Practice improves peri-saccadic shape judgment but does not diminish target mislocalization

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Visual sensitivity is markedly reduced during an eye movement. Peri-saccadic vision is also characterized by a mislocalization of the briefly presented stimulus closer to the saccadic target. These features are commonly viewed as obligatory elements of peri-saccadic vision. However, practice improves performance in many perceptual tasks performed at threshold conditions. We wondered if this could also be the case with peri-saccadic perception. To test this, we used a paradigm in which subjects reported the orientation (or location) of an ellipse briefly presented during a saccade. Practice on peri-saccadic orientation discrimination led to long-lasting gains in that task but did not alter the classical mislocalization of the visual stimulus. Shape discrimination gains were largely generalized to other untrained conditions when the same stimuli were used (discrimination during a saccade in the opposite direction or at a different stimulus location than previously trained). However, performance dropped to baseline level when participants shifted to a novel Vernier discrimination task under identical saccade conditions. Furthermore, practice on the location task did not induce better stimulus localization or discrimination. These results suggest that the limited visual information available during a saccade may be better used with practice, possibly by focusing attention on the specific target features or a better readout of the available information. Saccadic mislocalization, by contrast, is robust and resistant to top-down modulations, suggesting that it involves an automatic process triggered by the upcoming execution of a saccade (e.g., an efference copy signal).

Significance

Visual sensitivity is markedly reduced during saccades, and peri-saccadic stimuli are misperceived as being closer to the saccade target. We show here that peri-saccadic shape discrimination improves significantly with practice. Unlike classical training paradigms that lead to better performance despite external masking, this perceptual learning occurs in the presence of natural, self-induced masking due to the eye movement (i.e., saccadic suppression). Improvement is generalized across saccade direction and stimulus location but is specific to the stimulus type and task. In contrast, stimulus mislocalization remains as pronounced. Thus, the representation of stimulus position probably involves an obligatory process triggered by the upcoming saccade. The results point to a dissociation between shape and location representations of peri-saccadic stimuli.

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we find that discrimination performance improves considerably with practice but localization does not. Learning is unlikely to be due to allocation of spatial attention to the visual stimulus. The observed learning uniquely demonstrates how the visual system may overcome perceptual degradation caused by self-induced masking.

**Results**
Participants were instructed to perform horizontal saccades and determine the orientation of ellipses that appeared briefly while their eyes were moving (Fig 1A and C). Initially, to maximize the ability of subjects to improve in the task, subjects were given feedback on their answers. Later, to verify that learning could also be achieved in an unsupervised manner, a second group of subjects performed the task without feedback (Fig 1). The performance of each subject was analyzed across repeated sessions to assess if and to what extent subjects improve in this task.

For each subject, we fitted the behavioral data of each session with a sigmoid psychometric curve based on logistic regression (Materials and Methods). Sensitivity to ellipse shape (e.g., horizontal or vertical: determined by the main axes aspect ratio) was assessed by the curve steepness (b1; a shallow curve indicates less sensitivity to the ellipse axes aspect ratio). Fig. 2A depicts the psychometric curves of two representative subjects: one trained in an unsupervised manner (no feedback; *Top*) and the other in a supervised manner (with feedback; *Bottom*). The continuous gray curves indicate performance during the baseline (first) session (b1 = 19.66 for the supervised learning subject, b1 = 18.3 for unsupervised), and the hatched black curves denote performance in the fourth training session (b1 = 67.64 supervised, b1 = 65.45 unsupervised). This clear improvement in performance was typical. Indeed, a 1-way repeated measures ANOVA on the data of both supervised and unsupervised-learning groups showed a highly significant learning effect across the 4 learning sessions (*F*(3,42) = 12.69, *P* < 0.001; and *F*(3,21) = 11, *P* = 0.003 respectively). Fig. 2B shows the group-normalized performance (solid black line; performance in the first session is considered as 100%) for the first four training sessions, and in later transfer-testing sessions. We took a closer look at the time course of perceptual improvement within sessions, by computing the percent of vertical ellipse choices across all subjects in each repetition of a specific experimental condition (thereby obtaining a group psychometric curve per trial repetition, see Supporting Information for details). The fitted psychometric curves to the group data allowed assessment of the group slope (i.e., sensitivity, per stimulus repetition. Thus, improvement at a fine time scale could be assessed at the group level (see details in Supporting Information).

Fig. 2C shows these data for the unsupervised learning subjects. Performance increased throughout the first day.

