Competition between salience and informational value for saccade adaptation

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What we see is influenced by where we look. When confronted with multiple relevant targets, inaccurate saccade target selection can impair perceptual performance. Here we ask whether endpoint selection can be optimized by the mechanism maintaining saccade accuracy: saccade adaptation. Therefore, we introduce a double-target adaptation task, where a presaccadic peripheral stimulus (plaid) splits vertically into its two components (Gabor patches) during horizontal saccades. While both targets were task-relevant, one of them provided more information for the perceptual task, because it could only be identified after the saccade with near-foveal vision. The other target was highly salient and could also be identified in the presaccadic plaid using peripheral vision. This double-target paradigm induced saccade adaptation: Without a perceptual task, participants adapted to the salient target. When both targets were judged sequentially, participants mostly adapted to the target they had to judge first. When targets were judged simultaneously, endpoints were biased toward the informative target but showed no gradual learning and fell short of optimality. We observed gradual adaptation when targets shifted randomly such that a strategic adjustment of endpoints was not possible. Overall, these findings show that when multiple targets compete, our oculomotor system can learn to adjust endpoints in order to maximize information for perception. Yet individual variability and other factors affecting target priority play a crucial role.

Introduction

How well we can see an object strongly depends on its position on our retina. Only the central regions of our two retinas, the foveae, can provide us with information about fine visual details. However, the foveae span only a tiny part of the visual field, about 1° of visual angle. Beyond that, visual acuity drops drastically with increasing eccentricity, and peripheral vision only allows us to identify coarse patterns. To explore details across the whole visual field, we move our eyes to objects or regions of interest by means of saccade eye movements. After a saccade, the fine visual details of the saccade target can be best identified when the saccade's endpoint is accurate. Inaccurate saccades can either go along with a loss of perceptual information or require further corrective saccades. Therefore, saccade accuracy is fundamental for quick and precise visual perception.

When confronted with multiple perceptually relevant targets, selecting a saccade endpoint that maximizes information for perception is less trivial. Whereas some studies have found that saccade endpoints support perception optimally (Najemnik & Geisler, 2005, 2008; Renninger, Verghese, & Coughlan, 2007), others have found contradictory results (Morvan & Maloney, 2012; Verghese, 2012; Ackermann & Landy, 2013; Clarke & Hunt, 2016; Nowakowska, Clarke, & Hunt, 2017). Morvan and Maloney (2012), for instance, investigated whether human observers can select saccade endpoints that

optimize target identification. In their paradigm, participants had to discriminate a dot that appeared either in a left or in a right square, but never in the central one. Depending on the distance of the squares, the optimal strategy would be either to saccade to the central square and monitor the left and right squares with peripheral vision or to saccade to one of the lateral squares and monitor only that square with foveal vision. Participants behaved clearly suboptimally, because they did not adjust their saccade behavior as a function of target distance (see also Clarke & Hunt, 2016), leading to suboptimal perceptual performance. But what if our visual system is repeatedly confronted with the same multiple target arrangement? Will our eyes continue to land at the same perceptually suboptimal endpoint? Or will our oculomotor system learn to adjust to meet the demands of perception despite an initially suboptimal strategy?

For saccades to single targets, accuracy is maintained by a mechanism called saccade adaptation (McLaughlin, 1967; for reviews, see Pélisson, Alahyane, Panouillères, & Tilikete, 2010; Herman, Blangero, Madelain, Khan, & Harwood, 2013). Saccade adaptation is thought to minimize an error signal (McLaughlin, 1967; Wallman & Fuchs, 1998; Bahcall & Kowler, 2000; Wong & Shelhamer, 2010; Collins & Wallman, 2012) and is typically studied using the double-step paradigm (McLaughlin, 1967). In this paradigm, the fixation target steps to the periphery. During the saccade to the new target location, this target is shifted so that the eye does not land on the target as intended. If the target is shifted repeatedly over several trials, the motor system learns to adjust its motor command to the postsaccadic target location. Adaptation can be induced by shifting the target in the direction of the saccade (forward adaptation), opposite to it (backward adaptation), and perpendicular to it (cross-axis adaptation; e.g., Wallman & Fuchs, 1998; Chen-Harris, Joiner, Ethier, Zee, & Shadmehr, 2008; Schütz & Souto, 2011).

Recent studies have highlighted the contribution of behavioral goals for saccade adaptation. For example, adaptation can be voluntarily inhibited in the presence of a postsaccadic error, at least for forward adaptation (Heins, Meermeier, & Lappe, 2019). Moreover, saccade adaptation can be induced in the absence of a bottom-up visual error, either by reinforcement (Madelain, Paeye, & Wallman, 2011) or by the presence of a perceptual task (Schütz, Kerzel, & Souto, 2014). Madelain et al. (2011) made use of the natural variability of saccade amplitude and reinforced saccades within a certain amplitude range either via an auditory tone or by presenting the target in the fovea after saccade offset. That reinforcement procedure evoked saccade adaptation with a similar

overall amplitude change compared to the conventional double-step paradigm. Schütz et al. (2014) showed that saccade adaptation can be induced by the presence of a perceptual task. In that paradigm, participants made eye movements to a horizontally stretched compound stimulus containing multiple characters. Participants had to discriminate individual characters within the character array. Depending on which target within the array was task-relevant, saccades adapted either backward or forward. These adaptation time courses were best captured by a model that included an immediate strategic adjustment in addition to slow, gradual learning. There were further similarities with traditional adaptation induced by target steps: Endpoints changed gradually with an adaptation magnitude similar to a double-step paradigm, and adaptation transferred to reactive saccades and affected saccadic curvature as it does with an intrasaccadic step (Chen-Harris et al., 2008). The time course and magnitude of saccade adaptation induced by a perceptual task is similar to saccade adaptation when participants were explicitly instructed to select a particular target within the compound stimulus (Schütz & Souto, 2015). These findings on task-induced adaptation suggest that saccade adaptation not only maintains saccade accuracy but also optimizes saccade endpoints depending on the behavioral goal.

The aim of the present study is to test whether and to what extent saccade adaptation optimizes endpoints for perception and thus for a specified behavioral goal. To this end, we introduce a new adaptation paradigm, the double-target adaptation task, where a presaccadic target—a plaid stimulus consisting of two overlaid Gabor patches—appeared to the right of fixation (Figure 1A and 1B). As soon as participants made a saccade to the plaid, it split vertically into its two components. These two components constituted the two postsaccadic targets. One of them was shifted upward, the other downward. Participants had to judge the orientation of both postsaccadic Gabors and received score points only when both judgments were correct. Thus, both postsaccadic targets were equally task-relevant. However, one of the two postsaccadic targets was highly salient, because it was displayed at high contrast and had a low spatial frequency. We refer to this target as the *salient target* (Figure 1A). The other target had a high spatial frequency and was displayed at low contrast. Considering the different sensitivity profiles for high and low spatial frequencies across the retina (Hilz & Cavonius, 1974; Rovamo, Virsu, & Näsänen, 1978), these spatial-frequency values were chosen so that the salient target could still be identified when viewed from the periphery, whereas the other target could be identified only when seen with near-foveal vision. For this second target, successful
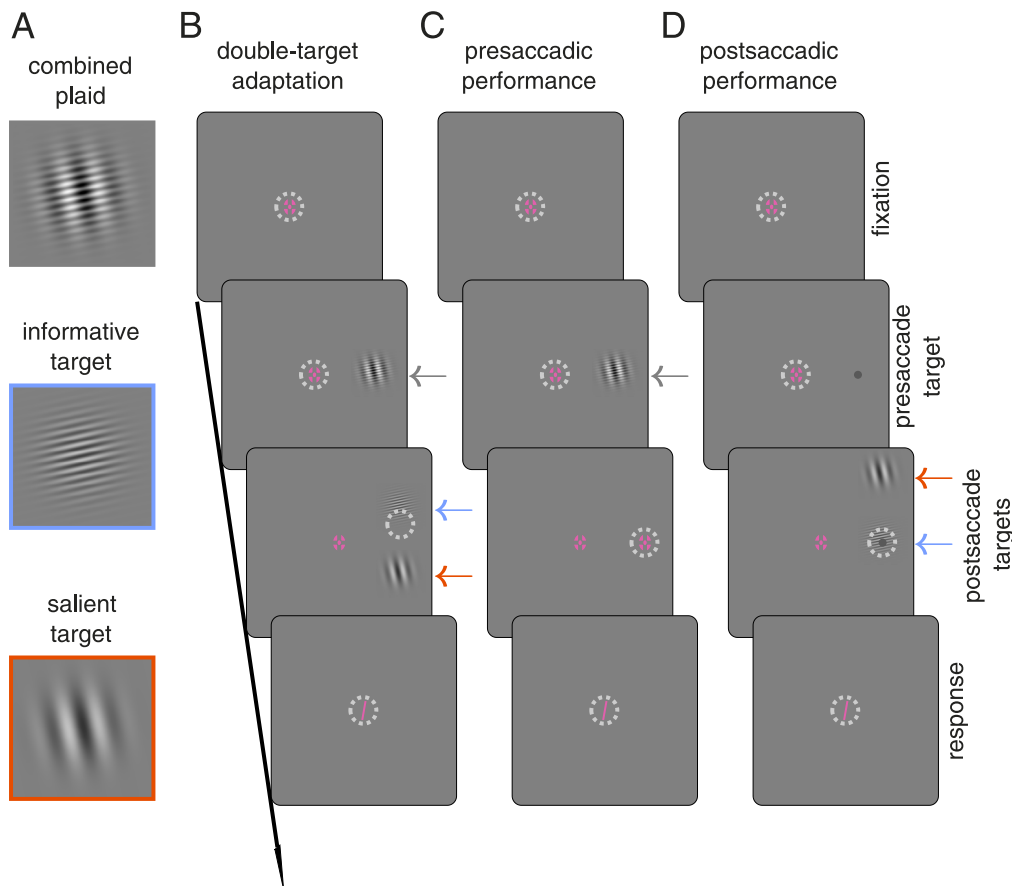
Figure 1. Stimuli and trial procedure. (A) Stimuli used in the present study. Gray and colored frames were added for illustrative purposes. (B–D) Trial procedure for the (B) double-target adaption task as well as the (C) pre- and (D) postsaccadic performance tasks. Gray and colored arrows, as in (A), indicate the identity of a target and its vertical position. Light-gray dashed circles depict the current gaze position and were not displayed during the experiment. (B) In the double-target adaptation task, participants fixated a central fixation cross at the beginning of a trial and the combined plaid appeared 12.5° to the right (presaccade target). During adaptation, the plaid was split into its two components, the informative and salient targets, as soon as participants moved their eyes to the plaid (postsaccade targets). One target was consistently shifted upward and the other downward by ±2°. Afterwards, participants judged the orientation of both components one after the other (response). At the end of a trial, participants received feedback about their perceptual judgment (not shown in figure). They received one point when they judged both orientations correctly. (C) In the presaccadic performance task, the plaid was replaced by a fixation cross during the saccade. (D) In the postsaccadic performance task, participants saccaded to a dark-gray dot and the two gratings appeared during the saccade. Gratings were vertically off by 4°, but unlike in (B), their relative position was not consistent across trials—they could appear at five different vertical locations: +4, +2, 0, −2, −4. Figure and stimuli are not drawn to scale.

identification should depend more strongly on the saccade endpoint. Thus, saccade endpoints closer to this second postsaccadic target should help to judge both orientations correctly. Therefore, although both targets were equally task-relevant, the overall perceptual performance should depend more strongly on this second, low-contrast, high-spatial-frequency target. Thus, we refer to this second target as the *informative target* (Figure 1A).

In three experiments we measured saccade endpoints using the double-target adaptation task. In Experiment 1, we measured saccade adaptation using sequential perceptual judgments. We compared endpoints to optimal endpoints derived from separately measured pre- and postsaccadic performance values. Moreover, we recorded adaptation time courses without a perceptual task and when only one of the two task-relevant targets appeared after the saccade. In Experiment 2, we measured endpoints in the double-target adaptation task when both postsaccadic targets were judged simultaneously. In Experiment 3, we recorded endpoints when the two postsaccadic targets split randomly with regard to their direction. This allowed us to test whether we could observe gradual oculomotor learning even when there is no possibility to strategically adjust saccade endpoints.

