

Miniature eye movements enhance fine spatial detail

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Our eyes are constantly in motion. Even during visual fixation, small eye movements continually jitter the location of gaze^{1–4}. It is known that visual percepts tend to fade when retinal image motion is eliminated in the laboratory^{5–9}. However, it has long been debated whether, during natural viewing, fixational eye movements have functions in addition to preventing the visual scene from fading^{10–17}. In this study, we analysed the influence in humans of fixational eye movements on the discrimination of gratings masked by noise that has a power spectrum similar to that of natural images. Using a new method of retinal image stabilization¹⁸, we selectively eliminated the motion of the retinal image that normally occurs during the intersaccadic intervals of visual fixation. Here we show that fixational eye movements improve discrimination of high spatial frequency stimuli, but not of low spatial frequency stimuli. This improvement originates from the temporal modulations introduced by fixational eye movements in the visual input to the retina, which emphasize the high spatial frequency harmonics of the stimulus. In a natural visual world dominated by low spatial frequencies, fixational eye movements appear to constitute an effective sampling strategy by which the visual system enhances the processing of spatial detail.

It was originally hypothesized¹⁰ that fixational eye movements might contribute to the perception of fine spatial details, a proposal later refined into the dynamic theories of visual acuity^{11–13}. Classical experiments that eliminated retinal image motion did not support these theories^{7,19–22}. These pioneering experiments, however, suffered from significant technological limitations. Most notably, the devices used to stabilize images on the retina did not allow selective

stabilization during periods of visual fixation between saccades, as would have been necessary to study fixational eye movements in their natural context^{23–25}. Instead, all trials with stabilized vision had to be run in uninterrupted blocks while the subject maintained fixation—a highly unnatural condition that unavoidably led to visual fatigue and fading.

In this study, we examined the influence of fixational eye movements on the discrimination of targets at different spatial frequencies (grating spacings). We compared discrimination performances measured in two conditions: with and without the retinal image motion produced by fixational eye movements. To overcome the limitations of previous experiments, we developed a new retinal stabilization technique based on real-time processing of eye-movement signals¹⁸. Like previous stabilization methods, this technique does not guarantee perfect elimination of retinal image motion; however, unlike previous methods, it combines a high quality of stabilization with experimental flexibility (see Supplementary Information). This flexibility enabled us to display and selectively stabilize the stimulus after a saccade, a method that isolates the normal fixational motion of the eye. It also allowed us to randomly alternate between trials with retinal stabilization and trials with normal retinal motion, a procedure that prevents visual fatigue and allows rigorous comparison of the two conditions, and to assess the accuracy of retinal stabilization independently from the subject's own judgement, a development that allows inexperienced and naive subjects to participate in experiments.

In a forced-choice task, subjects reported whether a grating was tilted by 45° clockwise or anticlockwise. Two separate experiments investigated the discrimination of the stimuli shown in Fig. 1a. In

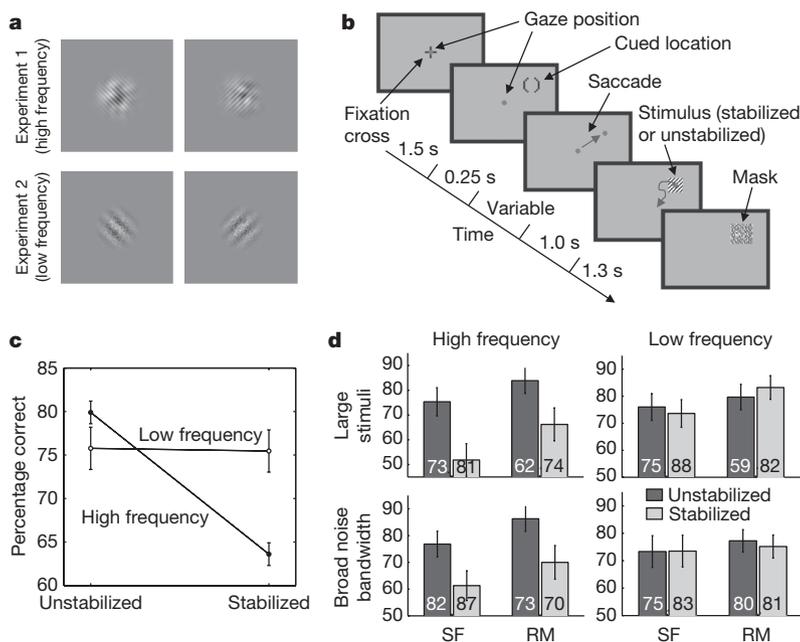


Figure 1 | Impact of retinal stabilization.