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**Fig. 1.** Experimental design. (A)Trial design: Participants were asked to fixate a red dot. Upon detecting fixation, the fixation point disappeared and reappeared on the opposite side of the screen, signaling subjects to make a saccade to the new fixation point. When the saccade was detected, an ellipse was flashed briefly (~12 ms) at the vertical meridian of the screen. Participants reported the orientation of the ellipse (vertical or horizontal) by left or right key press. (B) Experiment I protocol: The ellipse schematically depicts the location of the stimulus to be discriminated, and the arrow refers to the direction of the saccade. The stimulus was only present during the saccade. The first four training sessions (2 days) repeated the same condition, in this case a leftward saccade with an above-midline stimulus. The next six sessions (3 days) consisted of transfer sessions; in this case, a different saccade direction on day 3, a different stimulus position on day 4, and a random stimulus position (either above or below the horizontal midline) on day 5. Later the subjects were tested on a Vernier task under the same peri-saccadic conditions. Subjects were also tested if learning effects persisted over a long-term period, and when the stimuli appeared while fixating (Materials and Methods and Supporting Information). A different group of subjects performed the first four training sessions under conditions in which no feedback was given (Materials and Methods). (C) Trajectory of the eye in one representative trial. In this trial, a horizontal ellipse was displayed in the bottom part of the screen (centered 2.5° below the horizontal midline), and a saccade was made from the right fixation point to the left fixation point (red filled circles). Highlighted trajectory (in cyan) represents the gaze direction path (e.g., the location of the fovea) during the brief period in which the stimulus was present on the screen. The cyan rhombus is the midpoint of that path. (D) The distribution of the fovea’s position during stimulus presentation in one representative subject. Each data point is the path midpoint, while the stimulus was presented in a specific trial. The blue, purple, and green large rhombi denote the grand average for all trials in the first, fourth, and direction sessions, respectively. Axis values are degrees from the screen center. The exact ellipse position was jittered from trial to trial.
(within and between the first and second training sessions) and continued in the second day. Results for the supervised learning group followed an overall similar pattern (Fig. S1). Finally, performance after several months did not differ significantly from that at the end of the second day (green data point in Fig. 2B; long-term session vs. fourth session performance, Z = 0.157, P = 0.87). Overall, this pattern of improvement matches the properties of perceptual learning found in previous classical paradigms (15).

Previous studies testing visual sensitivity during saccades typically found that detection levels were most affected when low frequency grating stimuli were used (9, 24–26). We therefore verified that the ability to discriminate between ellipse shapes (which have broadband frequencies) was indeed hindered during saccades. For that purpose, participants performed an additional task, in which the ellipses appeared well after saccade completion. This “fixation” condition resulted in superior performance (pink point in Fig. 2B) in all subjects. The difference between this condition and the peri-saccadic control session following it was highly significant (Z = 2.85, P = 0.004), indicating that visual discrimination performance indeed dropped dramatically during rapid eye movements. It is worth noting, however, that the performance level of a relatively large number of subjects (17/60, 28%) was too noisy to be fit with a psychometric curve and establish a reliable baseline. This variability in perceptual skills is not unusual: individual differences in threshold levels of detection and discrimination of stimuli that appear during or around the onset of saccades have been prevalent in previous studies (11, 27). The above-mentioned 17 subjects were barred from continuing the tests and were not included in the analysis. The remaining subjects (n = 43, 72%) may represent a part of the population whose suppression of visual information during saccades is somewhat less pronounced, although they clearly performed worse in the peri-saccadic conditions than during fixation. Finally, we verified that the observed learning was not a result of any change in the saccade dynamics (e.g., becoming slower, more accurate, or systematically different in any way that could have improved the quality of the retinal image; see details in Supporting Information).

Saccadic Mislocalization. Until now we have shown that practice can improve the discrimination of peri-saccadic stimuli. As noted in the introduction, peri-saccadic stimuli are also characterized by their mislocalization in space. Naturally, we wondered if
training may also lead to changes in the perceived location of the peri-saccadic stimulus (i.e., changes in saccadic mislocalization). To assess this, a different group of subjects performed experiment II, which started with four localization sessions. In these sessions, subjects had to report the location of the ellipse in each trial (by a mouse click, while keeping fixation on the saccade target) rather than its orientation. For each subject, we calculated a mislocalization index (MLI) per session: the ratio between the mean perceived distance of the stimuli from the saccade target (PD) and the actual distance from the saccade target (AD), along the horizontal axis. Lower MLI values indicate larger mislocalization of the stimulus toward the saccade target (see example in Fig. 3B). MLI values were usually low (average of 0.18 ± 0.06 SEM for subjects in the first sessions and 0.13 ± 0.02 SEM in the fourth session), suggesting considerable compression of space. These values are comparable with those found in other studies during saccades of similar amplitude, in which stimuli also appeared at similar distances from the saccade target (4, 5, 28).

Following these localization sessions, the subjects went on to perform four discrimination sessions, after which they did an additional localization session (Fig. 3). MLI values remained low after practicing in the discrimination task (0.2 ± 0.04 SEM). A repeated-measures ANOVA over the different sessions indeed showed that MLI values did not change with repeating the localization task, nor were they altered after practice (and improvement) in the discrimination task ($F_{(1,3,3)} = 1.95, P = 0.18$; Fig. 3C).

Although MLI values remained unchanged (suggesting that the bias in target mislocalization remained the same), subjects’ position estimation became more reliable with practice (e.g., the trial-by-trial variability in the reported stimulus locations was diminished with practice; repeated-measures ANOVA on the SD of the reported locations in four sessions: along the horizontal axis, $F_{(3,2,9)} = 4.05, P = 0.018$; and in the vertical axis, $F_{(3,2,9)} = 6.72, P = 0.002$). Note, however, that the reduction in trial the trial to trial variation in the localization task could be due (at least in part) to the motor aspects of the task (e.g., marking with the mouse the location of the ellipse center). Variability was greater in the horizontal axis (as expected it was along the saccade axis), but the reduction in the trial to trial variability across sessions was similar in the in the two axes (reduction of $0.53 ± 0.72°$ and $0.83 ± 0.53°$ in the Sds between the first and fourth sessions in the $x$ and $y$ axes, respectively).

