B) but not identical, since reported mislocalization was not influenced by saccade kinematics in the same way as perisaccadic discrimination (see Figures 2D and 4C). The difference between these two measures could reflect the fact that one is an objective measure, whereas mislocalization is more subjective. Alternatively, one possibility is that unmasking could be associated with not only spatial but also temporal distortions occurring around saccade onset time (see, e.g., Binda, Cicchini, Burr, & Morrone, 2009).

Discussion

We found that a combination of saccade amplitude and peak velocity modulated subjects' performance on a perisaccadic unmasking task. When the target (face or house) was shown prior to saccade onset, faster/larger saccades led to better performance than slower/smaller saccades. This same pattern was replicated using a previously published data set (De Pisapia et al., 2010). Despite the differences between these data sets (e.g., stimulus type, background color, masking type, and experimental procedure), we found the same effect of saccade kinematics on perisaccadic performance (see Figure 2D, E). Consistent with our hypotheses, we found that the combination of saccade amplitude and peak velocity modulated perisaccadic unmasking performance only for the presaccadic trials, whereas we found no modulation of saccade kinematics for the postsaccadic trials.

The current pattern of results is consistent with the theory that the efference copy contains specific information about the upcoming eye movement. Additional control analyses showed that the perceptual effects are not due to eye motion per se, since the retinal distance between the stimuli and the mask could not explain the modulation of saccade kinematics on unmasking performance (Figure 4A). There was a small influence of saccade kinematics on retinal distance (Figure 4A), with faster/larger saccades leading to larger retinal distance differences between the target

and mask than slower/smaller saccades, but this difference was limited to postsaccadic trials in the range of 0 to 100 ms. This is expected given the larger retinal distance between target and mask while the eyes are actually moving. For the effects found during the presaccadic interval (−100, 0], larger retinal distances cannot account for the improvement in discrimination of faster/larger saccades. Furthermore, the improvement in discrimination for faster/larger saccades cannot be explained by the saccadic reaction time distribution, as mask onset times did not differ between faster/larger and slower/smaller saccades in the presaccadic interval.

Our findings provide support for previous studies showing a link between saccade amplitude and perisaccadic effects (Kaiser & Lappe, 2004; Morrone et al., 1997; Ostendorf et al., 2007). For example, Ostendorf et al. (2007) focused on the relation between participant variability of peak saccade velocity and the amount of perceived visual compression (Ross, Morrone, & Burr, 1997). They found a significant correlation between the average saccade velocity for each participant and the reported compression (but not mislocalization). Our study goes beyond earlier results by providing an analysis of both the presaccadic and postsaccadic perceptual effects in a within-subject analysis using discrimination accuracy as perisaccadic performance. We took advantage of the objective discrimination accuracy of the saccadic unmasking paradigm and built a novel predictor based on the combination between saccade amplitude and peak velocity to unveil a presaccadic modulation of subjects' performance. Thus, we show the close link between the efference copy, saccade kinematics, and perisaccadic perception in the interval prior to saccade onset.

The sensorimotor theory of visual spatial attention suggests a strong coupling between spatial attention and the oculomotor system (Sheliga, Riggio, & Rizzolatti, 1995). Both saccade preparation and covert attention increase visual sensitivity and perceived contrast (Carrasco, 2011; Rolfs & Carrasco, 2012; Treue, 2004). Nonetheless, a crucial difference between saccade preparation and the deployment of covert attention resides in the time scale over which these processes seem to operate (Rolfs & Carrasco, 2012). The influence of saccade preparation on perceived stimuli occurs as fast as 60 ms after cueing, whereas covert attention enhancements can be detected around 300 ms after cueing (Carrasco, 2011). This suggests that covert attention operates later than the mask and target onset of our experiments. Moreover, it has been reported that presaccadic perceptual consequences of an impending eye movement are tightly coupled with saccade execution (Born, Mottet, & Kerzel, 2014).