Experiment 1: Double-target adaptation with sequential judgments

When multiple task-relevant targets compete to be selected as a future saccade target, do we learn to adjust our saccades so that saccade endpoints maximize the information available for visual perception? If yes, then participants should adapt toward the informative target in our double-target task. Moreover, the amount of adaptation should depend on the individual saccade endpoint variability, how well participants can identify both targets before the saccade using peripheral vision, and how strongly postsaccadic perceptual performance depends on the actual saccade endpoint for each target. Here, we test double-target adaptation and compare it to optimal endpoints based on these three variables. Additionally, we compare double-target adaptation to adaptation with just one postsaccadic target (salient target only and informative target only) and to adaptation without any perceptual task. All adaptation time courses were compared by fitting a gradual-learning model (Srimal, Diedrichsen, Ryklin, & Curtis, 2008) and a two-component model (Schütz et al., 2014) that combines gradual learning and an immediate strategic endpoint adjustment.

Methods

Participants

Participants of all experiments provided written informed consent prior to testing and were unaware of the purpose of the experiment. All experiments were conducted in accordance with the ethical guidelines laid down in the 1964 Declaration of Helsinki and were approved by the local ethics committee of the Department of Psychology of Marburg University (Proposal 2017-27k). All participants had normal or corrected-to-normal vision. We recorded 16 participants for Experiment 1, one of whom was excluded because perceptual performance was below chance, and the participant stated after the experiment that he/she had difficulties performing the experiment. The remaining 15 participants (12 women, three men) had a mean age of 23 years (age range = 18–29, all right-handed). We recorded eight different participants for each of the three control conditions: no-task (three women, five men; all right-handed, mean age = 26, age range = 22–32), salient-only (all women; mean age = 22, age range = 19–28, one left-handed), and informative-only (all women; mean age = 23, age range = 19–31, all right-handed). Participants received course credit for participation or were compensated with 8 €/h.

Setup, apparatus, and stimuli

Experiments were conducted using the Psychtoolbox (Brainard, 1997) in MATLAB (R2016a; The Math-Works, Natick, MA) and presented on a VIEWPixx monitor (VPixx Technologies Inc., Saint-Bruno, Canada) at a viewing distance of 60 cm. The monitor had a spatial resolution of 1920 × 1080 pixels and a size of 51.5 × 29 cm. We recorded eye movements of the right eye using a desktop-mounted EyeLink 1000 (SR Research Ltd., Ottawa, Canada) with a sampling rate of 1000 Hz and the Eyelink Toolbox (Cornelissen, Peters, & Palmer, 2002). We used the combination of crosshair and bull's-eye as a fixation cross (Thaler, Schütz, Goodale, & Gegenfurtner, 2013).

Stimuli were two Gabor patches, the informative and the salient target (Figure 1A). They were either presented separately or overlaid (i.e., summed) as a plaid stimulus. In the latter case we refer to these overlaid targets as the plaid's *components*. The two targets differed with regard to their spatial frequency and their contrast. The salient target's underlying sine-wave grating had a spatial frequency of 1.5 c/° and a Michelson contrast of 0.6, whereas the informative target had a spatial frequency of 9 c/° and a contrast of 0.3. These stimuli characteristics were chosen so that the salient target could easily be identified using peripheral vision, whereas the informative target could be identified only when the fovea was brought in close proximity. Both targets were seen through a Gaussian window with a standard deviation of 0.4°. Thus, the distance from −2 to +2 standard deviations of this Gaussian envelope was 1.6°.

Consistent within one participant and balanced between participants, each of the two targets deviated in its orientation from a different cardinal axis. Deviations were 12° clockwise (cw) or counterclockwise (ccw) relative to the cardinal axes. For example, for one participant the informative target's orientation was either 12° cw or ccw relative to vertical throughout all trials and the salient target's orientation was either 12° cw or ccw relative to horizontal. The two components' orientation deviations were independent of each other. Bars during the response period also deviated by 12° from the cardinal axes.

Design and procedure

The main part of Experiment 1 comprised three tasks: a double-target adaptation task, a peripheral presaccadic performance task, and a foveal postsaccadic performance task. The purpose of the latter two was to measure presaccadic peripheral and postsaccadic foveal performance separately. This served as a manipulation check and allowed us to predict optimal saccade endpoints during the adaptation phase (see Eye movement and data analysis). Additionally, we re-

corded three control conditions, each with a distinct group of participants: the no-task, salient-only, and informative-only conditions. The no-task condition was mostly identical to the double-target adaptation task, except that participants did not have to perform a perceptual task. The salient-only and informative-only conditions were also mostly identical to the double-target adaptation task, except that after the saccade only one of the two targets was displayed and had to be evaluated.

Double-target adaptation task: The double-target adaptation task consisted of 200 trials. After calibrating the eye tracker, participants could start the experiment by pressing the space bar on a keyboard. The experiment was automatically paced. Thus, at the end of a trial, the experiment automatically proceeded to the next trial. After Trials 50, 100, and 150, we included a break of 10 s. During the break, the display turned black and participants were instructed to close their eyes. At the end of the break, three consecutive beep tones signaled participants that the experiment was about to continue.

At the beginning of a trial, a fixation cross was displayed at the screen center. After a uniformly distributed random interval between 1 and 1.5 s, a plaid stimulus appeared 12.5° to the right of the fixation cross. Participants had to look at the plaid and judge the orientation of its two components. During the initial baseline phase (Trials 1–50), the plaid stimulus remained at its location and did not change during the saccade. In the adaptation phase (Trials 51–200), however, the plaid stimulus was split into its two components during the saccade. One of these two targets was shifted upward and the other downward by 2°. Within every participant, the shift direction of every target was consistent. Between participants, we balanced the shift directions of the salient and informative targets.

Because the presaccadic target was exchanged during the saccade, the presentation duration of the presaccadic target (plaid; row 2 in Figure 1B) thus depended on the saccade latency in every trial. The two postsaccadic targets (row 3 in Figure 1B) were removed from the screen as soon as their presentation duration exceeded 100 ms. Additionally, we restricted the overall target presentation (presaccadic + postsaccadic; i.e., rows 2 and 3 in Figure 1B) to a maximum of 500 ms to limit the maximum trial duration. Thus, if the saccade latency was below 400 ms, the two postsaccadic targets were shown for 100 ms. Please note that only trials with saccade latencies below 400 ms were considered for the final analysis (see Eye movement and data analysis). If the saccade latency was in the range of 400–500 ms, the two postsaccadic targets were displayed for less than 100 ms. If no saccade was made within 500 ms after

onset of the presaccadic target, the two postsaccadic targets were not shown during that trial.

After stimulus removal, participants had to judge the orientation of the informative and salient target. A bar appeared at the screen center and participants had to indicate via two buttons on the keyboard whether or not the displayed bar matched either of the two directions. After the first response, a second bar appeared and participants had to indicate whether or not the bar's orientation matched the orientation of the remaining target. For every participant, the response order was consistent across the whole task. Across participants, the response order was balanced. Thus, half of the participants judged the informative target first, whereas the other half first responded on the salient target. For every response, participants were given 2.5 s.

After every trial, participants received feedback about their trial performance. The visual feedback contained the score from the current trial as well as their overall score, separated by a vertical bar (e.g., "+1 | 42"), and was displayed for 2.4 s. Participants received one point if they judged both targets correctly, if their gaze was located at the fixation cross during target onset, and if their saccade latency was between 80 and 400 ms. If any of the three criteria was not fulfilled, they lost one point. If there was a fixation or latency error, the feedback was displayed in red, otherwise in black. A high or a low beep tone was played to signal to participants which of the two targets was judged incorrectly. If both judgments were wrong, the two beeps were played consecutively.

Before the actual task, participants performed 30 demonstration trials. This demo contained two breaks (after Trials 10 and 20), four adaptation trials (Trials 14–17), and 26 baseline trials. For the first 10 trials, the foveal presentation duration was 0.5 s, the overall maximum stimulus presentation was 0.9 s, and the maximum response time per judgment was 4 s. For Trials 11 through 20, we increased the trial pace (0.3-s maximum foveal presentation, 0.6-s maximum overall presentation, 3-s maximum response time). For the last 10 trials, the pace was set like in the actual experiment. If a participant signaled that they were not yet confident with their task, the demo was repeated.

Presaccadic and postsaccadic performance tasks: The pre- and postsaccadic performance tasks consisted of 80 and 120 trials, respectively, and included breaks after every 40 trials. The trial procedure was identical to the double-target adaptation task with regard to timing, response, and feedback, but differed with regard to the presented stimuli. In the presaccadic performance task, the plaid stimulus disappeared during the saccade and was replaced by a fixation cross. Thus, the postsaccadic stimulus contained no information about orientation and participants had to base

their perceptual judgments on presaccadic peripheral information only.

In the postsaccadic performance task, a dark-gray dot appeared at the target location. During the saccade, the informative and salient targets appeared on the screen at a horizontal eccentricity of 12.5°. The two targets were vertically off by 4° and appeared at one of five possible location combinations along the vertical: (+4, 0), (+2, −2), (0, −4), (−2, +2), (−4, 0), with 0 being the vertical location of the dot and positive numbers referring to the upper screen half. In contrast to the double-target adaptation task, it was not consistent which target was shifted upward and which was shifted downward. If a Gabor appeared at the dot location—thus, (+4, 0) and (0, −4)—then the dot was displayed on top the Gabor. Thus, in the postsaccadic performance task participants solved the perceptual task solely based on postsaccadic (para)foveal information. For both targets, we thus measured performance in the fovea (0) as well as for 2° and 4° in the parafoveal region.

No-task condition: The no-task condition was identical to the double-target adaptation task with regard to trial number, timing, and stimuli, but here participants had no perceptual task at hand. After the foveal stimuli were extinguished, two bars appeared consecutively at the screen center. Every bar was presented for 1 s, the approximate average response duration measured in the double-target adaptation task. There was no feedback. Instead, the central fixation cross was shown for a longer duration at the beginning of the trial. Due to the effects of time on saccade adaptation (Ethier, Zee, & Shadmehr, 2008; Kim, Oh, & Schweighofer, 2015), we aimed to have a trial duration that was similar to the average trial duration in the double-target adaptation task. The average trial duration in the no-task condition was 8.6 s, and in the double-target adaptation task it was 8.5 s.

Salient-only and informative-only conditions: These two conditions differed from the double-target adaptation task only with respect to the fact that only the salient (salient-only) or the informative target (informative-only) was shown and had to be judged postsaccadically. The presaccadic target was the plaid containing both targets. During the saccade, one of the two targets consistently shifted up or down by 2°, whereas the other one was removed from the screen.

Eye movement and data analysis

We used the EyeLink algorithm to detect saccade onsets. Latencies were defined as the first saccadic sample relative to target onset. For the adaptation tasks, we considered only trials in which gaze did not deviate more than 2° from the fixation-cross location at any time from −20 to 80 ms relative to the plaid's onset in the periphery. Moreover, we included trials with

latencies above 80 ms and below 400 ms, trials with horizontal amplitudes above 8.75° (i.e., gain above 0.7), and trials with only one saccade during stimulus presentation. In the double-target adaptation task, 90.5% of all trials were considered for the final analyses. We recoded vertical endpoints when the informative target was shifted downward during adaptation. Thus, positive vertical endpoints always denote a shift toward the informative target, and negative vertical endpoints denote a shift toward the salient target. Endpoints of every individual were baseline-corrected by subtracting the mean vertical endpoint during the baseline phase (Trials 1–50).

Figures of adaptation time courses were complemented with a moving average. Moving averages were computed separately for every phase of 50 trials. For every trial, we averaged the current trial with up to (if available) three previous and subsequent trials. For group comparisons, we used *t* tests and Wilcoxon signed-rank tests if the normality assumption was violated. Inferential statistical tests were conducted in SPSS (Version 25; IBM Corp., Armonk, NY). All other analyses were conducted in MATLAB.

Receiver-operating characteristic analysis: For receiver-operating characteristic (ROC) analyses, we split trials from the double-target adaptation task into correct (both targets judged correctly) and incorrect trials. We sorted vertical saccade endpoints for correct and incorrect trials and computed hits and false alarms for 50 linearly spaced criteria from the minimum to the maximum vertical endpoint. Hits were defined as the proportion of correct trials above a criterion, and false alarms as the proportion of incorrect trials above a criterion. These 50 combinations of hits and false alarms define the ROC. We computed the area under the ROC curve (AUC) as an index of discriminability between correct and incorrect saccade endpoint distributions. For identical distributions, the AUC would yield a value of 0.5. If correct trials go along with endpoints closer to the informative target, this would go along with AUC values above 0.5.