a, Examples of stimuli. **b**, Experimental procedure. The grey arrows and dots represent the subject's eye movements and the centre of gaze, respectively. **c**, Mean subject performance ($N = 6$). For every subject, in each condition, percentages were evaluated over a minimum of 80 trials. Individual performance differences between stabilized and unstabilized conditions were all significant in experiment one and were statistically indistinguishable in experiment two ($P < 0.05$; one-tailed z -test). **d**, Results of control experiments. The large stimulus was 5.6° . For the broad bandwidth control, the frequency band of noise was 0–14 cycles per degree. For both subjects, performance dropped under stabilization using a grating with 11 cycles per degree (high frequency, experiment one) ($P < 0.05$; one-tailed z -test), but not using a grating with 4 cycles per degree (low frequency, experiment two). The numbers of trials are indicated on each bar. In both **c** and **d**, error bars represent 95% confidence intervals. SF, RM, subjects.

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experiment one, the stimulus was a high-frequency grating perturbed by noise at low spatial frequencies. In experiment two, the frequency bands of the grating and the noise were reversed: the grating was at low spatial frequencies and the noise was at high frequencies. In both cases, the power of the noise was inversely proportional to the square of the spatial frequency, similar to the power spectrum of natural images²⁶.

As shown in Fig. 1c, when high-frequency gratings were used, mean percentages of orientation discrimination dropped by more than 16% in the presence of retinal stabilization, a change that was highly significant (experiment one: $t = 19.1$, $P < 0.01$; one-tailed paired t -test). By contrast, the retinal image motion produced by fixational eye movements did not improve performance with low-frequency gratings (experiment two: $t = -0.2$, $P > 0.05$). Thus, fixational eye movements improved discrimination of the orientation of a high-frequency grating masked by low-frequency noise but did not help with a low-frequency grating masked by high-frequency noise. This result is surprising because it contradicts traditional views of the influence of fixational eye movements on vision. Indeed, the pronounced reduction in contrast sensitivity at low spatial frequencies measured by previous experiments with prolonged retinal stabilization^{19–21} predicts a more significant drop in performance with low-frequency than with high-frequency gratings.

Control experiments examined the robustness of this result. As shown by Fig. 1d, the same pattern of results was obtained in a first control experiment, which used a larger stimulus, and in a second experiment, in which the noise bandwidth was broadened to overlap the frequency of the grating. Furthermore, a beneficial effect of fixational eye movements was also found in the contrast thresholds—the lowest detectable contrast of a grating—measured at high spatial frequencies (Fig. 2). We concluded that the high-frequency discrimination impairment observed under retinal stabilization was not affected by the precise size of the stimulus or by the bandwidth of low-frequency noise.

To establish further evidence for the causal relationship between fixational modulations of luminance and performance, we eliminated retinal image motion on a selected axis while leaving motion on the orthogonal axis unaltered. As shown in Fig. 3, discrimination was impaired when retinal image motion was restricted to the axis parallel to the grating but was normal when motion occurred on the orthogonal axis. These results are consistent with the informational content of the modulations of luminance introduced by fixational eye movements. These modulations only convey information about the pattern of noise during motion parallel to the grating, but provide maximal information about the grating when motion occurs on the axis orthogonal to the grating. For one subject, we also artificially reconstructed the visual input signals resulting from fixational eye movements by moving an otherwise stabilized stimulus. Passive exposure to the fixational motion of the retinal image, obtained by motion of the stimulus instead of the eye, was sufficient for re-establishing a normal level of performance. These results confirm

