Microsaccades precisely relocate gaze in a high visual acuity task

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The image on the retina is never stationary. Microscopic relocations of gaze, known as microsaccades, occur even during steady fixation. It has long been thought that microsaccades enable exploration of small regions in the scene in the same way saccades are normally used to scan larger regions. This hypothesis, however, has remained controversial, as it is believed that microsaccades are suppressed during fine spatial judgments. We examined the eye movements of human observers in a high-acuity visuomotor task, the threading of a needle in a computer-simulated virtual environment. Using a method for gaze-contingent display that enables accurate localization of the line of sight, we found that microsaccades precisely move the eye to nearby regions of interest and are dynamically modulated by the ongoing demands of the task. These results indicate that microsaccades are part of the oculomotor strategy by which the visual system acquires fine spatial detail.

The possible visual functions of microsaccades have long been debated[1-3]. Proposed functions range from contributions to the prevention of image fading, the gradual disappearance of the visual percept experienced in the absence of retinal image motion[4-6], to participation in the oculomotor strategy by which the eye maintains precise fixation on a cue[7,8]. One hypothesis is that microsaccades may contribute to visual tasks that require high acuity[9]. According to this proposal, microsaccades serve the same function as larger saccades; as the visual system uses saccades to explore the scene, microsaccades enable exploration of a narrow region around the point of fixation when necessary.

Experimental data have not supported this proposal. A seminal study, which examined microsaccades while observers aimed and shot a rifle and threaded a sewing needle found that, in both conditions, microsaccade rates decreased just before the end of a trial, even when the task was successfully performed[10]. Furthermore, microsaccades are, on average, less frequent during these tasks than during maintained fixation on a small cue[10]. Similar results were also reported by another study[11]. On the basis of these findings, it was concluded that microsaccades are detrimental and therefore suppressed during the execution of finely guided visuomotor tasks and/or tasks that require high visual acuity.

Although the previous experiments found that some high-acuity judgments can be accomplished without microsaccades, a few observations caution against concluding that microsaccades are not used for exploring small regions in the scene. First, sustained fixation on a marker, the condition used as control reference by previous studies, might not provide an adequate baseline for comparing changes in microsaccade frequency. Many microsaccades performed under this condition might originate from the very requirement of maintaining precise fixation and therefore serve a different function than the microsaccades that occur when accurate fixation is not demanded[7,12,13]. Second, a reduction in the rate of microsaccades at the end of an experimental trial may reflect a change in the subject's attention and does not necessarily

entail that microsaccades were detrimental for perceptual judgments. These judgments could have benefited from information acquired by means of microsaccades occurring at earlier times during a trial.

To re-examine the role of microsaccades in fine spatial vision, we recorded eye movements in human observers while they were threading a needle in a virtual environment. Recent advances in gaze-contingent display technology[14,15] enabled us to accurately localize the portion of the scene examined with the preferred retinal region, as well as precisely analyze the timing of occurrence of microsaccades relative to adjustments in the thread-needle alignment. Our results indicate that microsaccades moved the preferred retinal location back and forth between the tip of the thread and the eye of the needle and were generated to evaluate the relative alignment of these two objects.

RESULTS

Participants were asked to insert a horizontal bar (the thread) into a small aperture at the center of a stationary vertical bar (the needle) (**Fig. 1a**). Both bars were displayed on a CRT monitor and embedded in a noisy background. This task enabled replication of the results reported by previous studies (**Fig. 1b**,**c**). In one experiment, as done previously[11], subjects had no control over the thread's position and were asked to maintain accurate fixation on the eye of the needle, while the thread approached the needle with constant velocity and stopped at a fixed distance (**Fig. 1b**). Consistent with previous results, the mean frequency of microsaccades at the end of the trial was substantially lower than at the beginning of the trial. Thus, microsaccades appeared to be suppressed at the time of high-acuity judgments.