Thus, improvement in localization reliability may well have been due to motor aspects. To explicitly test this, an auxiliary localization task was performed by 10 different, naïve, subjects (Supporting Information). In this new task, subjects were presented with a vertical bar that appeared at different locations along the horizontal axis after saccade completion. The peri-saccadic ellipse size and position was as in the original experiment. The task was to report the relative position of the postsaccadic bar with respect to the peri-saccadic ellipse center (left or right), eliminating any motor components in the task. Furthermore, this new location discrimination task involved a binary decision (as in the previous shape discrimination task), allowing for a clearer comparison between shape and location representation changes with practice (29).

The task was repeated in four sessions. The individual data from each session was fitted with a psychometric curve, allowing separate assessment of the position bias [i.e., saccadic mislocalization; by measuring the point of subject equality (PSE)] change across sessions, as well as position sensitivity (by measuring the psychometric function slope) changes between sessions. As in the previous localization task, we find no significant shift (e.g., change in the PSE value) toward the veridical position of the peri-saccadic stimuli with training (see further details in Supporting Information). In addition, no improvement was found in location sensitivity (i.e., location report reliability; $F_{(3,2,7)} = 1.76, P = 0.178$; Fig. S2). Thus, although practice clearly improved the subjects’ ability to judge the shape of peri-saccadic stimuli, it did not alter their mislocalization in space.

**Generalization of Discrimination Learning.** Our next goal was to study the degree of transfer of learning to novel conditions, in an effort to better understand the mechanisms responsible for the obtained improvement in shape discrimination performance. To that end, after completing the four training sessions of experiment I, the subjects performed additional sessions (see Fig. 1B) that differed from the original training in either the saccade direction (termed direction), stimulus location (termed position; in the upper visual field for subjects who were previously trained with the stimulus at the lower visual field and vice versa), or the degree of uncertainty regarding the location of the stimulus (termed random: in each trial the stimulus could appear in either the trained location or the new location, with equal probability). The “position” session tested if learning was confined to a certain retinotopic location of the stimuli.

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**Fig. 3.** Localization task. (A) Experiment II protocol. A different group of subjects performed four localization sessions, followed by four discrimination sessions. Next, they performed a Vernier session, and finally another localization session. (B) In each localization trial, we calculated the distance between the reported location of the ellipse (marked in dark blue diamonds, an example trial is denoted by light blue) and the saccade target. This distance was termed the “perceived distance” or PD. The PD was divided by the “actual distance” (AD) along the horizontal axis between the ellipse vertical position and the saccade target to obtain an MLI. MLI = 0 means that the stimulus is perceived at the same horizontal displacement as the saccade target (maximum shift, or full compression of space), whereas MLI = 1 indicates that the stimulus is seen at its veridical location (along the horizontal, saccadic axis). The MLI values were averaged across individual trials within a session per subject. Black ellipse represents the average location of the vertically jittered stimuli. (C) MLI remained the same through the localization sessions of experiment 2. Each line represents a single subject. The dashed black line is the grand average. The first four sessions were before the discrimination task, and the fifth session was after the discrimination task.
The “random” session tested if learning was mainly due to better allocation of spatial attention due to prior knowledge of the location of the stimulus position. The “direction” session was designed to test if automatization of the trained saccadic motor plan is the main cause for better perceptual performance. Conceivably, improvement might result from a shift from a “double task” requiring both planning a saccade and discriminating the stimulus to a greater focus on the discrimination task (e.g., allowing spatial attention to be directed to a location other than the saccade target).

In general, most of the learning gains were carried over to the different transfer sessions (Fig. 2B). Performance level remained close to that of the trained condition when the task parameters were manipulated [72 ± 20%, 99 ± 26%, and 89 ± 23% (SEM) for the degree of transfer for the position, direction, and random sessions, respectively]. Although the transfer to a different stimulus position was somewhat smaller than for the other two conditions, a one-way ANOVA performed on these generalization indices proved them to be statistically indistinguishable \( F_{(2,28)} = 0.21, P = 0.815 \). When comparing directly the performance of each of the three sessions with its matching control (a session identical to the first four sessions that was performed at the same day as the transfer test), performance in the position session was slightly lower \( Z = 2.33, P = 0.020 \); red rhombus in Fig. 2B), whereas the direction and random sessions were not different from their control sessions (yellow triangle, \( Z = 1.24, P = 0.22 \); blue rectangle, \( P = 0.113 \)). Altogether, the results point to marginal sensitivity to stimulus position, and no sensitivity to the direction of the saccade or to the level of certainty of the next stimulus position. It is therefore unlikely that better deployment of spatial attention contributed to the improvement in performance. The relatively low sensitivity for the fine retinotopic position of the stimuli (~5° across the horizontal meridian) indicates that higher level visual areas (V4 and above) (30) are likely to be involved, at least in part, in the learning (Discussion).