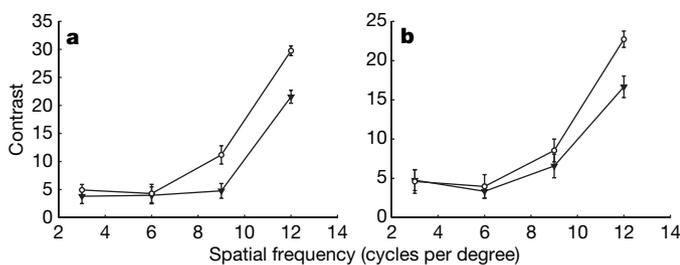


Figure 2 | Contrast thresholds. Mean levels of Michelson contrast \pm s.d. for two subjects: **a**, subject AR and **b**, subject GD. Consistent with the results of Fig. 1, the two conditions—normal retinal image motion (filled triangles) and retinal stabilization (open circles)—only produced different thresholds at high spatial frequencies.

that the discrimination impairment shown in Fig. 1 was caused by the absence of the retinal image motion produced by fixational eye movements.

To understand the mechanisms by which fixational eye movements improve the discrimination of high spatial frequency stimuli, we analysed the frequency contents of the spatiotemporal signals entering the eye in the unstabilized (stimuli fixed at a location on the screen) and stabilized (stimuli moved with the eye to cancel the retinal motion resulting from fixational eye movements) conditions of experiments 1 and 2 (the signals $I_U(\mathbf{x}, t)$ and $I_S(\mathbf{x}, t)$ received at time t by a receptor located at position \mathbf{x} on the retina, see Fig. 4a). Under retinal stabilization, $I_S(\mathbf{x}, t)$ did not change with time, and its power was confined to the spatial frequency plane at zero temporal frequency. In contrast, in the unstabilized condition, the motion of the eye spread the spatial power of the stimulus across temporal frequencies away from zero frequency. As shown by Fig. 4b, the extent of this temporal spreading was not uniform throughout the spatial frequency plane; it increased with spatial frequency. This dependence on spatial frequency occurred because the average change in luminance produced by a small displacement of a grating increases with the grating frequency. This effect had a different impact on the visual input signals of the two experiments.

Figure 4c compares the power spectrum of the stimulus with the spatial frequency distribution of the power in I_U , which, as a consequence of oculomotor activity, left the temporal zero frequency plane and became available at non-zero temporal frequencies. This dynamic power is identical to the power of the change in luminance that occurs as a result of the motion of the eye—the signal $\dot{I}_U(\mathbf{x}, t)$ in equation (2). With the stimuli of experiment one, these input modulations exhibited both attenuation of the low-frequency noise and