In another experiment, subjects were free to move their eyes normally and fully controlled the position of the thread (similar conditions as ref. 10; **Fig. 1c**). Each trial ended when the thread successfully passed through the eye of the needle. Again, the rate of microsaccades dropped at the end of the trial,

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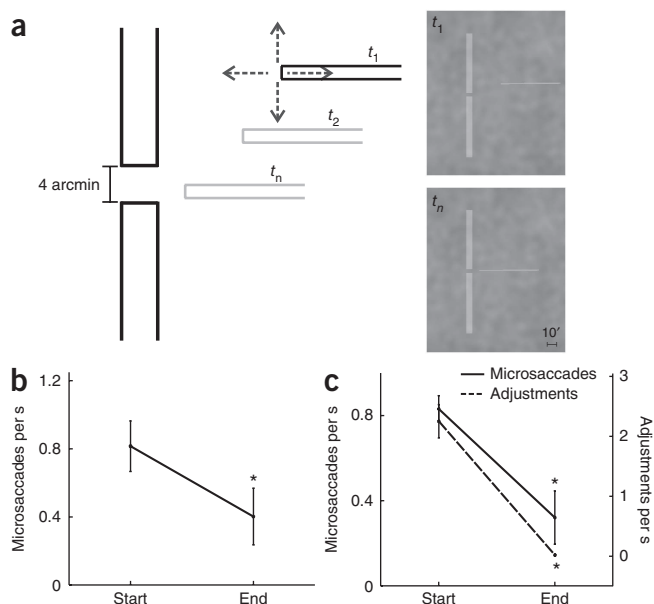
Figure 1 Threading a virtual needle. (**a**) The arena in which all of the threading experiments were conducted. Subjects used a joypad to align a horizontal bar (the thread) with the gap in a vertical bar (the needle). The gray bars represent the positions of the thread at various times during the trial. The actual stimulus on the display is shown on the right at two different times, t_1 and t_n. (**b**,**c**) Results from two experiments with conditions similar to those of previous studies[10,11]. In **b**, subjects maintained fixation on the needle's eye and had no control over the thread's position. In **c**, subjects were free to move their eyes and fully controlled the thread. The two intervals refer to the initial 4 s (start) and the last 0.5 s (end) of each trial. Both the mean microsaccade rate and the frequency of adjustments in the thread's vertical position are shown in **c**. *$P < 0.01$, one-tailed t test. Error bars represent s.e.m.

as previously reported[10]. Thus, microsaccades also appeared to be suppressed during finely guided visuomotor tasks.

Previous studies of microsaccade suppression[10,11] have suggested that microsaccades are detrimental in tasks that require high visual acuity. However, a reduction in microsaccade rate before perceptual reports (**Fig. 1b**) and at the completion of the visuomotor task (**Fig. 1c**) does not imply that microsaccades were not helpful at earlier times during the course of the trial, when perceptual judgments were formed. When subjects maintained fixation and had no control over the thread's position (**Fig. 1b**), the requirement for sustained fixation could have influenced microsaccade production. When subjects were free to move their eyes and fully controlled the thread (**Fig. 1c**), the probability of correcting the vertical position of the thread decreased with the microsaccade frequency at the end of the trial. That is, microsaccade rates reached their minimum at a time at which observers no longer adjusted the position of the thread.

To further investigate the possible contributions of microsaccades in high-acuity vision, we simulated threading using intermediate conditions. Subjects were allowed to freely move their eyes and control the thread's position, but the trial ended when the thread and the needle were at a distance at which evaluation of their correct alignment was still difficult. To ensure that modifications in the thread position were always the result of perceived misalignment between the thread and the needle, we restricted control of the thread to the vertical axis only. On the horizontal axis, the thread approached the needle at a constant velocity (1.4 arcmin s^{-1}).

We compared the saccades measured in this experiment to those recorded from the same observers during prolonged fixation on a stationary marker and during free viewing of images of natural scenes (**Fig. 2**). Both the frequency and amplitude of saccades varied greatly with the task. Amplitude distributions were very similar during threading and

sustained fixation. In both cases, the median was around 20 arcmin. In contrast, the amplitudes of saccades were spread more uniformly in free viewing, a condition in which saccades were more frequent than during the threading task (saccade rate during free viewing = 2.49 ± 0.46, threading = 1.56 ± 0.25, $P = 0.002$, paired t test). Consistent with previous reports, the rate of microsaccades was lower on average during threading than during sustained fixation, even though this difference fell short of statistical significance ($P = 0.074$, one-tailed paired t test). This rate was, however, fivefold higher than the rate measured during free viewing of natural images. Thus, the condition chosen for comparison is critical for evaluating microsaccade frequency.