It is also important to note that we found an unmasking effect for a stimulus that was displayed at a different position than the saccadic target. In contrast,

other studies on the relation between attention and saccade programming have consistently found perceptual facilitation at the saccadic goal rather than elsewhere (Kowler, Anderson, Dosher, & Blaser, 1995). Thus, the time scale and spatial location of our effects are not consistent with covert shifts of attention as the main factor in our results. Our model is parsimonious in capturing the anticipatory influence of saccade kinematics on perisaccadic perception without recurring to attentional resources, proposing a simpler explanation of the phenomenon.

Previous models of perisaccadic perception (Dassonville et al., 1992) have incorporated saccade kinematics to explain the influence of eye trajectory on perception. Our model does not propose a new mechanism to explain the underlying phenomenon but rather demonstrates how the combination of saccade amplitude and saccade peak velocity might play an important role in such models. We have represented the efference copy as a shifted and low-pass filtered version of the eye trace (Dassonville et al., 1992). The shifted representation of the eye trace leads to different read-out values between target stimuli and masks when they are presented before the onset of the eye movement, whereas the model predicts no systematic difference in the postsaccadic interval (Figure 3A, read-out section). Thus, we were able to model the anticipatory nature of perisaccadic perception (see Figure 2D, E) by incorporating saccade amplitude and saccade peak velocity into an already-existing model of perisaccadic perception (Dassonville et al., 1992).

The current results are of interest for the debate regarding the underlying nature of perisaccadic perceptual effects, such as mislocalization and unmasking. Some recent studies have argued that mislocalization is not unique to saccades or is caused by other aspects of the saccade, such as uncertainty or averaging of the saccadic target location with the flashed target location (Atsma et al., 2014; Zimmermann, Born, Fink, & Cavanagh, 2014). It seems unlikely that perisaccadic unmasking can be accounted for by mechanisms such as uncertainty or averaging. Instead, we suggest that models incorporating corollary discharge and active changes in visual processing around the time of saccades are better candidates for explaining unmasking.

Perisaccadic discrimination and perisaccadic mislocalization are two measures of performance that are correlated but not identical. There are at least two possible explanations for this difference between perisaccadic mislocalization and perisaccadic unmasking performance. First, unmasking performance is based on an objective evaluation of whether participants correctly report the identity of the stimuli, whereas subjective mislocalization reports lack an objective correct or incorrect answer and can be biased by the participant's response criterion. Second, the intention to make a saccade has been shown to induce temporal distortions in visual processing in addition to spatial ones (Morrone, Ross, & Burr, 2005). This raises the question of whether some aspects of saccadic unmasking result from temporal aspects of masking, such as changing the effective duration of the target or mask or the delay between the two, rather than just the spatial displacement of the target with respect to the mask.

What might be the functional advantage of having a detailed efference copy for the visual system? Saccades induce a specific spatial change, and so an estimate of kinematic parameters of the saccade could provide useful information for maintaining visual stability. Recent theoretical approaches have simulated efference copies with forward dynamic models that convert the motor signal into a sensory reference frame (Crapse & Sommer, 2008; Sommer & Wurtz, 2008; Vaziri, Diedrichsen, & Shadmehr, 2006; Wolpert & Miall, 1996). Within these models, the motor system initially provides the sensory systems with the expectation about the consequences of the movement that is going to be executed. Then, the sensory expectation is compared with the sensory input, and the magnitude of the discrepancy between the two is evaluated. In order to build a forward model that captures the dynamics of perisaccadic perception, the efference copy signal must store precise saccade kinematics.

The current findings suggest that the efference copy is not a dichotomous on–off motor signal and that it conveys information about saccade direction, amplitude, and velocity. These results are consistent with the idea that the efference copy carries a precise estimate of oculomotor error (Bahcall & Kowler, 1999; Collins, Rolfs, Deubel, & Cavanagh, 2009) and is compatible with a strong and active role of the efference copy. Such a precise copy would seem necessary to link visual stability to predictive remapping of receptive fields around saccade onset (Cavanagh et al., 2010; Melcher & Colby, 2008). A precise and detailed corollary discharge could provide the visual system with the information for predicting the dynamics of the entire perisaccadic input and thus estimate the perceptual consequences of the saccade to be executed.

Acknowledgments

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