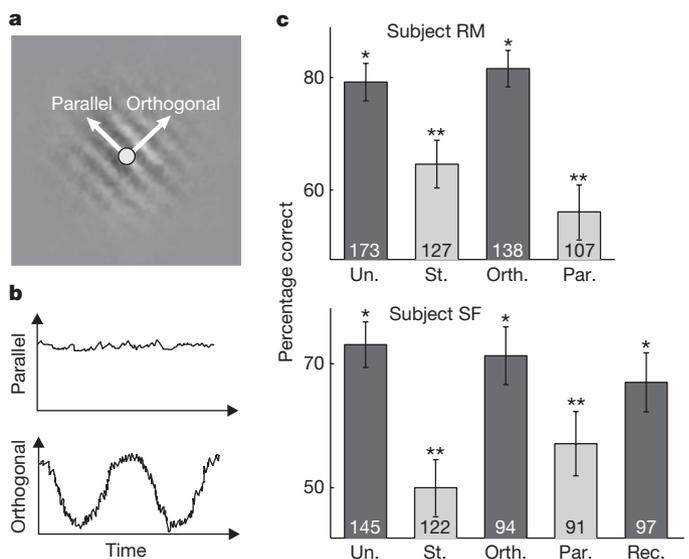


Figure 3 | Controlled retinal image motion. **a**, Selective stabilization of the stimulus on a single axis enables control of the signal-to-noise ratio of the visual input signals resulting from fixational eye movements. **b**, The fixational modulations of luminance experienced by a retinal receptor (the circle in **a**) convey no information about the grating when motion occurs on the axis parallel to the grating (Par.) and convey maximal information when motion occurs on the axis orthogonal to the grating (Orth.). **c**, Mean percentages of correct discrimination \pm s.e.m. for two subjects. Subject SF was also tested in an additional condition (Rec.), in which we reconstructed the fixational motion of the retinal image under retinal stabilization. In this condition, a recorded eye-movement trajectory was superimposed on the motion of an otherwise stabilized stimulus. In each trial, this trajectory was randomly selected from the pool of all previously recorded unstabilized trials that did not include fixational saccades. Significant differences from complete retinal stabilization (St.) and from normal retinal image motion (Un.) are indicated by * and **, respectively ($P < 0.05$; one-tailed z -tests). The numbers of trials are indicated on each bar.

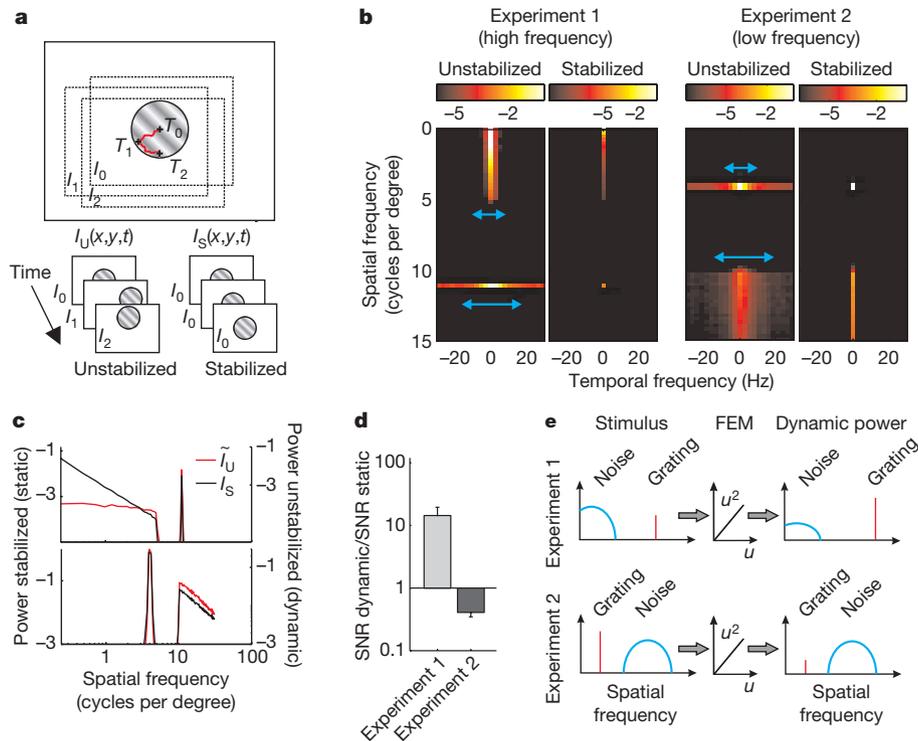


Figure 4 | Influence of fixational eye movements on visual input. **a**, For every trial in experiments one and two, a movie was generated to reconstruct the spatiotemporal input to the retina during the period of stimulus presentation. In the movie $I_U(x,y,t)$ of an unstabilized trial, the frame at time T_i was an image I_i centred at the current location of gaze. In the movie $I_S(x,y,t)$ of a stabilized trial, each frame was the same image I_0 . Examples of these are included as Supplementary Movies. **b**, **c**, Power spectra of the signals entering the eye of subject MD. The full space–time spectra are shown in **b**, **c**. Spatial spectral densities, after integration over temporal frequency,

enhancement of the power of the high-frequency grating. That is, the signal-to-noise-ratio (SNR, the ratio of the power of the grating to the power of the noise) of \tilde{I}_U was much higher than that of the stabilized input (SNR \tilde{I}_U /SNR $I_S = 21$). In contrast, in the case of the low-frequency grating of experiment two, fixational modulations enhanced the noise relative to the grating. In this case, the SNR of \tilde{I}_U was lower than that of the stimulus (SNR \tilde{I}_U /SNR $I_S = 0.33$). Therefore, fixational eye movements introduced temporal modulations that enhanced the grating with respect to the noise in experiment one but not in experiment two. On average, the SNR of the changes in luminance caused by oculomotor activity was more than 30 times larger with high-frequency gratings than it was with low-frequency gratings (Fig. 4d). This effect can be seen in the Supplementary Movies, which reconstruct the input to the retina.