Unlike during fixation on a stationary marker and free viewing of static pictures, the stimulus displayed during threading changed dynamically according to the subject's commands. We examined whether these changes in the stimulus modulated the characteristics of saccades. The frequency of microsaccades increased during the course of a trial (**Fig. 3**). Both saccades smaller than 20 and 10 arcmin were significantly more frequent ($P = 0.014$ and $P = 0.031$, respectively; one-tailed t test) during the final 7.5 s of a trial than during the initial 7.5 s. This increment in microsaccade rate coincided with a decrement in the mean amplitude across all saccades (**Fig. 3c**). That is, saccades became progressively smaller during the course of a trial, a change that reflected the narrowing of the separation between the thread and the needle. This effect was not a consequence of background noise, which could have forced subjects to look for points in which the thread and the needle were more visible. Indeed, highly similar results were obtained in the absence of background noise, when the thread and the needle were clearly visible.

These data suggest that the visual system calibrated saccades on the basis of the distance between the thread and the needle: the closer the

Figure 2 Comparison of saccade characteristics in three different tasks: threading, sustained fixation on a marker and free viewing of natural images. (**a**–**c**) Distributions of saccade amplitudes. The triangles mark the medians of the distributions. The insert in **c** shows the range of small amplitudes. (**d**) Mean rates of microsaccades, defined as saccades smaller than 20 arcmin (ANOVA with Scheffe *post hoc* comparisons, *$P = 0.009$, **$P = 0.004$). Error bars represent s.e.m. Individual trials of the threading task are shown in **Supplementary Videos 1** and **2**.
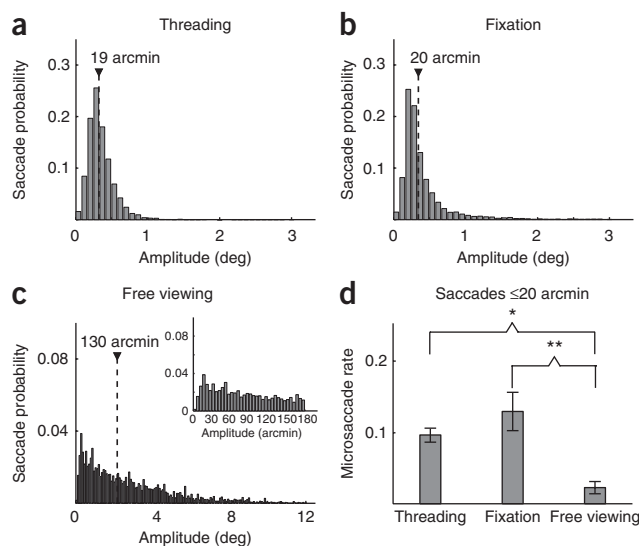
Figure 3 Modulation of saccade characteristics. (**a**,**b**) Mean instantaneous frequency of microsaccades, defined as saccades smaller than 20 arcmin or saccades smaller than 10 arcmin. (**c**) Mean instantaneous saccade amplitude. The two curves in each panel represent data obtained in the presence and absence of background noise. In this latter condition, the background was at a constant gray level and the stimulus was displayed at maximum contrast. Horizontal lines in each panel indicate mean values during sustained fixation (dashed line) and free viewing (dotted line). The asterisk indicates conditions in which measured values were significantly higher during the last 7.5 s of a trial than during the initial 7.5 s ($P < 0.04$, one-tailed t test in **a** and **b** and Wilcoxon signed-rank test in **c**).
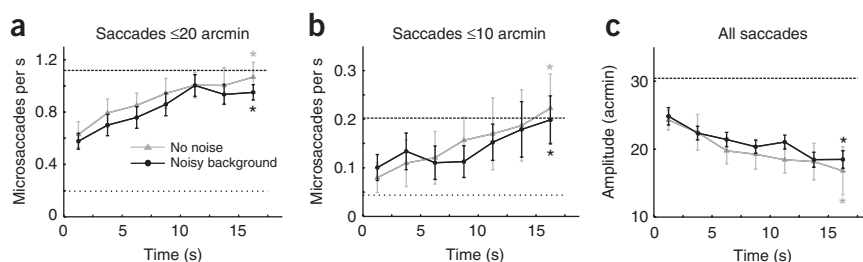
tip of the thread to the needle, the smaller the saccade (**Fig. 3**). This dependence might originate from an oculomotor strategy in which microsaccades relocate the line of sight back and forth between the two objects. To determine whether this was indeed the case, we examined the spatial distribution of fixations during a trial.