Modeling optimal endpoints: We modeled perceptually optimal vertical endpoints in the double-target adaptation task using optimal decision theory (Trommershäuser, Maloney, & Landy, 2008). Optimal vertical endpoints maximize task performance and were modeled based on an individual's endpoint variability in the baseline phase (first 50 trials of the double-target adaptation task) as well as performance in the pre- and postsaccadic performance tasks. Figure 2B and 2E illustrates the procedure and results of perceptually optimal endpoint prediction.

In a first step, we subtracted chance performance from the pre- and postsaccadic performance data (Figure 2A and 2B): If a participant correctly identifies a target in an *n*-alternative forced-choice task with a
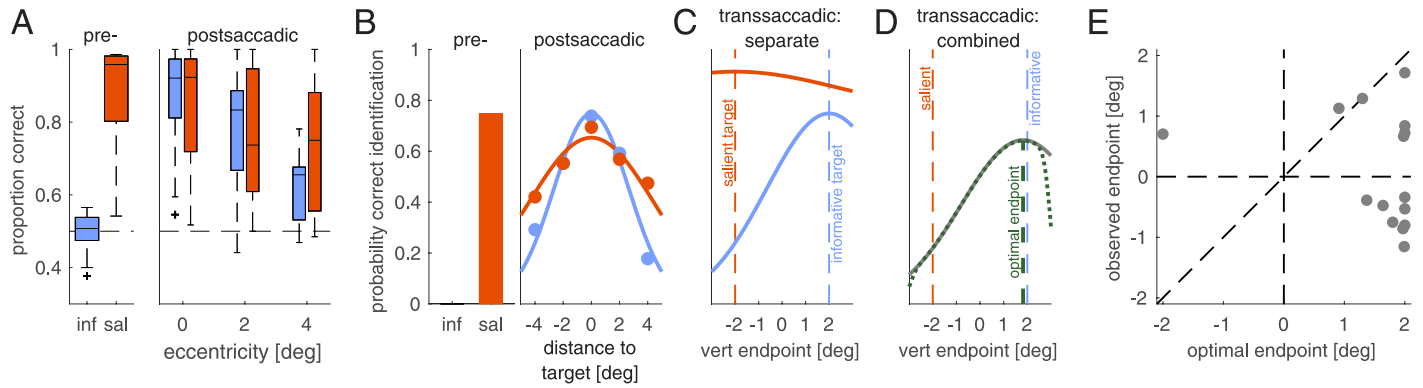
Figure 2. Experiment 1: pre- and postsaccadic performance tasks and optimal endpoint prediction. (A) Box plots depicting performance in the presaccadic (left panel) and postsaccadic (right panel) performance tasks for the informative (blue) and salient (orange) targets. The horizontally dashed line indicates chance. (B) Optimal endpoints were computed based on performance in the presaccadic (left) and postsaccadic (right) performance tasks. The depicted data are aggregated values from 2A with chance subtracted. Note that the postsaccadic target was displayed for shorter durations than the target in the presaccadic performance task and therefore can yield lower performance despite lower retinal eccentricity. (C) The values in 2B were used to compute transsaccadic identification performance (thick lines) separately for each target. Dashed vertical lines denote the center of the targets. (D) The solid gray line denotes transsaccadic identification performance for the joint task (both targets judged correctly) for a single saccade endpoint. To compute expected performance not only for a single endpoint but for the whole endpoint distribution, we additionally considered the vertical saccade-endpoint variability from the baseline phase (dotted green line). The dashed green vertical line is the optimal endpoint (1.82°) for the aggregated pre-/postsaccadic performance data and the mean endpoint variability. (E) Observed endpoints during late adaptation (Trials 151–200) as a function of optimal endpoints. Every data point denotes an individual participant. Optimal endpoints fall along the diagonal.

probability of p, then p reflects both correct identifications and correct guessing. For an n-alternative forced-choice task, the probability p' of correctly identifying a target without guessing can be estimated as

$$p' = p - \frac{(1-p)}{(n-1)}. \quad (1)$$

In the second step, we fitted two Gaussians to the data from the postsaccadic performance task, one for the salient and one for the informative target (Figure 2B). The Gaussians had two free parameters: standard deviation and a scaling parameter. The latter was multiplied with the Gaussian to scale it up and down. Gaussians and p' values were restricted to lie between 0 and 1.

Third, we predicted transsaccadic identification performance for both targets separately (Figure 2C). The probability of correctly identifying a target when presaccadic peripheral and postsaccadic foveal information is available can be estimated as

$$p'_t(d) = 1 - \left(1 - p'_p\right)\left(1 - p'_f(d)\right), \quad (2)$$

where $p'_f(d)$ and $p'_t(d)$ denote postsaccadic and transsaccadic identification performance as a function of the postsaccadic distance d between target and fovea, and p'_p denotes the presaccadic peripheral identification performance. Equation 2 assumes that

pre- and postsaccadic information arise from independent samples. Transsaccadic perception of orientation has been successfully modeled by assuming independence of pre- and postsaccadic vision (Ganmor, Landy, & Simoncelli, 2015; Wolf & Schütz, 2015; Stewart & Schütz, 2019). The lower asymptote of the transsaccadic performance (see Figure 2C) for every target is thus given by the presaccadic performance p'_p.

In a fourth step, we predicted the transsaccadic performance for the combined judgment of both targets, $p'_{t;c}$, as a function of the vertical saccade endpoint s. Therefore, we combined first the transsaccadic probability of identifying the informative target, $p'_{t;i}$, as a function of the postsaccadic distance d_i between the eye and the informative target, and second the transsaccadic probability of identifying the salient target, $p'_{t;s}$, as a function of d_i:

$$p'_{t;c}(s) = 1 - \left(1 - p'_{t;i}(d_i)\right)\left(1 - p'_{t;s}(d_s)\right). \quad (3)$$

Equation 3 yields the probability of identifying a target for a single vertical saccade endpoint s. In the fifth and final step, we modeled performance for a whole-endpoint distribution by considering the individual variability in saccade endpoints. We assumed that vertical saccade endpoints were normally distributed. Thus, the probability p_s of making a saccade to a certain vertical endpoint s depends on the saccade

endpoint variability σ_s and the mean endpoint μ:

$$p_s(s|\mu, \sigma_s) = \frac{1}{\sigma_s\sqrt{2\pi}} e^{\frac{-(s-\mu)^2}{2\sigma_s^2}}. \quad (4)$$

The integral of the multiplication of the endpoint distribution with the transsaccadic probability of identifying both targets, $p'_{t;c}$, yields the expected probability of identifying both targets for a given mean endpoint μ (green dotted line in Figure 2D). The optimal mean endpoint is given by the maximum of the resulting distribution (green dashed vertical line in Figure 2D).

Saccade adaptation models: We fitted two adaptation models to the adaptation time courses, based on the state-space model by Srimal et al. (2008) with gradual learning and an extended version that adds an immediately adapting process to the gradually adapting process and was introduced by Schütz et al. (2014). We chose these two models, because the model by Srimal et al. (2008) is appropriate to model saccade adaptation with random target steps (see Experiment 3). The two-component model, on the other hand (Schütz et al., 2014) allows inference of whether endpoints are gradually adjusted (like in a classical double-step paradigm) in addition to an immediate change in saccade endpoints due to task requirements. Other saccade adaptation models—for instance fast and slow learning (Smith, Ghazizadeh, & Shadmehr, 2006; Ethier et al., 2008)—would have required implementing multiple delays and error-clamp trials. Thus, fitting this model to our data could have resulted in uninformative parameter combinations.

According to the gradual-learning model by Srimal et al. (2008), the saccade gain y_n displayed at trial n is determined by the adaptive state of the adaptor z_n and random noise ε_n:

$$y_n = z_n + \varepsilon_n. \quad (5)$$

The adaptive state of the next trial, z_{n+1}, is determined by updating the current predicted saccade gain z_n. It is updated by a proportion B of the difference between the current gain z_n and the target position u_n:

$$z_{n+1} = z_n - B(z_n - u_n). \quad (6)$$

Parameter B thus determines the learning rate of the system. Since our participants were confronted with two targets, we replaced the target position u_n with an aim point $u_{a,n}$. The aim point was a weighted imaginary target between the informative target $u_{i,n}$ and the salient target $u_{s,n}$:

$$u_{a,n} = W(u_{i,n}) + (1 - W)u_{s,n}. \quad (7)$$

The variable W denotes the weight given to the informative target by a participant. If $W > 0.5$, then a

participant prioritized the informative target. A preference for the salient target would be reflected by $W < 0.5$. The closer W is to 1 (0), the stronger the preference is for the informative (salient) target.

The two-component model by Schütz et al. (2014) additionally distinguishes between an immediate adjustment z_i and a slowly adapting process z_s. The relative contribution of both processes to a saccade's gain is determined by the weight I:

$$y_n = Iz_{i,n} + (1 - I)z_{s,n}. \quad (8)$$

The state of the slow process is updated every trial by a proportion S of the difference between the adaptation state $z_{s,n}$ and the aim point $u_{a,n}$:

$$z_{s,n+1} = z_{s,n} - S(z_{s,n} - u_{a,n}). \quad (9)$$

Like the B parameter in the gradual-learning model (Equation 6), the S parameter determines the amount of gradual learning. The state of the immediate process is also updated from trial to trial by the full difference between adaptation state and target position:

$$z_{i,n+1} = z_{i,n} - (z_{i,n} - u_{a,n}). \quad (10)$$

To compare model fits, we computed information weights (Burnham & Anderson, 2002) based on the Bayesian information criterion. Information weights specify the relative likelihood of each of the two models and range between 0 and 1. Higher values for a particular model indicate that this model is superior over the other model. We then compared information weights across all participants by using Wilcoxon signed-rank tests.

Results

Pre- and postsaccadic performance

We measured saccade adaptation in a double-target adaptation task, where a presaccadic plaid stimulus splits vertically into its two components during the saccade. One of these two targets is highly salient, whereas the other is supposed to be more informative for the task at hand. After every trial, participants had to respond to the orientation of the two targets sequentially. They received a score point only when they judged both target orientations correctly. For all 15 participants in our double-target adaptation task, we measured pre- and postsaccadic performance separately in a presaccadic and a postsaccadic performance task, where the targets were displayed only either before or after the saccade (Figure 2A). The results from these two experiments also served as a manipulation check, because they allow us to test whether the informative target was indeed hardly visible in the periphery and whether postsaccadic

performance on the informative target depended more strongly on the vertical saccade endpoint.

In the presaccadic performance task (left panel in Figure 2A), mean performance for the informative component of the plaid was at chance level ($M = 0.5$, $SD = 0.05$). Presaccadic performance for the plaid's salient component was $M = 0.87$ ($SD = 0.15$), different from chance performance, $t(14) = 9.63$, $p < 0.001$, and better than the informative component, $t(14) = 9.7$, $p < 0.001$. This highlights that the informative component (unlike the salient component) could not be identified with presaccadic peripheral vision.

In the postsaccadic performance task, participants saccaded to a gray dot, and the two targets (salient and informative) appeared with a vertical distance of 4° but different absolute positions. Each of the two targets could be displayed at the saccade target location (eccentricity of 0°), 2° away, or 4° away. The right panel in Figure 2A depicts postsaccadic performance for the two targets and the three eccentricities. Descriptively, performance decreased with postsaccadic eccentricity, and this decrease in mean values was more pronounced for the informative (0°: 0.87, 2°: 0.79, 4°: 0.62) compared to the salient target (0°: 0.85, 2°: 0.78, 4°: 0.73). We analyzed postsaccadic performance in a 3×2 analysis of variance (ANOVA) with the two repeated-measures factors of target (informative, salient) and eccentricity (0°, 2°, 4°). The ANOVA revealed a significant main effect of eccentricity, $F(2, 28) = 27.19$, $p < 0.001$, and most importantly, a significant Target × Eccentricity interaction, $F(2, 28) = 4.37$, $p = 0.022$. This shows that successful orientation discrimination depended more strongly on the postsaccadic target distance for the informative than for the salient target. There was no main effect of target ($p > 0.5$).

Double-target adaptation

Seven of our 15 participants adapted toward the informative target (mean vertical endpoint of the last 50 adaptation trials: $M = 1°$, $SD = 0.39°$, range = 0.67°–1.71°), and the remaining eight adapted toward the salient target ($M = -0.66°$, $SD = 0.28°$, range = −0.34° to −1.15°). Figure 3A depicts aggregated adaptation data for the participants who adapted toward the informative target (blue) and the salient target (orange). All individual adaptation time courses can be found in Supplementary Figure S1.

