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The extraordinarily rapid disappearance of entoptic images

(stabilized images/blood vessels/visual persistence/capillary shadows)

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ABSTRACT **It has been known for more than 40 years that images fade from perception when they are kept at the same position on the retina by abrogating eye movements. Although aspects of this phenomenon were described earlier, the use of close-fitting contact lenses in the 1950s made possible a series of detailed observations on eye movements and visual continuity. In the intervening decades, many investigators have studied the role of image motion on visual perception. Although several controversies remain, it is clear that images deteriorate and in some cases disappear following stabilization; eye movements are, therefore, essential to sustained exoptic vision. The time course of image degradation has generally been reported to be a few seconds to a minute or more, depending upon the conditions. Here we show that images of entoptic vascular shadows can disappear in less than 80 msec. The rapid vanishing of these images implies an active mechanism of image erasure and creation as the basis of normal visual processing.**

J. E. Purkinje (1) was the first to describe the rich variety of perceptual phenomena that arise from objects within the eye (called entoptic images; see also refs. 2–5). As can be readily demonstrated with an ordinary penlight, a source of illumination applied to the sclera through the closed eyelid will, when moved, elicit a striking image created by the shadows of the larger retinal vessels (Fig. 1). A much more detailed entoptic image of retinal vessels is obtained by illuminating the pupil with a point source of light, as described by Helmholtz (ref. 3; see also ref. 6). When light is presented through a pinhole held at the focal point of the eye, the cornea and lens collimate the rays, which, therefore, cast well-defined shadows of the foveal capillaries onto the underlying retina (Fig. 2). Because of their close and constant relationship to the photoreceptor sheet, such shadows can move only slightly across the retina compared with exoptic images, and, like other stabilized images, disappear when their movement is stopped. Entoptic vascular shadows, therefore, provide a simple means of studying the effect of retinal image motion on the continuity of vision, a relationship that remains controversial despite several decades of study (10–17).

To determine how long these entoptic images persist in the absence of motion, we constructed two devices that translated a light source to produce moving shadows of the retinal vessels that could be readily stilled. To observe the larger vessels, a light guide was held in a conical collar that was moved back and forth in the horizontal plane by an oscillating motor (Fig. 1*A*). When the collar was drawn gently across the closed eyelid, the shadows of the major retinal vessels and their branches (save the capillaries) were easily seen. The second apparatus moved a smaller light guide back and forth over a similar horizontal path in front of the open eye, allowing visualization of the foveal capillary shadows (Fig. 2). Both devices were interfaced with a computer so that subjects could indicate the persistence time of the images from the moment the shadows of the blood vessels ceased moving. Alternate trials were used to determine reaction time. By subtracting the values for the reaction time controls from the trials testing image persistence, we could estimate the perceived duration of the stabilized images.

The persistence of the images of larger vessels seen by transcleral illumination was measured in five subjects. On average, the perception of vascular shadows observed in this way lasted for nearly a second (Table 1). When the trials were repeated with the instruction to estimate the persistence time of only the smallest vessels that could be seen in this manner (i.e., the arterioles and venules that approach the fovea—see Fig. 1*C*), the duration of image persistence was reduced in four of the five subjects, averaging about 0.5 sec.

To examine the persistence of capillary shadow perception in central vision, we used the smaller light source to deliver collimated rays through the pupil of the open eye (Fig. 2). (The capillary shadows are not seen by transcleral illumination because of the divergence of the light rays, the larger source, and scattering of the light by the eyelid and sclera.) The average persistence time of the foveal capillary images was less than any of the larger blood vessels viewed transclerally (Table 1). After stopping the collimated light source, the image of the stabilized shadows vanished in less than 80 msec, on average (see also refs. 4 and 5). Thus, foveal images can disappear far more rapidly than implied by most previous work on the perceptual fading of stabilized retinal images (which typically report persistence times of at least a few seconds after stabilization; for review, see refs. 17–20).