**Specificity to Stimulus and Task.** We also explored the possibility that learning is specific for the task and/or stimuli at hand. For that purpose, subjects who trained on the ellipses and reached asymptotic performance shifted to performing a Vernier discrimination task under the same spatial and temporal settings as in the previous sessions (Materials and Methods). Specifically, subjects had to judge the relative positions of two vertical black stripes that appeared while the eyes were moving. The horizontal distance between the bars varied between trials, allowing us to fit a psychometric curve for each subject, and to extract the sensitivity (slope) to the task parameters (Materials and Methods). An example curve is shown in Fig. 4A (Bottom). We also trained a separate group of naïve subjects on the Vernier task. Fig. 4A (Top) shows an example of a shallow baseline psychometric curve \( b_1 = 0.08 \) and a steep posttraining curve \( b_1 = 0.29 \) of one such subject. We compared Vernier task performance in subjects who previously trained with ellipses with that of naïve subjects. As can be seen in Fig. 4B, performance of the previously-ellipse-trained subjects was similar to the baseline level of the naïve Vernier subjects \( Z = 1.442, P = 0.16 \) and far from the
level that the Vernier subjects achieved after further training ($Z = 3.13$, $P = 0.002$). These data suggest that a significant part of what was learned in the ellipse task could not be used to better perform the Vernier task. The results also serve as an additional argument against the involvement of spatial attention in the learning: because the stimuli were presented at the same location, efficient deployment of spatial attention to that location should have led to better discrimination of both types of stimuli.

These results could be interpreted either as indicating that learning was specific for the type of stimuli used in the two tasks or specific to the task used (although the two are not necessarily mutually exclusive). To discriminate between these two options, we compared between the results of the first ellipse discrimination session in subjects who previously had four localization sessions (in experiment II) to the baseline and fully trained performance of the ellipse discrimination group (that had no prior localization training: experiment I). If mere exposure to the stimuli during the localization task is enough to induce changes in discrimination performance, subjects with previous experience in the localization task should show clear gains in their first discrimination session in comparison with the naïve group. However, this was not the case, as can clearly be seen in Fig. 4C: practice in a localization task resulted in performance that was almost identical to the baseline performance of the original ellipse discrimination group ($Z = 0.283$, $P = 0.80$) and significantly different from performance after training ($Z = 3.974$, $P < 0.001$). These results indicate that the observed learning was context dependent, suggesting possible recruitment of feature-specific attention, while arguing again against optimized allocation of spatial attention (because the same stimuli appeared at the same location in both tasks).

**Discussion**

In this study, we used a gaze-contingent paradigm to show that an initially reduced ability to judge peri-saccadic object shape can improve considerably with practice. However, this improvement was not accompanied by better judgment of the veridical location of the stimulus. Even explicit practice on a task requiring to report the position of the stimulus did not change its (mis)perceived location, nor did it lead to better discrimination of the stimulus’ shape later, when switching to the ellipse orientation discrimination task. Thus, the use of spatial attention (e.g., ellipse orientations) was dissociated from the ability to perceive the true location of the peri-saccadic stimuli.

The mechanisms responsible for saccadic suppression and the mislocalization of stimuli during saccades are not completely clear. Both effects can be seen even slightly before the saccade is initiated (5, 31, 32) and are therefore likely to be due (at least in part) to an efference copy signal that affects the processing of information in visual areas. The mislocalization of stimuli (or compression of space) has been suggested to result from a change in the activity pattern in visual areas that have an explicit retinotopic map (e.g., V4). Hamker et al. (22) suggested that the efference copy of the saccade command is sent to retinotopic areas in visual cortex where it generates a second locus of activity on top of the classical activity peak evoked by the visual stimulus at its retinal location. If stimulus position is indeed represented by the neural activity pattern in visual areas. The mislocalization of stimuli (or angular location) has been suggested to result from compression of space (37). These neuronal populations probably serve as a major input to higher level neurons in inferior-temporal cortex that are selective to global 2D shapes (38). Critically, the sensitivity of V4 neurons is also modulated by top-down signals from oculomotor areas such as the frontal eye fields (FEF) (39). Moreover, V4 neurons are less sensitive to luminance contrast (but not color contrast) just before an impending saccade (40), mirroring the classical characteristics of saccadic suppression (9). It has also been shown that following training in an orientation discrimination task, V4 orientation-informative neurons exhibit stronger responses and narrower orientation tuning curves (41). Furthermore, such changes were more pronounced in V4 than in V1 (42). Together, these pieces of evidence suggest that V4 may be the relevant site for changes that occur via learning in our task. As stated above, improvement may be due to the development of greater sensitivity to local features in the stimulus. Discrimination between vertically and horizontally aligned ellipses could be achieved by comparing the degree of curvature of contours in these two specific orientations (as described in Fig. 5). Learning could also involve readjustments in a higher readout area that integrates local information to establish global shape assessment (e.g., giving more weight to reliable signals). As many higher-level shape selective cells have large receptive fields centered on the fovea (43), their involvement can explain the high specificity to features of the stimulus and somewhat lower specificity to the location of the stimuli that was observed in our case.
Fig. 5. Schematic representation of the perceptual capabilities in our experiment and possible encoding schemes of stimulus location and shape that may account for it. (Top Row) Perceptual aspects. During fixation, the perceived (P) and veridical (V) locations of the stimulus match (Left). During eye movement, a flashed stimulus is perceived closer to the saccade target (Center), an effect that was not diminished with practice (Right). (Second Row) The misperceived location of the stimulus during saccades (dotted line) might be due to neurons activated by top-down signals from the oculomotor system (dashed line) that encode the saccade target location in the retinotopic map. These signals are combined with those from neurons firing at the veridical location of the stimulus (solid line), generating a compression of space toward the saccade target (22). Practice does not alter this automatic mechanism. (Third Row) Schematic psychometric curves describing shape discrimination performance in our study. Shape discrimination was initially severely hindered during saccades (compared with fixation), but significantly improved with practice. (Bottom Rows) A simplified scheme allowing for the better discrimination of shape with practice. Each dot represents a neuron which has preference to a specific degree of curvature acuteness (r) and orientation (θ); see example neuron with preference to specific parameters depicted as a 2D Gaussian in the Inset. Horizontal ellipses evoke activity in the blue neurons, whereas vertical ones activate the red neurons. We assume that an ellipse shape might be encoded by a population of such neurons, sensitive to different curvatures and orientations, which converge into global shape detectors. During saccades, the oculomotor signal reduces the sensitivity of the curvature selective cells (e.g., lowered activation levels, represented by faded colors in the middle column). Training may improve shape discrimination by gating the top-down signal resulting in higher signal strength in the curvature selective cells (indicated by brightened colors) and/or by giving more weight in the readout to neurons showing clear preference for vertical or horizontal curvature (depicted by enlarged dots within the black dashed squares in the bottom right).