In the periods in between successive saccades, slow movements keep the eye continually in motion. With the low velocity of the thread that we used, no sign of pursuit was present in the recorded data. Ocular drift was highly similar to that measured during sustained fixation on a marker and kept the eye in a region with a mean radius of 6 ± 3 arcmin. Because of this motion, we classified each intersaccadic interval as a fixation on the thread, the needle or the background according to the location of the mean position of the eye's trajectory during the considered interval (**Fig. 4a**).

Fixations were clustered around the eye of the needle and the tip of the thread (**Fig. 4b**). Very few fixations fell far from these two regions. Notably, the distributions of fixations covered the path followed by the thread during the course of the trial, suggesting that subjects precisely calibrated microsaccades to fixate on the moving thread. Subjects fixated more often on the thread than on any other part in the image; more than 50% of fixations were on the thread (**Fig. 4c**). This preference is understandable, given that the thread was the only component of the stimulus that changed position during a trial. Subjects also fixated often on the eye of the needle, with approximately one every three fixations in this area of the image. This distribution of fixation locations remained constant during the course of the trial (**Fig. 4d**).

We then examined how microsaccades contributed to oculomotor strategies. Microsaccades were often used to relocate the line of sight across objects (**Fig. 5a**). While fixating on the needle, microsaccades

most often moved the line of sight to the thread. While fixating on the thread, however, microsaccades had a higher probability of maintaining fixation on the thread. This difference occurred because subjects made multiple consecutive fixations on the thread and spent more time looking at this object before moving their gaze, via a microsaccade, to another region of the image (median interval consecutively spent on the thread = 876 ms, on the needle = 578 ms). It should be noted that these probability distributions might underestimate the number of relocations of gaze between the thread and the needle, particularly toward the end of the trial, when the two objects were very close to each other. During the last 2.5 s in each trial, the horizontal direction of a microsaccade was very likely to be opposite to that of the previous microsaccade (**Fig. 5b**).

We wondered whether microsaccades contributed to the estimation of the alignment between the thread and the needle. To this end, we first determined the fixations during which subjects were more likely to adjust the position of the thread. Adjustments were more likely to occur while subjects fixated on the thread than on other parts of the image (**Fig. 6a**). This result was, however, a consequence of the uneven distributions of fixations in the scene, as most fixations were also dedicated to the thread (**Fig. 4c**). Indeed, the mean rates of adjustments, that is, the mean numbers of corrections per fixation, were actually quite similar during fixations on the thread and the needle (**Fig. 6b**).

We examined the oculomotor strategies preceding and following adjustments in the thread's position. To this end, we estimated the probabilities of correcting the thread/needle alignment immediately after different types of microsaccades and the probabilities of performing microsaccades immediately after changing the thread's position. Subjects were more likely to correct the thread's position after executing a microsaccade that moved the preferred retinal location from one object (the thread or the needle) to the other than after prolonged fixation on the same object (**Fig. 6c**,**d**). This effect occurred for microsaccades of all amplitudes, but was particularly pronounced after microsaccades smaller than 10 arcmin (**Fig. 6d**). In contrast, after performing an adjustment, microsaccades were likely to move the preferred retinal location toward the thread (**Fig. 6e**,**f**).
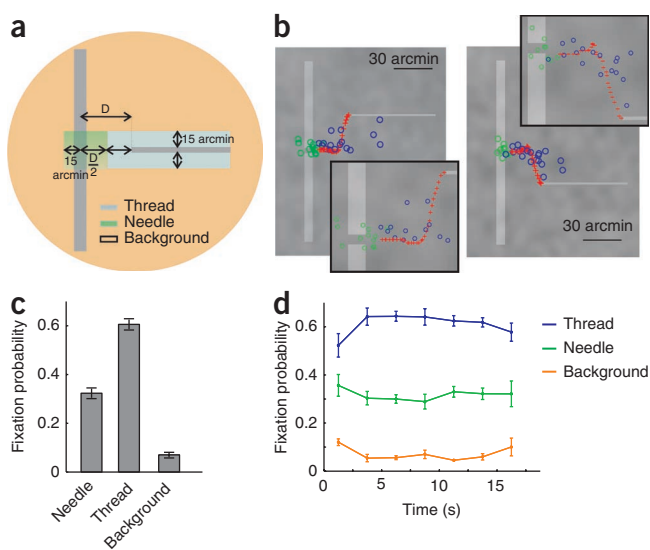