Closer inspection of the double-target adaptation data revealed that the adaptation direction almost perfectly coincided with the order in which participants had to respond to the two targets (see Supplementary Figure S1 for individual adaptation courses). The response order was consistent within every participant but balanced between participants (i.e., eight of our 15 participants always judged the informative target first

and the salient target second). All participants but one adapted to the target they had to judge first. One participant who judged the informative target first adapted toward the salient target (Supplementary Figure S1). One explanation for this twofold adaptation pattern might be that participants focus more strongly on one of the two targets when performing the task. If this is the case, then it should also be reflected in performance during the double-target adaptation task. We analyzed perceptual performance during the baseline phase (Trials 1–50), because here the target did not yet split, and performance was not yet affected by adaptation direction. Overall baseline performance (both targets judged correctly, chance = 0.25) was $M = 0.7$ ($SD = 0.2$). For the individual targets (chance = 0.5), mean performance was $M = 0.87$ ($SD = 0.11$) for the informative target and $M = 0.85$ ($SD = 0.17$) for the salient target. For every individual, we computed the performance difference between the informative and salient targets, and thus positive values indicate better performance for the informative target (Figure 3C). The performance difference was $M = 0.14$ for informative-first responders and $M = -0.12$ for salient-first responders, $t(13) = 2.97$, $p = 0.011$ (independent-samples t test). Thus, participants showed better baseline performance for the target they had to respond on first. This indicates that they indeed prioritized one of the two targets based on response order.

We fitted two adaptation models (see Methods for details) to the data from the double-target adaptation task, based on the state-space model by Srimal et al. (2008) and its extension introduced by Schütz et al. (2014). The former describes saccade adaptation as a gradual learning process, whereas the latter includes an additional immediate adjustment as a second component. We adjusted both models to our two-target scenario by introducing an imaginary target in between the salient and informative targets.

The location of the imaginary target was determined by means of a relative target weight between the two locations. Mean parameter values for both models and all adaptation conditions can be found in Supplementary Figure S2. Model fits were evaluated using information weights based on the Bayesian information criterion. The two-component model including an immediate adjustment provided a better fit to the data for 12 out of 15 participants, $z = -2.9$, $p = 0.004$ (Wilcoxon signed-rank test).

Did adaptation time courses differ for participants who adapted to the informative versus the salient target? We compared model parameters for the two-component model for the two adaptation directions. The immediate-adjustment parameter quantifies how much of the target distance is compensated immediately (Figure 3A), whereas the gradual-learning parameter quantifies how much of the distance to the
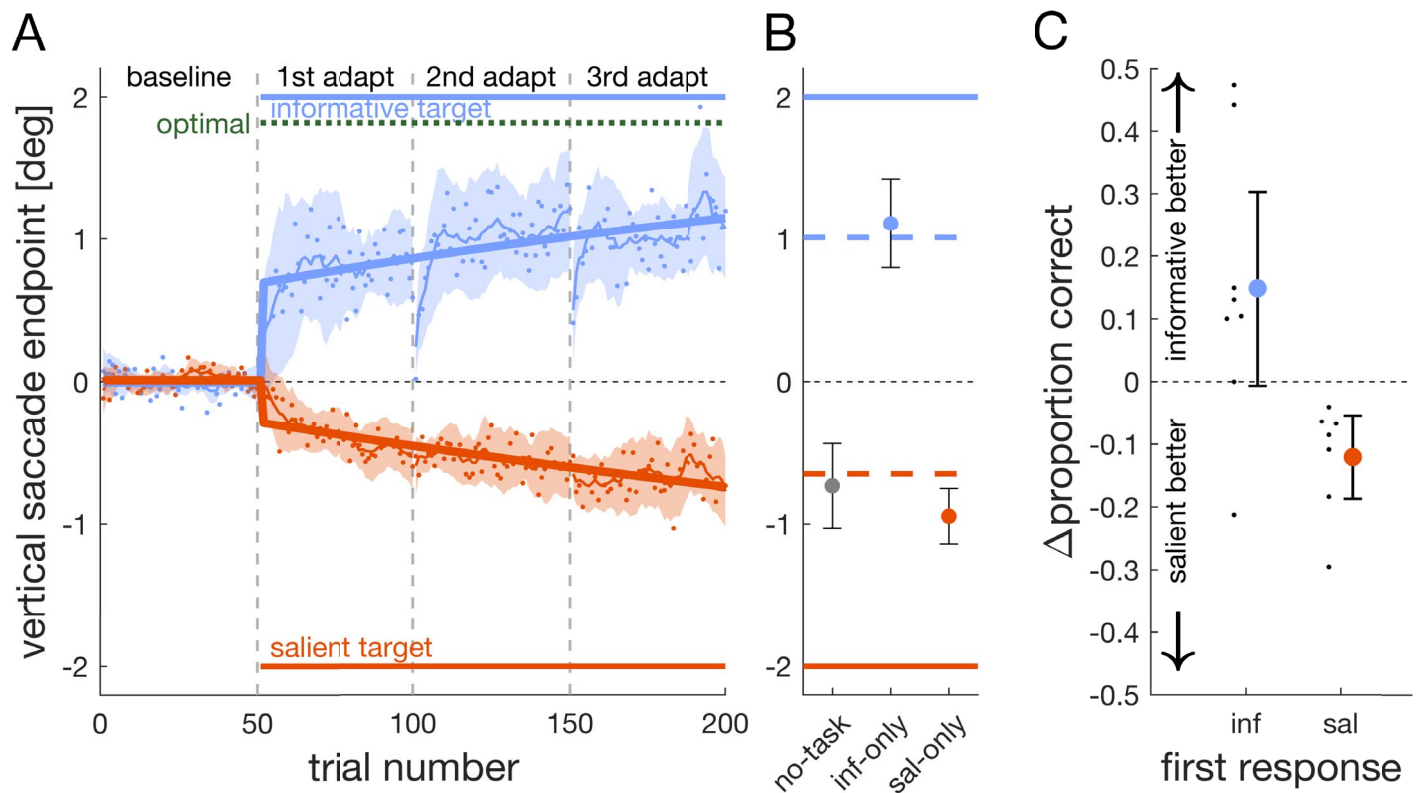
Figure 3. Experiment 1: main results. (A) Aggregated adaptation time courses and model fits split up according to adaptation direction (informative: blue; salient: orange). Blue and orange data points are aggregated vertical saccade endpoints for a given trial number. Thin lines denote the running average and shaded regions the 95% confidence intervals of between-participants variability. Participants mostly adapted toward the target they had to respond on first. Thick lines are the model fit of the two-component model (Equations 8–10) on the aggregated data. The green dotted line indicates the mean optimal saccade endpoint derived for the mean eye-movement variability during the baseline phase and the mean discrimination performance in the pre- and postsaccadic performance tasks. (B) Mean vertical saccade endpoints based on the last 50 adaptation trials for the three different control conditions (gray: double-target adaptation without a task; blue: informative-only; orange: salient-only). Solid lines indicate the target locations, dashed lines the mean vertical endpoints of the last 50 adaptation trials from the data in (A). (C) Baseline performance as a function of response order: difference in proportion correct between the informative and the salient target separately for participants who first responded on the informative (blue) or the salient (orange) grating. Blue and orange data points depict the mean, and black dots are data from individual participants. Error bars in (B–C) are 95% confidence intervals of between-participants variability.

target is adapted over the whole adaptation period (Schütz et al., 2014). The contribution of the immediate adjustment was $M = 0.32$ ($SD = 0.24$) for participants adapting to the informative target and $M = 0.14$ ($SD = 0.11$) for participants adapting to the salient target. The slow-learning parameter's contribution was $M = 0.0037$ ($SD = 0.0032$) and $M = 0.0023$ ($SD = 0.0025$), respectively. Neither the contribution of immediate adjustment, $t(13) = 0.96$, $p = 0.353$, nor that of slow learning, $t(13) = 1.94$, $p = 0.074$, was statistically different between the two adaptation directions (independent-samples t tests).

However, one distinction between adaptation toward the salient and the informative target becomes obvious from Figure 3A: Adaptation toward the informative target seems to decay during the 10-s breaks in which participants were asked to close their

eyes (vertical dashed lines in Figure 3A). To analyze this decay, we calculated the difference in vertical endpoints between the first two trials after a break and the last two trials before a break. We expressed this difference relative to the presaccadic target location, so that for both adaptation directions negative values would indicate a shift toward the presaccadic target location and positive values a stronger adaptation after breaks. For adaptation toward the informative target, the mean difference score was $M = -0.41$ after the first adaptation break and $M = -0.64$ after the second adaptation break. For adaptation toward the salient target it was $M = 0.02$ and $M = 0.02$. We compared these values using a 2×2 ANOVA with the within-participant factor of break (1st to 2nd adapt vs. 2nd to 3rd adapt) and the between-participants factor of adaptation direction. The ANOVA revealed a signifi-

cant main effect of adaptation direction, $F(1, 13) = 7.18$, $p = 0.019$. There were no other effects in the ANOVA (all ps > 0.4). Thus, adaptation toward the informative target decayed partially during the 10-s breaks.

Perceptual performance depended on vertical saccade endpoint

Average performance during the adaptation phase was $M = 0.7$ ($SD = 0.15$). To test whether performance in the double-target adaptation task depended on the vertical saccade endpoint, we computed ROC curves for every individual. To do so, we first divided all adaptation trials into correct (both targets judged correctly) and incorrect trials (both or one target judged incorrectly). The vertical endpoint distributions of correct and incorrect trials were then compared using ROC analyses (Figure 4). AUC values above 0.5 indicate better perceptual performance for endpoints close to the informative target, and below 0.5 indicate better performance for endpoints closer to the salient target. Values of 0.5 indicate that performance did not depend on the vertical saccade endpoint.

The average AUC value was $M = 0.54$ ($SD = 0.07$), significantly above 0.5, $t(14) = 2.60$, $p = 0.021$. Thus, saccade endpoints closer to the informative target went along with better perceptual performance. In a next step, we wanted to know whether not only the overall performance but also the perceptual performance of the two individual targets depended on the vertical saccade endpoints. To do so, we repeated the same ROC analysis, but this time we split trials based only on the judgments concerning either the informative or the salient target. Thus, we compared endpoint distributions for trials in which the informative (salient) target was judged correctly with those in which it was incorrect, independent of whether the salient (informative) target was judged correctly or not. When trials were split based on responses regarding the informative target, the average AUC value was $M = 0.57$ ($SD = 0.11$), significantly above 0.5, $t(14) = 2.47$, $p = 0.027$. When trials were split based on responses regarding the salient target, the average AUC value was $M = 0.50$ ($SD = 0.19$), not statistically different from 0.5, $t(14) = 0.01$, $p = 0.992$. Thus, saccade endpoints closer to the informative target led to better overall perceptual performance and better performance on the informative target, whereas we found no evidence that saccade
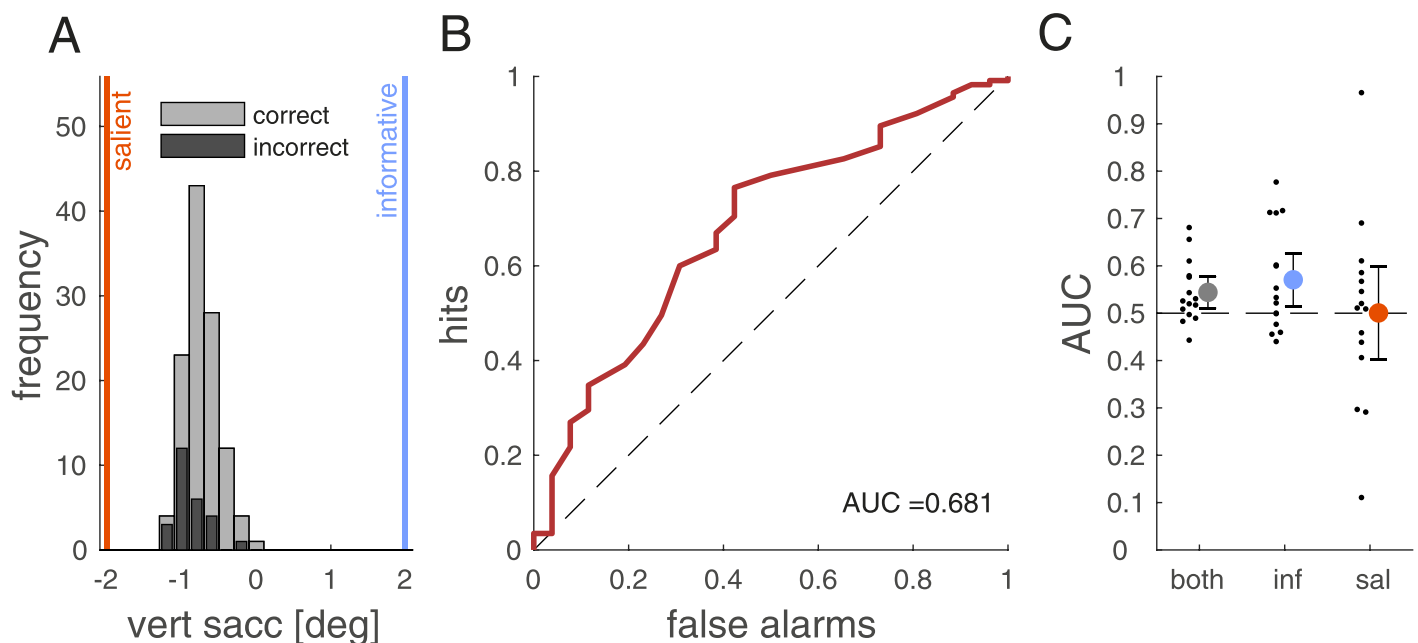