Fig. 5, bottom row, depicts this process schematically: it assumes that the core process is based on oriented curvature detectors (which are found in V4). Each dot represents such a neuron, sensitive to a specific degree of curvature and orientation. Red dots correspond to curvature detectors that will be activated by a horizontal ellipse of a given aspect ratio (say V/H = 1/2) and blue ones by a vertical ellipse (with an opposite aspect ratio: V/H = 2). Color saturation in the figure corresponds to the strength of response of a given detector. Ellipse orientation can be assessed by the general pattern of active curvature detectors (blue vs. red). During fixation, the curvature estimation is reliable enough to estimate global shape correctly (even when the ellipse V/H aspect ratio is close to 1; Left). However, during saccades, the neuronal signal is suppressed (as has been reported in V4) (40) resulting in a “fuzzier” representation of shape (due to lower sensitivity of the detectors; indicated by faded colors in the middle.
column). Learning may improve performance in several possible ways: it may allow for effective deployment of feature-based attention, focusing on the most relevant features for discrimination between vertically and horizontally oriented ellipses (e.g., the curvature detectors at the horizontal and vertical orientation indicated by hatched rectangles in Fig. 5, Right). A direct comparison between the activity level of these two detectors may be enough to judge the ellipse’s orientation correctly. Alternatively, learning may involve lifting of the suppression imposed by the impending saccade leading to a better sensitivity of the curvature detectors. Finally, learning could be implemented by optimizing the weights of these detectors allowing for better readout of the population code that represents the whole shape.

In accordance with current results, perceptual learning is often reported to be highly specific to the choice of task and stimuli (44–47, but see refs. 48–53). Unlike the present results, learning has been often shown to be restricted to the stimulus retinotopic position (16, 47, 54–56). However, this is not always the case, and the degree of generalization in learning has been associated with task difficulty (57), training length (58), the way attention is deployed during the task (59), and the spatial resolution required to solve the task (60). Furthermore, the notion that perceptual learning is highly position specific and therefore likely to be implemented at early processing stages (16) has recently been challenged. Generalization across spatial position was found in double-training paradigms, in which two stimuli (e.g., Gabor patches) are shown at different locations, and the task-relevant feature for each location is different (61, 62). All these pieces of evidence indicate that perceptual learning involves at least to some extent higher-order decision mechanisms. One possibility is that the “readout” of inputs from earlier areas is modified by giving more weight to the more informative neurons (63–67). Perceptual learning could also result from an interaction of higher-level areas with lower-level representations through feedback connections (68), leading to an efficient allocation of attention to specific features (so-called reverse hierarchy) (17).

To summarize, we demonstrate here that participants improve their peri-saccadic shape recognition with practice. This improvement is not accompanied by more accurate perception of the peri-saccadic stimulus location. We speculate that the improvement might be due to a combination of better readout of the information encoded in the stimulus, better allocation of attention, and reduced degree of peri-saccadic suppression of shape selective cells in the visual cortex. Future application of similar paradigms combined with electrophysiology in monkeys may allow to better characterize the visual information available during saccades and the mechanisms involved when learning to use it.