The result of Fig. 4d can be explained on the basis of the spatial characteristics of fixational instability. Because of the small scale of fixational eye movements, it is possible to use a Taylor expansion to approximate the visual input:

$$I_U(\mathbf{x}, t) \approx S(\mathbf{x}) + \zeta(t) \cdot \nabla S(\mathbf{x}) + \frac{1}{2} \zeta(t) H_S \zeta^T(t) \quad (1)$$

where $S(\mathbf{x})$ is the stimulus luminance, H_S its Hessian, and the vector $\zeta(t)$ represents the eye trajectory during the presentation of the stimulus. Equation (1) enables an analytical approximation of the frequency content of the dynamic change in luminance that occurs as a result of the motion of the eye. It predicts that the total power of \tilde{I}_U at a given spatial frequency $|\mathbf{u}|$ is proportional to $R_{SS}(|\mathbf{u}|)|\mathbf{u}|^2$, where R_{SS} is the power spectrum of the stimulus. That is, for small eye movements, the total power that becomes available at non-zero temporal frequency is given by the power spectrum of the stimulus multiplied by $|\mathbf{u}|^2$, a term that enhances high spatial frequencies and

of I_S and of the changes in luminance caused by oculomotor activity (\tilde{I}_U in equation (2)). **d**, Ratio between the SNRs of \tilde{I}_U and I_S in the two experiments. Bars represent mean \pm s.d. across all subjects. **e**, Theoretical explanation of the impact of fixational eye movements. Fixational instability acts as a filter (FEM) that enhances high spatial frequencies in the temporal modulations of luminance present in the input to the retina. The total power at spatial frequency u of these input modulations (dynamic power) is approximately equal to the power of the stimulus multiplied by u^2 .

attenuates low frequencies. As illustrated in Fig. 4e, this term amplifies the grating relative to the noise in experiment one and the noise relative to the grating in experiment two.

Our results show that vision is impaired at high spatial frequencies in the absence of fixational eye movements. This finding is consistent with the spatial frequency dependence of the temporal modulations resulting from fixational eye movements. Neurons in the early visual system are sensitive to these input modulations^{27–29}. As with the stimuli of experiment one, natural visual environments possess substantial power at low spatial frequencies. Our results indicate that sampling visual information by means of a jittering fixation is an effective strategy for analysing natural scenes, facilitating the processing of spatial detail in the face of otherwise overwhelming low-frequency power.

METHODS SUMMARY

Subjects reported the orientation ($\pm 45^\circ$) of a grating masked by noise. In experiment one, a grating with 11 cycles per degree was perturbed by low spatial frequency noise (low-pass cutoff frequency $f_c = 5$ cycles per degree). In experiment two, the stimulus was a grating with 4 cycles per degree overlapped by high spatial frequency noise (high-pass $f_c = 10$ cycles per degree). Stimuli were displayed at the onset of fixation after a saccade towards a randomly cued location. Stimuli were either fixed at a location on the screen (unstabilized condition) or moved with the eye to cancel the retinal motion resulting from fixational eye movements (stabilized condition). In both experiments, the contrast of the gratings was individually adjusted for each subject so that performance levels in the unstabilized condition were approximately 75%.

Contrast thresholds were evaluated under conditions similar to those of experiments one and two using an adaptive tracking method³⁰, both in the presence and in the absence of the retinal image motion originating from fixational eye movements.

In the experiment reported in Fig. 3, the task, stimuli and procedure were identical to those of experiment one, except that trials randomly alternated among all conditions. Random selections of the stabilization axis and the stimulus ensured lack of correlation between the direction of retinal image motion and the grating orientation.