Figure 4. Experiment 1: better performance for saccades closer to the informative target. (A) Vertical endpoint distributions for correct (light gray) and incorrect (dark gray) trials during adaptation for a representative participant. In the displayed case, trials were considered correct when both gratings were judged correctly. (B) Receiver-operating characteristic curve for the data in (A): hits against false alarms for 50 linearly spaced criteria along the vertical-endpoint distributions. An area under the curve (AUC) above 0.5 indicates that saccades closer to the informative target go along with better discrimination performance. (C) Mean AUC values when both judgments were considered (left; gray data point) or when only responses with regard to the informative (center; blue data point) or salient (right; orange data point) target were considered. Error bars denote 95% confidence intervals of between-participant variability. Black dots are AUC values of individual participants.
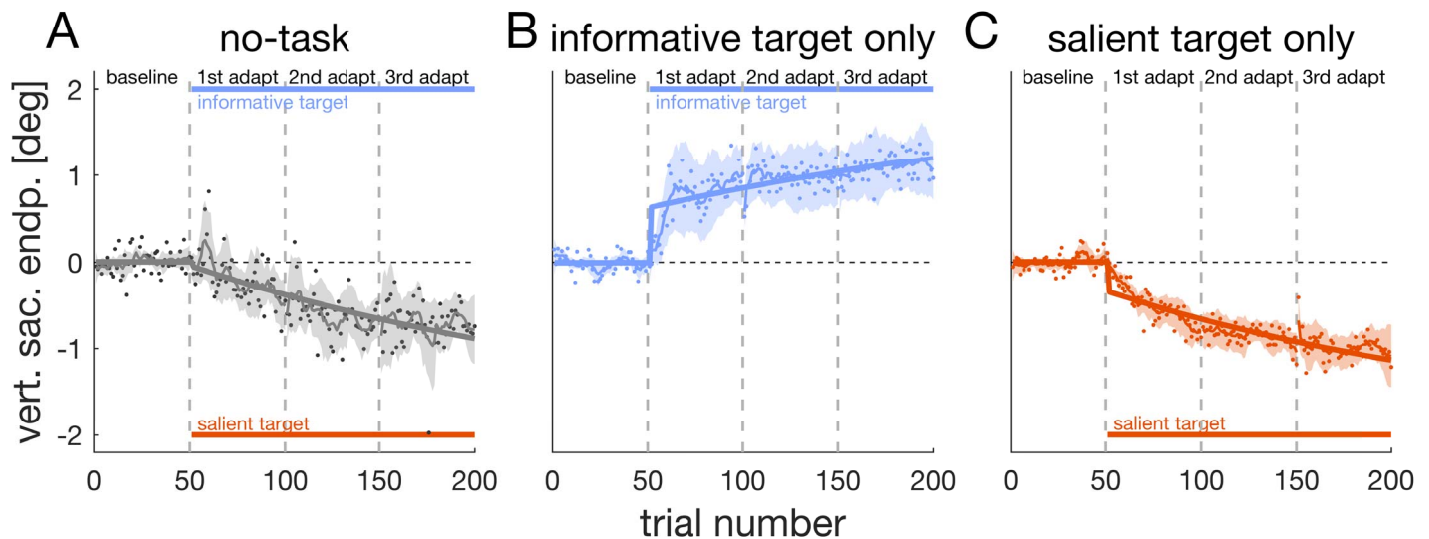
Figure 5. Experiment 1: adaptation control conditions. Aggregated adaptation time courses and model fits for the (A) no-task, (B) informative-only, and (C) salient-only condition. Thin lines denote the running average and shaded regions the 95% confidence intervals of between-participant variability. Thick lines are the model fit of the two-component model (Equations 8–10) on the aggregated data.

endpoints were related to performance with regard to the salient target.

Optimal endpoints

For every individual, we estimated the perceptually optimal vertical saccade endpoint based on their performance in the pre- and postsaccadic performance tasks and based on their saccade endpoint variability during the baseline phase (see Methods, Figure 2B through E). The mean optimal endpoint was $M = 1.53°$ ($SD = 1.03°$, median = 1.98°)—that is, very close to the informative target at 2°. For one outlier the predicted optimal endpoint was at the salient target at −2°, because this participant had close to chance performance for the salient target in the pre- and postsaccadic performance tasks. Figure 2E plots observed endpoints during late adaptation (Trials 151–200) against the predicted optimal endpoints. Observed endpoints deviated from optimal endpoints for participants who adapted toward the salient target, $t(7) = 16.23$, $p < 0.001$, but not for those who adapted toward the informative target, $t(6) = 0.3$, $p = 0.773$. Among the seven participants who adapted toward the salient target (positive values on the *y*-axis in Figure 2E), three achieved an endpoint that was close to optimal.

Predicting optimal endpoints also allows computation of an upper asymptote of perceptual performance. This asymptote is given by the predicted performance when participants would have immediately adjusted their vertical endpoints to the optimal endpoints. Thus, even when all participants achieved an endpoint that matched with the optimal one during late adaptation, perfor-

mance would still be lower than this upper asymptote when these endpoints were not reached immediately. Optimal perceptual performance was $M = 0.84$ ($SD = 0.15$). Actual performance during adaptation ($M = 0.7$, $SD = 0.15$) was significantly worse, $z = −2.95$, $p = 0.003$ (Wilcoxon signed-rank test). This was true for participants adapting toward the salient target, $z = −2.24$, $p = 0.025$, and those adapting toward the informative target, $z = −2.03$, $p = 0.043$. Thus, participants could have achieved better performance in the perceptual task by adapting (more immediately) toward the informative target (or toward the salient target for the one participant with an optimal endpoint at −2°).

Double-target adaptation without task and single-target adaptation

We measured three control conditions, each with a different group of participants, to compare the results of the double-target adaptation task to simpler adaptation conditions: double-target adaptation without a perceptual task (no-task, Figure 5A) and adaptation with only one postsaccadic target (informative-only and salient-only, Figure 5B and 5C). The no-task condition was identical to the double-target adaptation task, except that participants did not have to perform any perceptual task. Thus, neither target was task-relevant. Without a perceptual task, all participants adapted to the salient target. Mean vertical endpoints of the last 50 adaptation trials (Figure 3B) were $M = −0.73°$ ($SD = 0.43°$), statistically different from zero, $t(7) = 4.81$, $p = 0.002$, suggesting that saccade endpoints during late adaptation were different

from those during the initial baseline phase. However, endpoints in the no-task condition were not any different from the corresponding endpoints from participants adapting to the salient target in the double-target adaptation task (orange dashed line in Figure 3B), $t(15) = 0.43$, $p = 0.676$ (independent-samples t test).

Mean vertical endpoints during late adaptation were $M = 1.11°$ ($SD = 0.45$) for the informative-only condition and $M = −0.95°$ ($SD = 0.28°$) for the salient-only condition (Figure 3B). These values were different from zero for both groups—informative-only: $t(7) = 6.96$, $p < 0.001$; salient-only: $t(7) = 9.51$, $p < 0.001$. Whereas endpoints in the informative-only condition were not any different from vertical endpoints for late adaptation toward the informative target during double-target adaption, $t(13) = 0.46$, $p = 0.650$, vertical endpoints in the salient-only condition differed from their counterparts in the double-target adaptation task (Figure 3B), $t(15) = 2.18$, $p = 0.046$. This suggests a stronger adaptation magnitude toward the salient target with one compared to two targets.

We additionally fitted both adaptation models to the three control adaptation conditions (Figure 5). For the no-task condition, both adaptation models were superior to the other model for four out of eight participants each. Model parameters for the two-component model (Equations 8–10) were not any different from parameters for participants adapting to the salient target in the double-target adaptation task—contribution of immediate adjustment I: $t(14) = 1.38$, $p = 0.188$; of gradual learning S: $t(14) = 1.12$, $p = 0.283$.

For both single-target conditions, the two-component model provided a better fit to the data (informative-only: $z = −2.52$, $p = 0.012$; salient-only: $z = −2.1$, $p = 0.036$; Wilcoxon signed-rank test). To compare gradual learning between double- and single-target adaptation, we performed a 2×2 ANOVA with the between-participant factors adaptation target (informative vs. salient) and number of targets (single- vs. double-target) for each of the two parameters. For double-target adaptation, we grouped participants from the double-target adaptation task according to their adaptation direction. For the gradual-learning parameter, the ANOVA revealed no significant effects (all ps > 0.3). For immediate adjustment, it revealed no effect of target number ($p > 0.9$) but a main effect of adaptation direction, $F(1, 27) = 7.01$, $p = 0.013$; this was stronger with the informative target ($M = 0.32$, $SD = 0.24$) than the salient target ($M = 0.15$, $SD = 0.1$), $t(29) = 2.75$, $p = 0.015$ (Supplementary Figure S2A).

Discussion

We measured saccade adaptation in a double-target adaptation task where a presaccadic plaid stimulus splits vertically into its components, two Gabors, during horizontal saccades. One of the Gabor targets was highly salient and identifiable in the periphery, whereas the other, the informative target, could be identified only with near-foveal vision. Without a perceptual task, participants consistently adapted to the salient target (Figure 5A). When both postsaccadic targets were task-relevant, the direction of saccade adaptation strongly depended on the response order in which participants judged the two targets (Figure 3A). All participants but one adapted to the target they had to evaluate first. Even during the baseline phase, where the plaid had not yet split, performance was better for the target judged first (Figure 3C). During adaptation, endpoints closer to the informative target were associated with better performance within participants (Figure 4). Adaptation time courses during double-target adaptation were similar to those evoked with only one postsaccadic target, either the salient or the informative one (Figure 5B and 5C).

However, it is not possible to distinguish whether participants adapted toward the informative target in order to maximize the informational value or based on response order. The latter would highlight the potential role of visual memory in saccade adaptation, but it would conceal the potential effect of informational value on saccade adaptation. The effect of response order can be overcome when participants judge the two targets simultaneously, for example in judging the relative orientation of the two targets.

Experiment 2: Double-target adaptation with simultaneous judgments

The direction of saccade adaptation in Experiment 1 depended on the response order in which the two postsaccadic targets were judged. In Experiment 2 we eliminated the influence of response order by asking participants to judge whether both target orientations were orthogonal or not. This way, both targets were judged simultaneously and the response should not have prioritized one of the targets.

Methods

We recorded data from 18 participants. We had to discard data from two participants because of technical difficulties with the experimental setup. Moreover, we discarded data from two additional participants

because more than 50% of trials were invalid based on the criteria for fixation, latency, horizontal amplitude, and number of saccades. For the remaining 14 participants (10 women, four men; mean age = 21 years, age range = 18–25, two left-handed), 13.4% of trials on average were discarded (range = 4%–25%).