Materials and Methods

Participants. Forty-three subjects (average age, 23 y) took part in this study. Sixteen subjects (six females) completed experiment I fully, and eight additional subjects (five females) performed experiment Ii, and a third group of 10 subjects (three females) performed four Vernier sessions. Seventeen other individuals were excluded due to noisy behavioral performance in their first session (e.g., no reliable fit to a psychometric curve ($R^2 < 0.8$), suggesting poor ability to use easier stimulus conditions [greater ellipse axes (V/H) ratio] to achieve better performance]. In experiment I, all 16 subjects participated in the four learning sessions and the three transfer sessions: different saccade direction, different stimulus position, and random stimulus position. Twelve of those subjects participated in the long-term and fixation sessions. All subjects were naive and had no feedback, normal or corrected to normal visual acuity by self-report. All subjects were naïve and had no experience with the three transfer sessions: different saccade direction, a different stimulus position, or a random stimulus position; see Fig. 18 for an example), as well as an original learning session. The final day included the fixation session (Supporting Information) and a final control learning session. In addition, subjects who completed the transfer sessions performed one Vernier session (a different group of naive subjects performed a four-session training on the Vernier task to assess specificity to stimulus; see ref. 16). Finally, 12 subjects returned 10.2 ± 2.8 mo after completion of the protocol to test if learning gains have been maintained over a long-term period. Performance in each transfer session was always compared against its matching control, performed on the same day. The order of transfer sessions was counterbalanced across participants, with the exception of the random-position session that was always after the different-position session. The within-order of the transfer and control sessions was also counterbalanced across participants. The position of stimuli and saccade directions were kept constant within a single session, except for the random-position sessions in which each stimulus had an equal chance to appear either in the upper visual field or in the lower visual field. Each session included 160 valid trials, 20 trials for each specific condition (V/H: ellipse axes ratio), presented in pseudorandom order.

Stimuli. All stimuli were generated by the same software in which the experiment was written and deployed (Experiment Builder; SR Research) and were presented at 85-Hz on a 20-inch cathode ray tube (CRT) screen (model: StudioWorks N2200p). All stimuli were black (RGB gun values: 0, 0, 0; 0.01 cd/m²) on a gray background (100, 100, 100 RGB; 1.85 cd/m²).

Ellipse stimuli. The stimuli consisted of a family of ellipses, varying in the ratio of their main (horizontal (h) and vertical (v)) axes. The minimal axis length was ~4°, and the maximal length was about 6°. The basic set of stimuli comprised of eight different ellipses with different V/H ratios: (1.08, 1.16, 1.25, 1.85) and their counterparts with the opposite ratios (0.925, 0.865, 0.8, 0.54). Note that we use the log of these ratios to plot the psychometric curve so that the values are symmetric around zero [log(V/H) = 0: perfect circle]. To prevent using the distance from the screen horizontal midline as a cue for stimulus orientation, the vertical position of the ellipses’ center was randomly jittered across trials (0.5° above and below the stimulus original coordinates). Vernier stimuli. Vernier stimuli consisted of two straight black bars each subtending 18 arcminutes (~0.3°) wide and 2° long, positioned one above the other, with a horizontal offset between them: the lower bar appeared 10, 20, 34, or 47 arcminutes to the left or to the right of the higher bar (center of bar to center of bar). The vertical location of the stimulus was jittered in the same way as in the ellipse sessions.

Trial Design. Each trial began with a fixation point appearing 12 degrees left (or right) of the screen center (for different subjects). After 350 ms of fixation (in which the gaze was maintained within a 2° × 2° region centered on the fixation point), the point disappeared and a target point appeared in the mirror location on the opposite side of the screen. The participant was instructed to voluntarily initiate a saccade toward the target immediately after target appearance. Upon detection of the saccade by the tracking system (see details in Eye Tracking) an ellipse was flashed for one frame (12 ms) midway between the initial fixation target and the final fixation target points. The ellipse was centered on the midvertical screen axis: 2–2.5° above or below the screen midline, depending on session type and trial condition. Note that the actual presentation time of the stimulus was shorter than one frame and varied according to the vertical axis of the ellipse: the ellipse vertical axis was 3–6° long or 10–20% of the screen vertical size (27°), meaning that the actual rendering of the ellipse took roughly 1.25–2.5 ms, plus the phosphor decay time (2.4 ms). The stimulus disappeared by the time the participants had finished the saccade (verified by post hoc analysis of the eye position during stimulus presentation, see Eye Tracking and Fig. 1C for details). Once the eye landed on the saccade target, the target was replaced by a question mark and two prototypical ellipses: horizontal and vertical right and left of it, respectively. Participants had to indicate if they saw a horizontal or vertical ellipse by clicking the right or left mouse button. Participants had 3 s to answer and were given immediate feedback (the word correct or wrong appeared where the question mark was). In one session, termed “no feedback,” the participants were given no feedback, to check their performance in an unsupervised session. Unsupervised learning. Eight new subjects performed the same learning protocol as the original subjects (i.e., the first four learning sessions) with no feedback to test if learning could be achieved in an unsupervised manner.
Location report session. Localization sessions were identical to the learning sessions, but instead of reporting the orientation of the ellipse, participants had to indicate where was the ellipse by clicking the mouse on the center of the ellipse as they perceived it. There was no time limit for answering, and no feedback was given.

Vernier session. Vernier trials followed the exact structure of the ellipse trials, including the stimulus position on the screen and the position jitter. The only difference was the use of a different set of stimuli and discrimination task (Vernier). Each condition was repeated 25 times within a session.

Experiment II: Location Report Dynamics. Experiment II included four ellipse localization sessions, followed by four ellipse discrimination sessions. Next, subjects performed three Vernier sessions and finally one additional ellipse localization session (Fig. 3A). Session structure and the stimuli were identical to those of experiment I.

Data Analysis. Data from each session for each subject was filtered for the aborted trials and catch-trials. The data were then analyzed using Data Viewer (SR Research), Microsoft Excel (Microsoft), and Matlab in-house code (The MathWorks). Statistical analysis was done using SPSS (version 16.0 for Windows; IBM) and Microsoft Excel (Microsoft).