We next explored the velocities of motion across the retina that are sufficient—and optimal—for viewing capillary shadows. The minimum velocity necessary to see vascular shadows for the several seconds of testing was greater in all five subjects than the rates of slow eye movements (17, 18). This was true whether the head was immobilized (Fig. 3) or freely moving (data not shown). All subjects showed a similar relationship between shadow velocity and visibility, with optimum visibility occurring at values more than an order of magnitude faster than eye movements that have been measured with the head immobilized, and several times greater than eye movements reported for subjects free to move their heads (see ref. 17). Evidently the persistence of visual images can be enhanced by moving the retinal image over large distances (as occurs routinely for exoptic images) or moving the image rapidly back and forth over the same set of photoreceptors (as occurs for entoptic vascular shadows).

Finally, we asked whether movement of the vascular shadows is essential for their perception. To explore this point, we modified the apparatus used to visualize the retinal vessels so that both set-ups (see Figs. 1 and 2) could deliver a stroboscopic flash (15–30 μsec; Monarch Instruments, Amherst, NH). Such a brief period of illumination stimulates only one set of photoreceptors, there being no time for movement of the eye or head. Brief pulses of light shown through the sclera in the absence of movement clearly allowed momentary visual-

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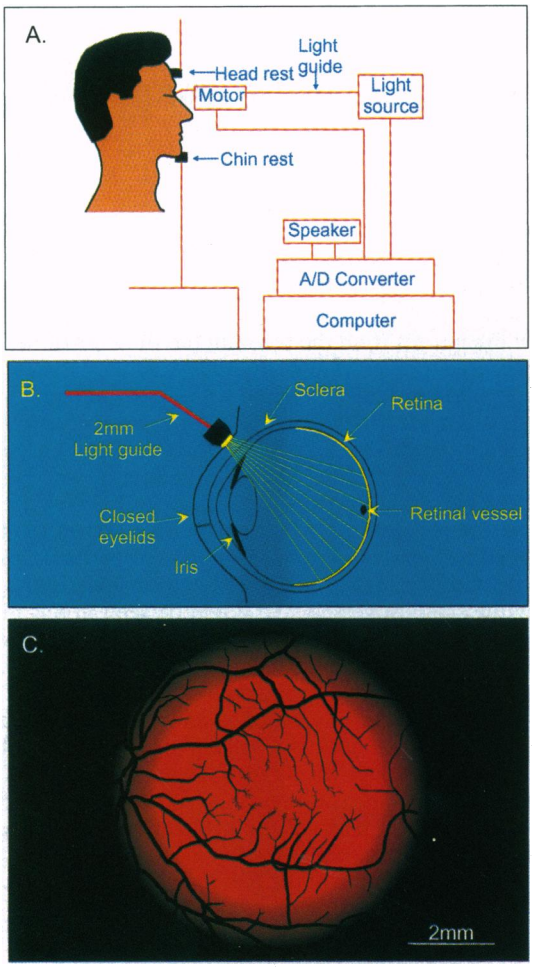

FIG. 1. Entoptic visualization of the retinal blood vessels (excluding capillaries) by transcleral illumination. (*A*) The head was immobilized with a chin and forehead rest, allowing a light guide (d = 2 mm) mounted in a conical aluminum collar to contact the closed lid of the right eye. The luminance at the light source was 90 cd/m^2 (measured by a PIN photo detector; UDT Sensors, Inc., Hawthorne, CA). An alternating motor controlled by a computer moved the light back and forth over a 6-mm horizontal path. Two seconds after the start of this movement, the computer switched the motor off, thus abruptly stopping the light. Subjects then indicated how long they continued to see the entoptic vascular image. Each of the five subjects made five such determinations in 10 different sessions for each category of vessel size (see Table 1). (*B*) This method of illumination casts discernible vascular shadows on the retina because the divergence of light rays from the source diminishes the vascular penumbras and increases the contrast of the umbras. (*C*) Diagrammatic representation of the vascular image produced by this method. Since the cornea and lens do not collimate the light in this circumstance, the capillaries are not seen.