Stimuli and procedure in this double-target adaptation task were mostly identical with those in Experiment 1, except for the gratings' orientations and the response. Here, both gratings deviated 15° cw or ccw from the cardinal axes. Thus, they either were perpendicular or intersected at angles of 60° and 120°. After extinction of the postsaccadic target(s), the fixation cross at the screen center changed its color from pink to green for 2.4 s or until participants made a response. While the fixation cross was green, participants had to judge whether the two gratings were perpendicular or not via two buttons on a keyboard. Afterwards, participants received feedback. Feedback was identical to that in Experiment 1, except that visual feedback was displayed for only 1 s and one tone was played for an erroneous perceptual task.

Instead of having two distinct pre- and postsaccadic performance tasks as in Experiment 1, we recorded performance in one joint pre/post performance task. This task comprised 200 trials and was mostly identical to the postsaccadic performance task from Experiment 1, except that the combined plaid appeared as the peripheral target with a dark-gray dot (diameter of 0.15°) on top. Participants were instructed to saccade to the dot. Like in Experiment 1, the two components were vertically offset by 4° and appeared at one of five possible location combinations along the vertical: (+4, 0), (+3, −1), (+2, −2), (+1, −3), (0, −4).

Results

Pre/post performance task

We analyzed the proportion of correct responses as a function of the informative target's eccentricity (Figure 6A). Performance was $M = 0.84$ ($SD = 0.1$) when the informative target was shown at the fovea and the salient target appeared 4° up or down. In the opposite case, when the salient target was shown at the fovea and the informative target was 4° away, performance was $M = 0.64$ ($SD = 0.17$). A one-way repeated-measures ANOVA comparing the five levels of eccentricity yielded a significant main effect, $F(4, 52) = 12.14$, $p < 0.001$.

Double-target adaptation with simultaneous judgments

When participants judged the orthogonality of the two targets simultaneously, and behavior was thus not affected by response order, endpoints for 13 out of 14 participants were biased toward the informative target (Supplementary Figure S3). Figure 6B shows the mean vertical saccade endpoints during the double-target adaptation task. During the adaptation phase, vertical endpoints reached an asymptote very early during adaptation. This is different from double-target adaptation with sequential judgments (Figure 3A), double-target adaptation without a perceptual task (Figure 5A), or adaptation to single targets (Figure 5B and 5C). The mean vertical endpoint during late adaptation (last 50 adaptation trials) was $M = 0.35°$ ($SD = 0.27°$, range = −0.22° to 0.67°), significantly different from 0, $t(13) = 5.09$, $p < 0.001$. To test whether vertical eye position was closer to the presaccadic target position, we compared these values to vertical endpoints from informative-first responders of Experiment 1 using an independent-samples t test. With orthogonality judgments, vertical endpoints were closer to presaccadic target position, $t(20) = 2.36$, $p = 0.029$. This was also the case when we considered only participants with endpoints biased toward the informative target, $t(18) = 4.48$, $p < 0.001$.

We fitted the same two models to the data as in Experiment 1. For 10 participants, the two-component model including an immediate adjustment received higher information weights, $z = −2.67$, $p = 0.008$ (Wilcoxon signed-rank test). For five participants, the model fit of the two-component model yielded a gradual-learning parameter of 0. Overall, learning parameters were significantly lower than in Experiment 1, $t(27) = 3.02$, $p = 0.005$. We found no difference in the magnitude of immediate adjustment between the two experiments ($p > 0.2$). Supplementary Figure S4 depicts all model parameters.

Performance during baseline and adaptation phases was $M = 0.89$ ($SD = 0.12$) and $M = 0.85$ ($SD = 0.12$), respectively. To test whether performance during adaptation was affected by the vertical saccade endpoint, we performed the same ROC analysis as in Experiment 1. The mean AUC was 0.55 ($SD = 0.15$). AUC values (Figure 6C) were not different from 0.5, $t(13) = 1.35$, $p = 0.199$.

Discussion

Here we measured saccade endpoints when a presaccadic target split into two task-relevant targets during the saccade and both targets had to be judged simultaneously by comparing them. Unlike in Experiment 1, participants were more consistent in their eye-movement behavior. Endpoints of all but one participant were biased toward the informative target. However, the time course of endpoints during adaptation was qualitatively different from double-target adaptation with sequential judgments, double-target
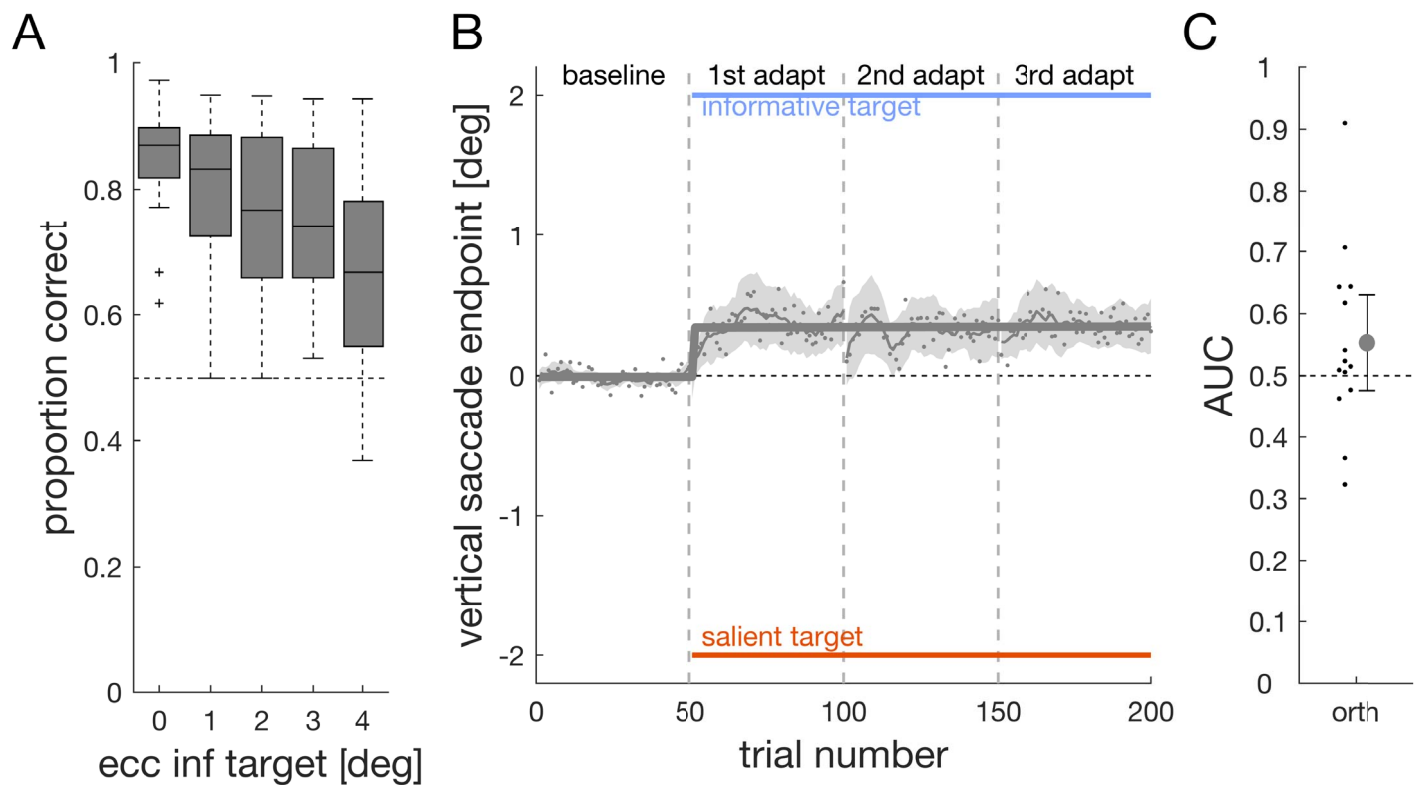
Figure 6. Main results of Experiment 2. (A) Box plots depicting proportion correct for the pre/post performance control condition as a function of eccentricity with respect to the informative target. (B) Aggregated adaptation time course and model fit for double-target adaptation with simultaneous judgment. Thin lines denote the running average and shaded regions the 95% confidence intervals of between-participant variability. The thick line is the model fit for the two-component model on the aggregated data. (C) Area under the receiver-operating characteristic curve when comparing endpoints of correct and incorrect trials during adaptation. Black dots denote values of individual participants, and the gray data point depicts the mean. The error bar is the 95% confidence interval of between-participant variability.

adaptation without a task, and adaptation to a single target (Experiment 1). There was almost no overlap between the two distributions of individual mean endpoints during late adaptation for Experiment 2 (maximum = 0.67°) on the one hand and for participants adapting toward the informative target in Experiment 1 on the other hand (minimum = 0.67°). Moreover, adaptation time courses from Experiments 1 and 2 differed with respect to the amount of gradual learning. Participants adapted their endpoints mostly, if not exclusively, by means of immediate strategic adjustment in Experiment 2.

Also, unlike in Experiment 1, we found no evidence that saccades closer to the informative target were associated with better perceptual performance. However, this might be because the perceptual task in Experiment 2 makes it harder to detect such an effect. Due to the doubled chance performance (0.5) compared to Experiment 1 (0.25), correct trials were more strongly affected by chance and thus less dependent on the actual saccade endpoint. Furthermore, there were fewer incorrect trials, and therefore the numbers of

correct and incorrect trials were less balanced, leading to noisier results from the ROC analysis. The fact that the mean AUC value is even higher than in Experiment 1 but more than twice as variable speaks in favor of this interpretation.

In sum, in order to overcome the effect of response order we asked participants to judge the relationship between the two stimuli. Although endpoints were biased toward the informative target, this bias was achieved by means of an immediate adjustment without any evidence of gradual learning. It could be that participants aim for an endpoint close to the presaccadic target location so that the error is small and can be fully compensated by an immediate adjustment without the requirement of further gradual learning. This raises the question whether it is possible to observe gradual adaptation of saccade endpoints when an immediate strategic adjustment is not useful. This would be the case when the location of the postsaccadic targets is random rather than consistent.

Experiment 3: Double-target adaptation with randomized target steps

To test whether we can observe saccade adaptation in the double-target adaptation task without immediate, strategic adjustment of saccade endpoints, we here recorded data for the double-target adaptation tasks of Experiment 1 and 2 when the vertical positions of the two postsaccadic targets were determined randomly in each trial of the adaptation phase. In this case, overall strategic adjustment of saccade endpoints is not helpful for the task at hand because the postsaccadic locations of the targets are no longer predictable. However, it is still possible to observe learning from one trial to the next (Srimal et al., 2008). This would indicate that double-target adaptation induces classical saccade adaptation and not just a voluntary, immediate adjustment of saccade targeting.

Methods

We recorded data from 20 participants; 10 performed the experiment with sequential judgments (same judgment as in Experiment 1) and the other 10 performed the experiment with simultaneous judgments (same judgment as in Experiment 2). For each group, we had to discard data from two participants because of more than 50% erroneous trials based on the same saccade criteria applied to the other experiments (latency, fixation, horizontal amplitude, number of saccades). Thus, we had two groups of eight participants each. For the remaining participants, the proportion of correct trials was 83% (range = 66%–96%) for the sequential-judgment group and 84% (range = 66%–94%) for the simultaneous-judgment group. The two groups had mean ages of 22 years (sequential judgment; six women, two men; age range = 19–25, two left-handed) and 24 years (simultaneous judgment; all women; age range = 20–28, one left-handed).

The procedure was mostly identical to that in the double-target adaptation tasks in Experiments 1 and 2 except that during the adaptation phase (Trials 51–200), the vertical shift of the salient and informative targets was not consistent. In half of the trials, the informative target was shifted upward, whereas in the other half of trials the salient target was shifted upward. The order of these trials was randomized. Like in Experiments 1 and 2, target shifts were +2° and −2°.

Results

To reveal whether we can observe adaptation in the absence of consistent target shifts, we measured saccade endpoints when the salient and informative targets stepped in a random direction. We fitted the gradual-learning model (Equations 5–7) to individual endpoint time courses (Figure 7; see Methods of Experiment 1 for model details). The mean learning parameter (B in Equation 6) was $M = 0.012$ ($SD = 0.008$) for the sequential-judgment group and $M = 0.015$ ($SD = 0.011$) for the simultaneous-judgment group (Figure 8). Learning parameters were thus in a similar range for adaptation toward a single target (Figure 8B; Supplementary Figure S2). To statistically ensure that the observed learning parameters were meaningful, we compared learning parameters against those when the model was fitted to the same data but the assignment of target steps and saccade endpoints was permuted. In the permuted case, the mean learning parameter was $M = 0.006$ ($SD = 0.004$) for the sequential-judgment group and $M = 0.006$ ($SD = 0.006$) for the simultaneous-judgment group. Moreover, we fitted the same model with a sequence of constant target steps, thus assuming that participants adapted to one of the two target locations (−2, +2). Mean learning parameters for the target-location sequence were $M = 0.0004$ ($SD = 0.0005$) for the individual and $M = 0.0002$ ($SD = 0.0003$) for the orthogonal judgment group.