Behavioral analysis. For each session, the percent of vertical responses for each of the eight ellipses was plotted against the log of the V/H ratio. A psychometric function was fitted using logistic regression (Excel Solver; Microsoft). The function was of the form \( \text{P Yale} = 1 \exp(-b0 - b1 \times \text{log V/H}) \), and the parameters \( b0 \) and \( b1 \) were determined by minimizing the sum of squares of the error.

The slope of the curve \( b1 \) indicates the sensitivity of the observer to changes in the V/H ratio (i.e., the ability to distinguish between horizontal and vertical ellipses for a small change in the V/H ratio); better sensitivity results in a higher slope (ideal performance would result in a step function; Fig. 2). The bias toward horizontal or vertical orientation is represented by \( b0 \): \( b0 = 0 \) means no bias, such that when \( \text{X} = \text{V/H} \), the probability \( \text{b1} \) shifts the function to the left, indicating a bias toward horizontal orientation. Using the slope of the first session of each subject as baseline (i.e., 100%), we calculated the level of performance in each of the sessions, per subject. The same procedure was used in the Vernier sessions. In this case, the "upper-right" responses (i.e., the responses in which subjects reported seeing the upper bar to the right of the lower bar) for each of the 10 possible distances between the vertical bars was plotted against the log of those distances.

Group level analysis. We used one-way repeated-measures ANOVAs to compare the performance (with respect to the baseline), saccade amplitude, velocity, and angle in the four learning sessions. A similar one-way repeated-measures ANOVA was performed on the performance in the learning sessions of experiment II. In addition, to investigate the changes in performance within session, we pooled together all trials from a given session, from all subjects, categorizing them according to the chrono-logon of each specific condition (i.e., first practice, second, etc.). The pooled data (per stimulus repetition) was fitted with a psychometric curve, yielding a group estimate of performance sensitivity at a much finer temporal resolution (see detailed explanation in Supporting Information).

Eye Tracking. A video-based, infrared, desk-mounted eye tracker (EyeLink1000; SR Research) with a sampling rate of 1,000 Hz was used for correcting eye movements. The manufacturer's software was used for stimulus presentation, calibration, validation, drift correction, saccade detection (at a 30°/s threshold), and determination of periods of fixation. The eye-position data were used to automatically monitor online performance of the task. Throughout the experiment, failure to maintain fixation, execution of unwarranted saccades, fixating at directly or around (7° × 7°) the visual stimuli, or fixating more than 2° above or below the screen horizontal middle line aborted the trial, and the trial was recycled at a random time later in the experiment. Eye-movement data were analyzed using the manufacturer's software and Matlab R2010b.

All eye-tracking data were drift corrected: the jitter of the gaze in a trial was determined by comparing the gaze position during fixation at the beginning of a trial to the location of the fixation point, and correcting the data of the trial so that the two would match. The saccades of the different sessions were analyzed for possible consistent differences in their amplitude, average velocity, and angle. We also analyzed the raw data to determine the fovea's position during the time window in which the stimulus was shown (see Fig. 1C and Supporting Information for details).

Supporting Information

Supporting Information

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Fixation Session
In the fixation sessions, participants performed the same ellipse orientation discrimination task as in the other conditions, and made a saccade in the same direction and amplitude as in a standard trial. However, the ellipse appeared after the saccade—500 ms after fixation has been established on the saccade target. Because performance in such conditions is far superior to that in the previous experimental conditions (in which the stimulus was shown during midflight), the ellipses used in this experiment were much closer to a perfect circle (e.g., their main axes aspect-ratio was closer to 1). We made an effort to present the stimulus at the same retinotopic position as in the standard session. To that end, we extracted the centroid of the location of the fovea while the stimulus was displayed (computed from the eye movement data) and compared it to the stimulus position (separately for left and right saccades sessions, see Eye Tracking and Fig. 1C for example data). We used the horizontal (x) coordinates of these centroids from all participants in all of the learning sessions to calculate a distribution of retinotopic distances of the stimuli from the fovea. This distribution of distances was then used to position the stimuli relative to the saccade target point in the fixation session. Accordingly, the stimuli appeared 2.08 ± 2.4° right of the saccade target in the leftward trials and 2.72 ± 2.5° left of the saccade target in the rightward trials. The y position of the stimuli was jittered exactly as in the other sessions.

Ellipse Discrimination: Improvement Within Session Analysis
To assess intrasession changes in performance, all trials from a given session, from all subjects, were pooled together and then divided according to the chronological order of occurrence of each condition (i.e., ellipse with a specific aspect ratio) in the session. For example, the first dataset of trials in session 1 included the first occurrence of ellipse with axes ratio of 1.08 (from all subjects), the first occurrence of ellipse with axes ratio of 1.16, and so on. Thus, the dataset of trials consisted of eight data points (first occurrences of the eight conditions), each made of the average data of 16 subjects. Because there were 20 repetitions of each condition throughout each session, there were 20 such datasets for each session. We fitted a psychometric curve for each dataset and extracted 20 slope values (b1) for each session. Finally, we smoothed the data by calculating a running average over the slopes (bin size = 9, step = 1). This procedure resulted in 12, chronologically organized slope values for each session. This process was done for each session, both when feedback was given and when it was not given. Fig. 2C shows the results for the no-feedback, unsupervised learning. Fig. S1 shows the same analysis for the supervised learning.