Power spectra were evaluated using the Welch periodogram technique. In the unstabilized condition, the input signal $I_U(\mathbf{x}, t)$ can be expressed as:

$$I_U(\mathbf{x}, t) = S(\mathbf{x} + \zeta(t)) = \bar{I}_U(\mathbf{x}) + \tilde{I}_U(\mathbf{x}, t) \quad (2)$$

where $\bar{I}_U(\mathbf{x})$ is the mean luminance received by the receptor over the period of stimulus presentation. Figure 4 shows the spectra of I_S , I_U and \tilde{I}_U . I_S and I_U possessed equal total power but differed in their spectral distributions.

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

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Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

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METHODS

Subjects. Five naive subjects and one experienced observer, all with normal vision, participated in the experiments. Informed consent was obtained from all subjects in accordance with the procedures approved by the Boston University Charles River Campus Institutional Review Board.

Apparatus and stimuli. To overcome the technical limitations of previous studies of retinal stabilization, the experiments of this study used EyeRIS (ref. 18), a custom-developed system based on a digital signal processor, which allows flexible gaze-contingent display control on a cathode-ray tube (CRT) monitor. This system processes eye movements in real time and guarantees refresh of the stimulus with a maximum delay equal to the time required to render two frames on the CRT display (10 ms at 200 Hz, typical delay 7.5 ms). Joint analysis of the performance of EyeRIS and eye-movement data shows that the error of retinal stabilization in the experiments was smaller than 1' (see Supplementary Methods). Such a high quality of retinal stabilization was possible because of the brief duration of stimulus presentation and the small amplitude of fixational eye movements.

Stimuli were designed on the basis of the predictions of equation (1) to enhance the impact of fixational eye movements on visual input signals. Gratings and noise fields were linearly superimposed, and the resulting patterns were weighted by a two-dimensional gaussian envelope so that the visible area covered approximately 30'. Such a small stimulus could be seen with a single fixation without the need for macroscopic eye movements. Stimuli were displayed on a grey background of uniform luminance equal to the mean luminance of the stimulus (21 cd m^{-2}). To compensate for individual differences in contrast sensitivity, contrast levels were adjusted for each subject in a preliminary experimental session, so that discrimination percentages were around 75% in the presence of the normally moving retinal image. Michelson contrast levels ranged from 4% to 9%.

Stimuli were displayed on a fast phosphor CRT monitor (Iiyama HM204DT) at a resolution of 800×600 pixels and a vertical refresh rate of 200 Hz. Movements of the head were prevented by use of a bite bar with a customized dental imprint and a headrest. Eye position was measured with a Generation 6 DPI eyetracker (Fourward Technologies, Inc.).

Procedure. Stimuli were displayed for 1 s at the centre of the visual field. To study the normal motion of the retinal image that occurs when periods of fixation are separated by saccades, stimuli were presented after the subject performed a saccade from the centre of the screen to a randomly cued location at 1.5° of visual eccentricity. A real-time routine running on EyeRIS displayed the stimulus as soon as it detected the onset of a fixation within 30' of the cued location. Offline analysis of eye-movement traces showed that activation of the display occurred with an average delay of 12 ms after the onset of fixation, as evaluated by a human expert.

In each trial, the grating had equal probability of being tilted by $\pm 45^\circ$ and was followed by a high-energy mask for 1.3 s. Subjects reported the orientation of the grating using a joystick after disappearance of the mask. Trials alternated randomly between the two conditions of normal retinal motion and stabilization. In the stabilized condition, the stimulus was actively translated on the screen under real-time computer control to compensate for the subject's eye movements and always appeared to be immobile at the centre of the fovea. Subjects did not report stimulus fading and were often unable to tell whether or not a trial was stabilized. Trials with saccades larger than 30', or in which the gaze exceeded a 30'-radius window centred on the stimulus, were discarded from data analysis.

Contrast thresholds were evaluated in the same conditions as experiments one and two. The grating contrast was changed at each trial following a 3-up-1-down rule, so that percentages of correct discrimination settled around 79%. To enable fine changes between trials, these experiments were conducted at a lower monitor contrast setting with a background luminance of 6 cd m^{-2} . Every few trials, an image randomly extracted from a database of natural scenes was presented for 2 s to ensure that fading did not affect the results. Each subject underwent a minimum of 60 trials until thresholds settled on steady values. The values shown in Fig. 2 are mean \pm s.d. evaluated over the last ten trials.