We compared learning parameters using a 3×2 ANOVA with the within-participant factor of sequence (original sequence vs. permuted sequence vs. target-location sequence) and the between-participants factor of judgment (sequential vs. simultaneous). The ANOVA revealed a main effect of sequence, $F(2, 28) = 22.18$, $p < 0.001$. For both judgment groups, learning parameters were higher for the original sequence compared to a randomly permuted sequence—sequential: $t(7) = 2.65$, $p = 0.033$; simultaneous: $t(7) = 2.55$, $p = 0.039$—and to adaptation toward the target locations—sequential: $t(7) = 4$, $p = 0.005$; simultaneous: $t(7) = 3.86$, $p = 0.006$.

So far, these results argue that participants gradually adjusted their eye-movement endpoints from one trial to the next, but not which target they adapted to. To analyze whether participants adapted toward the informative or the salient target, we analyzed the target-weight parameters (parameter W in Equation 7). A target weight $W > 0.5$ indicates that participants adapted toward the informative target, and below 0.5 indicates adaptation toward the salient target. For sequential judgments, four out of eight participants had target-weight parameters above 0.5 (0.64, 0.79, 0.84, 0.98), and the other four below 0.5 (0.09, 0.13, 0.33, 0.38). Like in Experiment 1, the majority of participants (six out of eight) adapted toward the target they
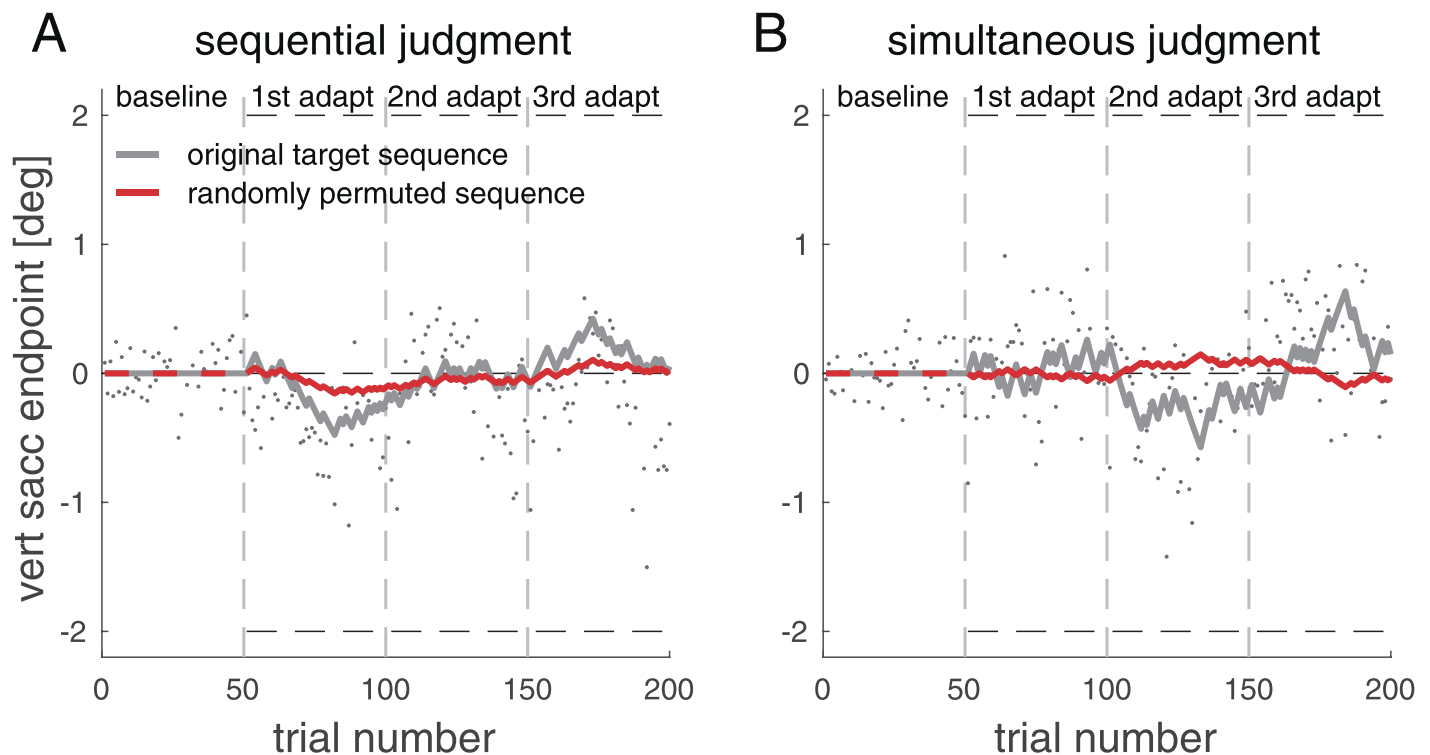
Figure 7. Experiment 3: Oculomotor learning with random target steps—individual data. Vertical saccade endpoint as a function of trial number when the postsaccadic targets were stepped in a random direction. Representative data of individual participants with (A) sequential and (B) simultaneous target judgment. Horizontal dashed lines indicate the presaccadic (0) and the two postsaccadic target locations (−2, +2). Data points are endpoints from individual trials. Solid lines are model fits (Equations 5–7) when either the original sequence of target steps (gray) or a randomly permuted sequence (red) was used.
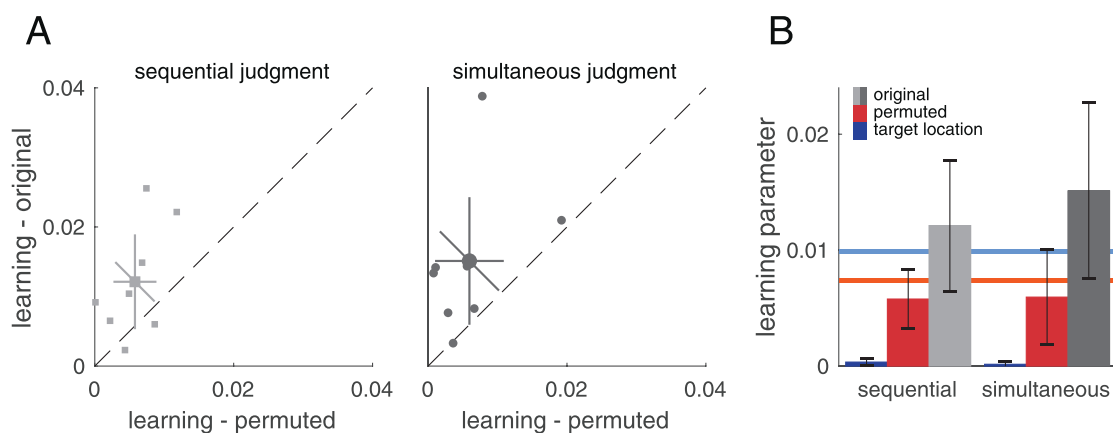

Figure 8. Experiment 3: Oculomotor learning with random target steps—aggregated data. (A) Learning parameter from the model by Srimal et al. (2008) for the original sequence compared to learning parameters derived from a permuted sequence for the (left) sequential-judgment and (right) simultaneous-judgment groups. Small data points denote learning parameters of individual participants. Larger data points indicate aggregated parameter values. Diagonal error bars denote the error of the difference between the two values and have to be compared to the identity line. Values above the identity line provide evidence for saccade adaptation with random target steps. (B) Aggregated learning parameters for original sequences (light and dark gray), permuted sequences (red), and adaptation toward a target location (purple) for the two different judgment groups. Lines are the median learning parameter (Equations 5–7) derived from the informative-only (blue) and salience-only (orange) tasks in Experiment 1. Error bars are 95% confidence intervals.
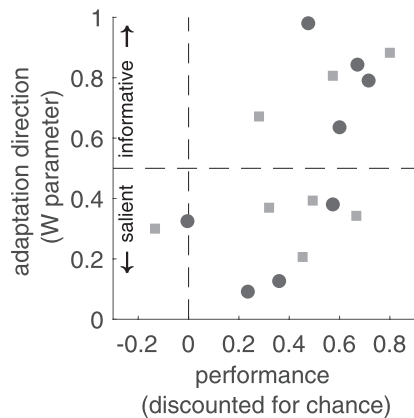
Figure 9. Experiment 3: relationship between adaptation direction and perceptual performance. Data points denote individual participants from the sequential-judgment (light-gray squares) and simultaneous-judgment (dark-gray circles) groups. Values of the *W* parameter above or below 0.5 indicate adaptation toward the informative or the salient target, respectively. Negative performance values indicate performance that was below chance.

had to respond to first. For the simultaneous-judgment group, three out of eight participants had a target weight above 0.5 (0.67, 0.81, 0.88) and thus gradually adapted toward the informative target. The remaining five participants had a weight below 0.5 (0.21, 0.30, 0.34, 0.37, 0.39) and thus adapted toward the salient target.

One potential explanation for the less homogeneous results compared to Experiments 1 and 2 might be the higher difficulty of the perceptual task with random steps. The mean performance was $M = 0.59$ ($SD = 0.18$) for the sequential-judgment group and $M = 0.72$ ($SD = 0.14$) for the simultaneous-judgment group. With random target steps, it is not possible to adjust saccade endpoints in order to optimize perceptual performance. We therefore wondered whether the adaptation direction is determined by the individual effort. Whereas some participants might have been highly engaged with the task and aimed to attend the perceptually informative target, others might have resigned and let their attention become caught by the physically more attractive stimulus. This might have contributed to differences in adaptation direction in the present random-step experiment. We used perceptual performance as an index of effort. We used Equation 1 to consider the different chance levels and correlated perceptual performance with the weight parameters *W* from the gradual-learning model (Equations 5–7). We observed a positive correlation, $r(14) = 0.55$, $p = 0.028$, indicating that better performance was associated with gradual oculomotor learning toward the informative target (Figure 9).

Discussion

We measured saccade adaptation in the double-target adaptation task when the direction of the perisaccadic shift was determined randomly for the two targets. Model fits with the gradual-learning model provided evidence for saccade adaptation. Gradual-learning parameters were comparable to single-target adaptation (Experiment 1) and higher than those derived from model fits when the relationship between saccade endpoints and target steps was permuted and thus nonsystematic. They were also higher compared to adaptation to one of the two target locations. This is evidence that participants displayed saccade adaptation in the present experiment, and that adaptation was driven by target identity, not target location. Like in Experiment 1, with sequential judgments, most participants (six out of eight) adapted toward the target they had to respond to first.

Here, we observed a positive correlation between perceptual performance and adaptation direction. The better the performance, the more strongly participants adapted toward the informative target. A correlation between two variables could arise due to several theoretically possible causal relationships. As the target was randomly stepped, it is more than unlikely that adaptation direction affected perceptual performance. When the eyes land closer to the location where the informative target was located in the previous trial, it might lead to a larger distance between fovea and informative target in the subsequent trial. Rather, we believe that this correlation reflects the contribution of effort. Participants who were highly engaged with the task might have aimed to attend the informative target and therefore showed stronger gradual learning toward that target and better overall performance.

General discussion

We measured saccades to a plaid target that was vertically split into its two components during horizontal saccades. One of these two postsaccadic targets was highly salient and could already be identified in the plaid before the saccade using peripheral vision. The other target could be identified only with near-foveal vision after the saccade, and identification performance thus depended more strongly on the saccade endpoint. Thus, this second target was more informative for the perceptual task at hand. Participants had to discriminate the orientations of both targets. When targets were consistently stepped in the same direction, we observed saccade adaptation when both targets were judged sequentially (Experiment 1). The data were best captured by a model that combines an immediate

strategic adjustment and gradual learning (Schütz et al., 2014). Participants mostly adapted toward the target they had to respond to first. This suggests a possible role of visual memory for saccade adaptation. Out of the seven participants who adapted toward the informative target in Experiment 1, three had an adaptation magnitude that was close to their optimal endpoint in this task (Figure 2E). When the two targets were judged simultaneously by judging whether their orientations were perpendicular or not (Experiment 2), endpoints were consistently biased toward the informative target, but we observed no evidence for gradual adaptation of saccade endpoints. Moreover, endpoints were closer to the presaccadic target location (i.e., the center between the two postsaccadic targets) than for participants from Experiment 1 who adapted toward the informative target. In contrast to that, we observed gradual adaptation when the two postsaccadic targets were randomly stepped (Experiment 3), no matter whether the targets were judged sequentially or simultaneously. With random target steps, a strategic adjustment was not possible. We observed that the adaptation direction with random target steps was related to perceptual performance.