Figure 4 Analysis of fixation locations. (**a**) Each intersaccadic period was classified as a fixation on the eye of the needle, the thread or the background according to the location of its centroid. The distance D between the needle and the thread varied during the course of the trial. (**b**) Two examples of spatial distributions of fixations. Each panel corresponds to a different experimental trial. Blue and green circles represent fixations on the thread and on the eye of the needle, respectively. The red crosses mark the trajectory followed by the thread. Inserts, higher magnification of the center of the display. (**c**) Mean probabilities of fixation locations. Differences across all conditions were significant (ANOVA with Scheffe *post hoc* comparisons, $P < 0.002$). (**d**) Fixation probabilities at successive intervals during the course of the trial.

Figure 5 Analysis of microsaccades. (**a**) Probabilities of various types of microsaccades during fixation on the needle and on the thread. Microsaccades were subdivided according to where they landed. Data refer to saccades smaller than 20 arcmin. (**b**) Influence of microsaccade direction on the direction of the following microsaccade. During the last 2.5 s in each trial, consecutive microsaccades possessed opposite directions on the horizontal axis. In both graphs, all differences within each group were statistically significant (paired *z* test with Bonferroni corrections, *P* < 0.001).

That is, the first microsaccade following an adjustment had a high probability of moving the line of sight onto the thread when the subject performed the adjustment while fixating on the needle, and keeping the center of gaze on the thread when the correction was performed during fixation on the thread. Thus, microsaccades were used to either look back or gain a new view of the moving thread after realigning its position. These data, together with the different patterns of eye movements observed in successful and unsuccessful trials (**Supplementary Results** and **Supplementary Fig. 1**), indicate that microsaccades are part of the oculomotor strategy by which subjects acquire information about the alignment between the thread and the eye of the needle.

DISCUSSION

Although microsaccades have attracted considerable interest since their first quantitative measurements[16,17], their visual functions have remained controversial[2,3]. We found that saccades smaller than 20 arcmin precisely relocated the line of sight according to the ongoing demands of the task. These results contradict the widespread assumption that microsaccades are suppressed during high-acuity judgments and support the proposal that microsaccades are exploratory movements, similar to larger saccades[9,12].
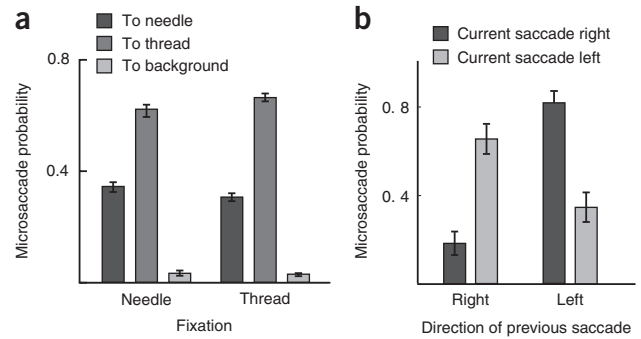
The proposal that microsaccades differ from saccades in amplitude, but not in function, is consistent with multiple experimental observations. It is known that the area of preferred target location in the retina is small, with a s.d. of only 3.4 arcmin[18,19]. Thus, targets displaced by more than a few minutes of arc are likely to fall outside of this region and the line of sight may need to be reoriented to ensure optimal vision. For example, under the assumption that the probability of target location is uniformly distributed in the preferred retinal region, a stimulus located only 5′ away from the current fixation would fall outside of the preferred retinal region in more than 50% of the cases. Furthermore, microsaccades and saccades exhibit similar motor characteristics and share a common neural substrate[20]. In fact, there is no clear distinction between the two types of movements and their amplitudes form a continuum (**Fig. 2c**). It is also known that saccades with amplitudes in the range of microsaccades can be voluntarily executed both to track small displacements of a fixated target[21] and to look away from a stimulus[22]. Thus, our findings are consistent with the observations that relocations of the line of sight of a few minutes of arc are sometimes necessary to ensure optimal vision and that the oculomotor system is capable of performing such relocations by means of microsaccades.