Determining the Fovea’s Position at the Time of Stimulus Presentation
We analyzed the raw data to determine the fovea’s position during the time window in which the stimulus was shown. For each trial, we extracted the coordinates of the gaze during the 12 sample points during the single video frame at which the stimulus was presented, corresponding to the locations of the center of gaze during stimulus presentation (although the stimuli were actually presented for a shorter time and prone to small variations; Trial Design). The mean of these points was calculated, resulting in one value per trial. In Fig. 1C, we plot these values for the first, fourth, and direction sessions of one subject. Note that the median value is usually in the first half of the horizontal axis in relation to the saccade direction: right half in the leftward trial and left half in the rightward trials as the stimulus display is triggered by saccade initiation. The stimuli disappeared well before the eye reached its target.

Saccade Dynamics and Learning
The saccade amplitude, velocity, and angle did not change significantly with learning (F(3,36) = 0.23, P = 0.72; F(3,36) = 0.6, P = 0.54; and F(3,36) = 0.97, P = 0.41, respectively). Similarly, the position of the fovea at the time of stimulus presentation did not change with learning (x coordinates: F(3,36) = 0.35, P = 0.79; y coordinates: F(3,36) = 0.94, P = 0.43; Fig. 1C and D) and was not significantly different between successful trials (where the orientation of the ellipse was accurately identified) versus unsuccessful trials (x coordinates: Z = 1.6, P = 0.11; y coordinates: Z = 1.05, P = 0.29).

Location Discrimination Task
The objective of the auxiliary location experiment was to test for changes in stimulus localization with practice using a position judgement task (between two alternatives), as in the shape discrimination task. Another advantage of this task was that it eliminated the requirement for motor precision, thereby focusing on its sensory aspects. Ten naïve subjects performed four location discrimination sessions, in which they had to determine the horizontal position of a post-saccadic stimulus (bar) relative to the center of a peri-saccadic stimulus (ellipse). Saccade parameters, as well as ellipses’ sizes and position, were the same as in the main experiment. Because we expected considerable variability in the perceived positions of the ellipses between subjects (as in the main localization experiment; Fig. 3), we first assessed the mean perceived position of the ellipse, per subject. For that purpose, each subject started with a short version of the main localization task (30 trials), from which the subject’s mean perceived ellipse position (mean X) and its SD were computed. The test bar in the location discrimination task was placed at 0.25, 0.5, 1, 2, and 4 SDs left or right to the reported mean X. Thus, each session of the location discrimination experiment included 10 conditions, repeated 18 times in a pseudorandom order.

Location Discrimination Analysis
For each subject, in each session, and for each condition, we calculated the proportion of trials in which the bar was perceived as farther away from the saccade origin than the ellipse center (e.g., in saccades to the right, the proportion of trials in which the bar was perceived as being to the right of the ellipse, and vice versa). We fitted a psychometric curve to the data for each subject, for each session, and extracted the slope and point of subjective equality (PSE) values (see example in Fig. S2). The PSE represents the perceived position of the ellipse (at which the bar is seen left or right of the ellipse at the same proportion), whereas the slope indicates the sensitivity of this relative position assessment to changes in the bar position. We ran a repeated-measures ANOVA to test for consistent changes in these values across training sessions. As in the previous localization task, we found no shift in the bias (e.g., change in the PSE) toward the veridical position of the peri-saccadic stimuli, with training. In fact, a mild effect at the verge of significance was found in the opposite direction (i.e., somewhat greater mislocalization with practice; repeated-measures ANOVA: F(3,27) = 5, P = 0.043). In addition, no significant change was found in sensitivity (Results). We conclude that practice does not improve the ability to assess the veridical position of peri-saccadic stimuli.
Within-session changes in performance, with feedback. Each data point represents the group slope for a certain stimulus repetition, ordered chronologically from left to right. Each repetition slope was smoothed by averaging it with the four preceding repetition slopes and the four following repetition slopes, resulting in 12 data points per session. The data presented here are taken from the four ellipse discrimination training sessions, with feedback. Dashed lines represent rest periods within the same day; solid line represents an overnight break between sessions.

A Single subject’s position judgement in the first (baseline, gray) and fourth (trained session, black) sessions. The abscissa corresponds to the bar position (in degrees) where zero corresponds to the veridical horizontal position of the ellipse, and 12° is the position of the saccade target. The ordinate corresponds to the proportion of times in which the subject reported that the bar was further from the ellipse center toward the saccade target. The data were fit with a psychometric curve using logistic regression (as in the shape discrimination experiment), to yield the slope and the PSE per session. The example subject experienced strong mislocalization [PSE: 8.14° and 8.66° in the first (baseline, B) and last session (trained, T), respectively]. Thus, the perceived ellipse position remained almost the same with training. (B) Perceived position of the ellipses (PSE values) for all subjects in the four sessions of training. Colored lines represent data from the different subjects. Dashed black line represents the mean perceived position across subjects. Saccades were made from −12 horizontal degrees to +12°. Values closer to 12 indicate stronger mislocalization, and values closer to zero indicate weak mislocalization.