Saccade adaptation with two task-relevant targets

We believe that all changes of saccade endpoints in the double-target adaptation task in Experiment 1 (and also Experiment 3) represent genuine saccade adaptation for the following reasons: First, participants showed gradual learning, no matter whether they adapted toward the informative or the salient target. Second, these time courses and their magnitudes were highly similar to time courses for a single postsaccadic target. The latter could be taken as a further example of single-target cross-axis adaptation that has been described before (e.g., Wallman & Fuchs, 1998; Chen-Harris et al., 2008; Schütz & Souto, 2011). A further possibility to highlight the similarities with saccade adaptation induced by the classical double-step paradigm (McLaughlin, 1967) would have been to show that adaptation effects persist after the adaptation period and transfer to reactive saccades. Here, we refrained from implementing these aspects in our experiments, as it has been demonstrated before that adaptation induced by a perceptual task persists after the adaptation period and transfers to reactive saccades (Schütz et al., 2014).

Another indicator that the time courses in Experiment 1 can be labeled saccade adaptation is forgetting and relearning induced by the 10-s breaks after Trials 100 and 150. Forgetting after the break was evident for participants adapting toward the informative target

(Figure 3A; Supplementary Figure S1). This observation is consistent with the suggestion that motor adaptation is supported by distinct processes operating at different timescales (Ethier et al., 2008): one process that learns slowly but has good retention, and one process that learns quickly but has poor retention. Stronger forgetting would thus imply a stronger contribution of the fast-learning process and thus also a stronger immediate adjustment at the beginning of the adaptation phase. This is consistent with the present results. However, we refrained from considering (fast and slow) forgetting for the models, because the experiment was not designed to include these aspects and it would have resulted in uninformative parameter combinations. In order to model forgetting, it would have been most informative to measure not only learning but also unlearning, and to implement multiple temporal intervals between trials (Ethier et al., 2008). Here, we observed that participants adapting toward the informative target displayed a stronger immediate adjustment and possibly also signs of forgetting after the 10-s breaks. This suggests that saccade adaptation, which is driven by task demands or other aspects of top-down control, might rely more strongly on the fast-learning process than adaptation toward targets that are mostly attractive due to their visual properties.

Target selection for saccade adaptation in a double-target scenario

When a person is confronted with more than just one small target, saccade adaptation is determined by a target-selection mechanism (Ditterich, Eggert, & Straube, 2000; Collins, Vergilino-Perez, Beauvillain, & Doré-Mazars, 2007; Madelain, Harwood, Herman, & Wallman, 2010; Schütz et al., 2014; Schütz & Souto, 2015). For example, Madelain et al. (2010) measured backward and forward saccade adaptation when the presaccadic target was stepped during the saccade and a distractor appeared at the presaccadic target location. They found that adaptation was essentially driven by the target and not by the distractor. Our paradigm differs from theirs, because both postsaccadic targets were task-relevant targets and neither of them appeared at the presaccadic target location. However, whether participants adapted toward the salient or the informative target in Experiment 1 probably reflects the same underlying target-selection mechanism.

But what determines whether participants select the informative or the salient target? Without a perceptual task, all participants consistently adapted toward the salient target. Saccade adaptation toward the salient target (Experiments 1 and 3) can be triggered by different aspects: the target's salience or the corre-

spondence with the presaccadic target. The presaccadic plaid combined the salient and informative targets. When participants had to judge the plaid using peripheral vision, they were able to discriminate only the salient target, whereas discrimination performance for the informative target was at chance. Therefore, participants might have perceived the postsaccadic salient Gabor as corresponding to the presaccadic plaid. With the current paradigm, it is not possible to dissociate whether saccade adaptation toward the salient target was triggered by salience or correspondence. Therefore, when neither of the two targets is task-relevant, the default target for saccade adaptation is either the most salient one or the one that corresponds to the presaccadic target.

With a perceptual task, target selection can additionally be determined by behavioral goals (Schütz et al., 2014). If the informational value of a target overwrites the default target-selection process, then participants should have consistently adapted toward the informative target. This way they could have optimized their perceptual performance. However, this was not the case. Instead, we observed a twofold pattern in adaptation direction (Experiment 1; Figure 3A). Which target participants adapted to highly coincided with which target they had to respond on first. The fact that participants showed better baseline performance for the target judged first indicates that they prioritized one of the two targets based on response order. Such a preference of one target over the other might be useful when visual-memory resources are limited. Storing multiple objects in visual memory causes a degradation of memory resources over time, leading to increased variability during the recall of memorized information (Pertzov, Manohar, & Husain, 2017). In consequence, it would be beneficial to maintain only a small number of items in visual memory at the same time, and sample the visual environment consecutively using saccades. This is in line with the observation that people tend to use the world as an external memory rather than relying on their internal memory resources (Ballard, Hayhoe, & Pelz, 1995). Given that the time between stimulus presentation and response is shorter for the stimulus judged first, it is a sensible strategy to prioritize this target, because it is less prone to memory decay (Pertzov et al., 2017).

However, in our double-target adaptation task, it is possible not only to select one of the two postsaccadic targets but also to select one location in between the two targets. When looking at individual time courses, it is not possible to infer whether participants selected one of the two targets and adaptation was incomplete or they selected an endpoint in between the two targets and adaptation to that endpoint was (more) complete. For Experiment 1, we additionally measured vertical endpoints when either only the informative or only the salient target appeared after the saccade (Figure 5B and 5C). This allows comparison of single-target and double-target adaptation between participants on an aggregated level. Adaptation toward the informative target in the double-target adaptation task was not different from adaptation when only the informative target was displayed—neither in terms of adaptation magnitude (Figure 3B) nor in terms of adaptation time course as revealed by the model parameters. This makes it likely that participants also selected the informative target in the double-target adaptation task. For the salient target, we observed a slightly reduced adaptation magnitude in double-target compared to single-target adaptation (Figure 3B). The direction of this effect might reflect that participants who adapted toward the salient target in the double-target task did not fully neglect the informative target and the constraints of the task.

Unlike in Experiments 1 and 3, we found no evidence for gradual adjustment of saccade endpoints when both postsaccadic targets were consistently stepped and judged sequentially (Experiment 2). However, vertical endpoints were consistently biased toward the informative target by means of a strategic adjustment. This adjustment was smaller than the overall adaptation magnitude observed with sequential judgments or single-target adaptation (Experiment 1). Therefore, it is possible that participants in this experiment selected endpoints in between the two targets, close to the presaccadic target location. These endpoints might reflect a weighted average between the top-down behavioral goal of looking at the informative target and the salience of the presaccadic target (and possibly also the postsaccadic salient target). However, we consider it unlikely that the present endpoints represent a weighted average of bottom-up and top-down information. When bottom-up and top-down information compete for oculomotor control, then the contribution of each is determined by the saccade latency: Early saccades are more strongly drawn toward salience, whereas later saccades are more strongly determined by behavioral goals (Schütz, Trommershäuser, & Gegenfurtner, 2012; Ghahghaei & Verghese, 2015). Moreover, in the experiment by Schütz et al. (2012), participants learned to adjust their latencies in order to adjust their endpoints and maximize their outcome over the course of the experiment. Here, we observed neither that endpoints were modulated by saccade latencies (data not reported) nor that participants adjusted their behavior over the course of the experiment. This argues against the notion that endpoints were caused by dynamically integrating salience and behavioral goals.

Alternatively, the results of Experiment 2 might be related to the global effect: When people make saccades to two targets, saccades typically land at an intermediate location. This observation has been termed the *global effect* (for review, see Vitu, 2008; van der Stigchel & Nijboer, 2011). Saccade endpoints in the global effect are biased toward the more salient of two targets (Deubel, Wolf, & Hauske, 1984), and they can be biased by task demands (Chou, Sommer, & Schiller, 1999; Findlay & Blythe, 2009). Here, saccade endpoints were directed away from the more salient target. However, our double-target adaptation task cannot directly be compared with the global effect, because in our task saccades were triggered by the peripheral image of one and not two targets. Therefore, it was impossible for the salient target and its postsaccadic target location to directly interfere with saccade planning. However, the present data might reflect the same top-down influence on saccade endpoints that can be observed in the global effect.

Do saccade endpoints support perception optimally?

In Experiment 1 we modeled individual optimal endpoints given individual endpoint variability, presaccadic peripheral identification performance, and postsaccadic identification performance as a function of the distance to the fovea. The optimal endpoint can be taken as the adaptation magnitude that maximizes perceptual performance for the combined perceptual task. Overall, an endpoint close to the informative target emerged as perceptually optimal (Figure 2D and 2E). The facts that participants in Experiment 1 did not uniformly adapt in the optimal direction and that they seemed to maximize performance for a single target instead of both targets show that, overall, participants did not adjust their eye movements in order to optimize visual-information uptake for the overall perceptual task. On the individual level, however, three participants reached an adaptation magnitude that closely matched the optimal-endpoint predictions (Figure 2E). In Experiment 2, participants were more consistent in their behavior, yet they showed no evidence of gradual oculomotor learning, and the bias toward the informative target was smaller than what would be considered optimal based on the results of Experiment 1.

The present results are a further example that humans do not optimally exploit their sensitivity across the retina when adjusting their oculomotor behavior (Morvan & Maloney, 2012; Ackermann & Landy, 2013; Clarke & Hunt, 2016; Nowakowska et al., 2017; Wolf & Schütz, 2017). Our task shares some similarities with the paradigm of Morvan and Maloney, where

participants could choose to saccade in between or directly at one of two squares to localize a target that would appear in one of the two squares. To behave optimally, participants should have changed their strategy (looking in between or at one of the squares) depending on the square distance or target size. Both paradigms require making a saccade to two targets or two potential target locations. Despite this similarity, the two paradigms differ with regard to several aspects: First, in our paradigm saccades are not classified as belonging to one or the other strategy (center or side); and second, in our paradigm the optimal strategy does not change from one trial to the next. Quite the contrary, it is essential for our paradigm that the optimal endpoint is the same across the whole experiment. This is why with our paradigm we are able to measure a gradual adjustment of endpoints in addition to (Experiment 1) or independent of (Experiment 3) a strategic adjustment.

Clarke and Hunt (2016) used the paradigm of Morvan and Maloney (2012) and applied it to other effectors and tasks. They replicated Morvan and Maloney's findings and showed that the same pattern can be observed when participants select a location to throw to or an item to memorize. In all experiments, participants were not able to adjust their decision of which target to select based on the task difficulty relative to their visual, motor, or memory uncertainty. This suggests that suboptimal target selection is not restricted to the oculomotor domain. Rather, this suboptimality seems to emerge whenever participants have to consider uncertainty about their own abilities. In a reaching experiment without any uncertainty, participants were well able to select the optimal target. Likewise, optimal eye-movement behavior and target selection seem to emerge whenever participants do not have to consider the capability and limitations of their visual system, but are confronted with the statistics of the external world. Then they are able to optimize temporal and spatial aspects of oculomotor behavior (Hoppe & Rothkopf, 2016; Wang & Theeuwes, 2018). On the other hand, the fact that participants in the present study adapted toward the target they had to respond on first can be taken as a hint that they did consider the limitations of their own visual memory and thus might have maximized their performance given their memory constraints.

Conclusion

Our results show that saccade adaptation can occur even when two postsaccadic targets compete with each other. Without a perceptual task, participants consistently adapt toward the salient target. With a percep-

tual task, this default mode can be overwritten. However, which target is selected for adaptation can be determined by various factors, including the relative salience and informational value of both targets as well as the target prioritization as set by the structure of a perceptual task. Thus, these findings highlight the flexibility of the oculomotor system in selecting postsaccadic targets to drive saccade adaptation.

Keywords: saccade adaptation, sensorimotor adaptation, visual perception, eye movements, target selection, memory, ideal-observer model

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