Our conclusions conflict with those of prior reports. We confirmed previous results (**Fig. 1b,c**), but our findings subject these results to a very different interpretation. The observation that microsaccades are rare immediately before shooting a rifle or threading a needle[10], two tasks in which shifts of attention between small details would be expected to be crucial, has been taken to imply that microsaccades are detrimental in tasks that require high visual acuity. However, a similar reduction in microsaccade frequency is also to be expected if microsaccades contribute information about the stimulus. Microsaccades might no longer be needed at the end of the trial, when the positions of the thread and needle practically overlap on
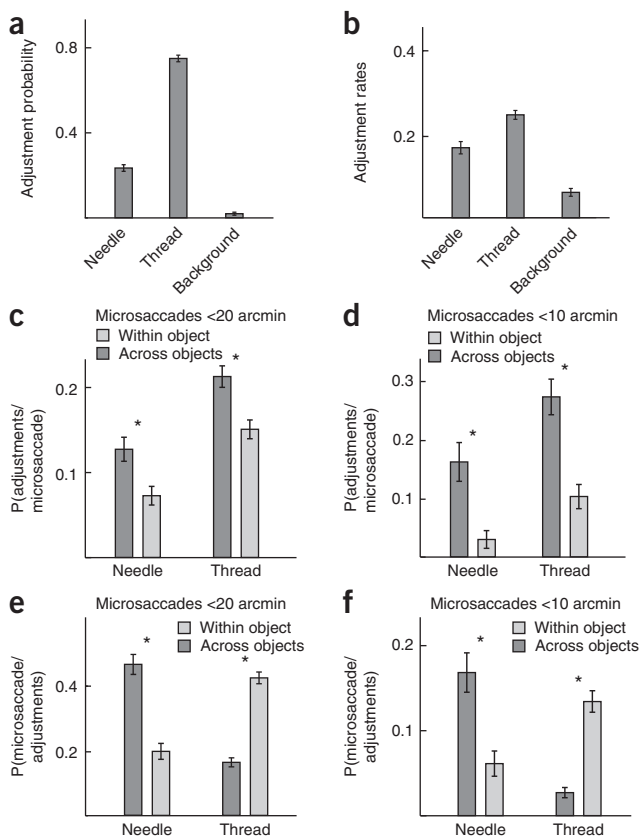

Figure 6 Interaction between microsaccades and corrections in the thread-needle alignment. (**a**) Probability distributions of adjustments to the thread's position as a function of the location of fixation during which they occurred. (**b**) Rates of adjustments. Data points represent the average numbers of changes in the thread's position per fixation. In both **a** and **b**, all differences were statistically significant (paired *z* test with Bonferroni corrections, *P* < 0.01). (**c,d**) Conditional probabilities of adjustments following different types of microsaccades. The fixation in which the adjustment occurred (*x* axis) is the target destination of the microsaccade. (**e,f**) Conditional probabilities of performing different types of microsaccades following an adjustment. The fixation in which the adjustment occurred (*x* axis) is the origin of the microsaccade. Data are shown for both microsaccades smaller than 20 arcmin (**c,e**) and 10 arcmin (**d,f**). In **c**–**f**, microsaccades are arranged according to whether they maintained fixation on the same object (thread or needle) or moved the line of sight from one to the other. *P* < 0.05, paired *z*-test with Bonferroni corrections.

the retina and their alignment can be assessed comfortably without the need for relocating the line of sight. In fact, a decrement in microsaccade rate also occurred when the thread was allowed to reach and go through the needle (see **Fig. 1c**). However, the frequency of microsaccades only dropped when the distance between the tip of the thread and the needle was smaller than 5′. In contrast, microsaccades occurred frequently at earlier times, when the thread was farther from the needle and subjects still adjusted the thread and needle alignment.

It is also known that the mean rates of microsaccades during threading and shooting are lower than those during sustained fixation on a marker[10]. Across the five naive subjects who participated in this previous study, the mean rate decreased by approximately 30%, a value similar to that measured in our experiments (26% for saccades smaller than 20 arcmin). Again, this reduction does not imply that microsaccades are not helpful in high-acuity tasks. We found that the mean rate of microsaccades measured during threading was lower than that observed during fixation, but was also substantially higher than that measured during free viewing of natural images. This task dependence of microsaccades emphasizes the difficulty of choosing a control condition to use as baseline.

Our results stress the need for distinguishing between different types of microsaccades[23,24]. As previously reported[11] and confirmed in our experiments (**Fig. 1b**), a reduction in microsaccade rate occurs when subjects are asked to maintain fixation on the eye of the needle and passively observe the motion of the thread. This effect is probably caused by a change in the accuracy of fixation control during the course of the experiment. Most (but not all) observers perform frequent microsaccades while attempting to maintain steady fixation on a marker, even if no stimulus other than the fixation cue is displayed. These fixational saccades appear to serve a different function from the exploratory microsaccades observed when subjects are free to move their eyes. Fixational saccades can be voluntarily suppressed[12] and their frequency depends on the precision of intended fixation[13]. A suppression of fixational saccades is to be expected at the time of perceptual judgments, as these saccades are not pertinent to the task and may impair performance. Exploratory microsaccades and fixational saccades can hardly be distinguished in experiments in which stimuli are observed while maintaining accurate fixation on a marker. Confusion between these two types of eye movements has probably contributed to the long-standing controversy over the visual functions of microsaccades.

In our experiments, the probability of correcting the thread's position was higher after a microsaccade shifted the line of sight from one object to the other than during prolonged fixation, a finding that is reminiscent of the way saccades precede hand movements in manipulation tasks[25–28]. The precision by which microsaccades relocated the line of sight between the thread and the needle suggests that these movements contributed to visual acuity. Such a contribution would also provide an explanation for previously reported improvements in fine spatial discrimination measured in the presence of microsaccades[29]. Our findings, however, do not exclude other hypotheses, including possible enhancements in contrast sensitivity following microsaccades. Further studies are needed to distinguish among hypotheses and investigate the physiological mechanisms by which microsaccades enhance the perception of fine detail.

METHODS

Methods and any associated references are available in the online version of the paper at http://www.nature.com/natureneuroscience/.

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ONLINE METHODS

Participants. Ten subjects with normal vision participated in this study. Six subjects participated in the experiments shown in **Figures 2–6**, with three of them also taking part in the experiments shown in **Figure 1**. Five subjects participated in the experiment described in **Supplementary Figure 1**. With the exception of one experienced observer, all subjects were naive about the purposes of the experiments and were compensated for their participation. Informed consent was obtained from all participants following procedures approved by the Boston University Charles River Campus Institutional Review Board.

Apparatus. Stimuli were displayed on a fast phosphor CRT monitor (Iyama HM204DT) at a resolution of 800 × 600 pixels and vertical refresh rate of 200 Hz in a dimly illuminated room. A dental imprint bite bar and a head rest prevented movement of the head and kept subjects at a distance of 126 cm from the monitor. Stimuli were observed monocularly with the right eye while the left eye was patched. Stimuli were rendered by means of EyeRIS[14], a hardware/software system for gaze-contingent display control that enables precise synchronization between eye movement data and the refresh of the image on the monitor, as well as accurate spatial localization of the line of sight. Vertical and horizontal eye position data were sampled at 1 kHz and recorded for subsequent analysis. Subjects used different buttons on a joypad to control the x and y coordinates of the thread on the screen. Adjustments occurred in discrete steps; each button press moved the thread by 1.4 arcmin.

Stimuli and procedure. Data were collected in separate experimental sessions, each of approximately 20 min. Every experimental session started with preliminary setup operations that lasted a few minutes and allowed the subject to adapt to the low level of light in the room. These preliminary operations included positioning the subject optimally and comfortably in the apparatus, tuning the eyetracker, and calibrating EyeRIS. Subjects were never constrained in the experimental setup for more than 30 min consecutively.

Accurate localization of the line of sight is necessary to examine the way eye movements scan the scene during high-acuity judgments. To optimize the transformation of the eye position measurements given by the eyetracker into screen coordinates, a dual-step calibration procedure, in which the subject observed and refined the estimated position of the preferred retinal location, preceded each block of trials. In the first phase of the calibration, the subject sequentially fixated on nine points evenly spaced in the working area of the display, as in standard calibration routines. For each point, the mean output voltage from the eye tracker was estimated over a period of 3.5 s. The mapping from eye-position coordinates to degrees of visual angle was determined by bilinear interpolation over the mean eye positions measured at these nine points. This transformation was made possible by virtue of the highly linear behavior of the DPI eyetracker in the central region of the visual field. In the second phase of the calibration procedure, subjects fine-tuned the gaze-to-pixel mapping using a gaze-contingent display technique. In this phase, subjects adjusted the position of a cross, displayed in real time on the screen at the estimated preferred retinal location, while sequentially fixating again on the nine points of the calibration grid. Subjects used the buttons on EyeRIS' joypad to finely adjust the position of the cross at each of these fixation points. These refinements were then incorporated into the offsets and gains of the bilinear interpolation. This method effectively reduces the dispersion of eye position measurements during calibration and improves the precision of the voltage-to-pixel mapping.

Subjects threaded a needle in a simulated virtual environment. The needle consisted of two aligned vertical bars (each 68 × 7 arcmin) with a 4 arcmin gap (the eye of the needle) in the center. A horizontal bar (68 × 1.4 arcmin) served as the thread (**Fig. 1**). The needle always remained immobile at the center of the screen. The thread started from a random location to the right of the needle and moved following the subject's commands (the initial distance from the needle was always 31 arcmin on the x axis). With the exception of the experiment shown in **Figure 1c**, subjects only controlled the vertical position of the thread; on the horizontal axis, the thread approached the needle with constant speed of 1.4 arcmin s^{-1} and stopped 7 arcmin from the needle, so that each trial lasted for 17.5 s. In the experiment shown in **Figure 1b**, the thread followed a previously recorded trajectory, which varied randomly across trials. Subjects evaluated whether or not the thread was correctly aligned with the eye of the needle after the thread stopped moving. In the experiment shown in **Figure 1c**, the thread went through the needle until its tip reached the needle's central axis.

The thread and the needle were displayed at the same contrast level over a noisy background. The spectral density of the background declined as $1/f^2$ with the spatial frequency f and was low-pass filtered with cut-off frequency at 5 cycles per degree. The mean luminance of the background was 16 cd m^{-2}. To normalize the difficulty of the task across subjects, we individually adjusted the contrast of the stimulus for each subject so that successful completion of the task occurred in approximately 85% of the trials in the main experiment (**Figs. 2–6**) and 50% of the trials in the experiment shown in **Supplementary Figure 1**. Contrast values were selected during preliminary experimental sessions. **Figure 3** also shows data collected in the absence of background noise; that is, when the stimulus was displayed at maximum contrast over a uniformly gray field (luminance = 16 cd m^{-2}). In this condition, the needle and the thread were clearly visible and subjects always successfully accomplished the task.

Figure 2 compares microsaccade rates measured during threading to those observed during sustained fixation and free viewing. In the sustained fixation condition, subjects maintained fixation on a black dot (4 × 4 arcmin) on a homogeneous gray background for 17.5 s. In the free-viewing condition, subjects freely explored gray-scale images of natural scenes extracted from a public domain database[30]. Each image subtended a visual angle of 18.1° × 13.6° and was displayed for 10 s.

Data analysis. Movements with maximum speed higher than 3° per s and amplitude larger than 1 arcmin were classified as saccades. Saccade amplitude was defined as the distance between the locations in which eye velocity became greater (saccade onset) and lower (saccade offset) than 2° per s. Classification of eye movements was performed automatically and then validated by human experts. Mean instantaneous rates and amplitudes were evaluated over consecutive, non-overlapping bins of 2.5-s duration. Periods of blinks were automatically removed from data analysis.

The conditional probabilities of **Figure 6c,d** and the distributions of **Supplementary Figure 1** were calculated by selecting all of the adjustments preceded by a microsaccade. To be included in the analysis, an adjustment had to occur within 1.5 s of the end of a microsaccade and no other saccade had to be present in between these two events. Similar criteria were applied to the interval between the time of an adjustment and the onset time of a later microsaccade to select microsaccades that followed adjustments and compute the conditional probabilities of **Figure 6e,f**.

30. van Hateren, J.H. & Ruderman, D.L. Independent component analysis of natural image sequences yields spatio-temporal filters similar to simple cells in primary visual cortex. *Proc. Biol. Sci.* **265**, 2315–2320 (1998).