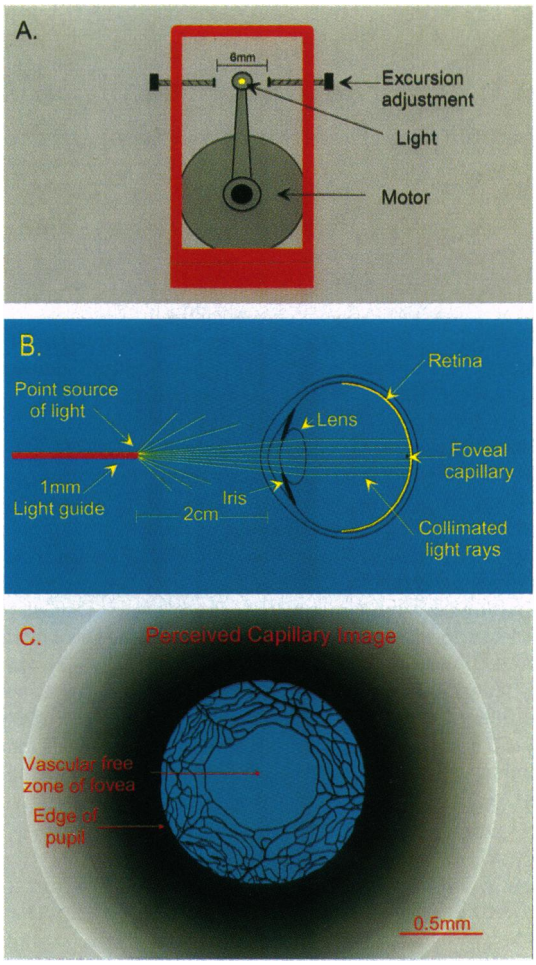

FIG. 2. Entoptic visualization of foveal capillary shadows by collimated light. (*A*) A light guide (d = 1 mm) mounted on the armature of a pen motor that moved between two stopped positions was positioned approximately 15 mm in front of the right cornea. A blue filter (Wratten 47B; 3M Company) was used to increase the visibility of the retinal capillaries by taking advantage of the light-absorbence characteristics of hemoglobin (6). The luminance 15 mm from the light guide was 1.1 cd/m^2. The apparatus, subjects and protocol were otherwise the same as described in Fig. 1. As in the transcleral observations, light moved in a 6-mm horizontal path at a frequency of 6 Hz. (An exception is the experiment shown in Fig. 3, in which the frequency of movement was varied between 1 and 15 Hz.) (*B*) Diagram of the collimation of rays from a point source located near the focal point of the eye. Parallel rays minimize the penumbra of entoptic objects, greatly enhancing their visibility. In particular, the foveal capillaries, which lie between the light source and the photoreceptors, are readily seen. (*C*) Diagrammatic representation of the entoptic capillary image seen by observers with collimated illumination. Remarkably, the capillary shadows visualized in this way are only 7–10 μm in diameter (7). Analysis of latex-filled vessels of the macaque fovea shows the average distance between capillaries to be about 28 μm (8). Assuming this value for human subjects, the entoptic capillary shadows would approximate exoptic grating patterns of 10 cycles/degree. Gratings of this sort can be seen in central vision at 1% contrast (9). The contrast of capillary shadows has been estimated to be between 20 and 40%, depending on the size of the light and its wavelength (6). The stimuli provided by the capillary shadows are, therefore, far above threshold (as indeed they appear to be subjectively).

ization of the larger retinal vessels in all five subjects. All the subjects also saw portions of the foveal capillary image when a single pulse of collimated light was delivered via the pupil. Although the observed image was judged to be less complete (i.e., to contain fewer capillaries) than the image observed over several seconds with the continuously moving light source, all the subjects reported seeing elements of the same scene. Since entoptic vascular shadows can be seen with illumination from a single stroboscopic flash, motion, while enhancing the visibility of entoptic shadows, is not a prerequisite for their perception.

The rapid and complete disappearance of these entoptic images is at odds with previous work (17–20) on stabilized exoptic images. In general, earlier studies have reported degradation of images measured in seconds or minutes (17–20). It is clear from our results that images in central vision are much more ephemeral. If retinal motion flags for even an instant, the perception of capillary shadows in central vision disappears. Comparing these results to the normal viewing of exoptic images, it is apparent that rapid eye movements (saccades) would not, by themselves, be frequent enough to maintain this percept since they occur only up to five times per second (ref. 18; cf. Table 1). Slow eye movements, which are

Table 1. Estimated persistence time of the entoptic images of retinal blood vessels

Illumination	Vessels	Subject 1	2	3	4	5	Mean
Transcleral	All vessels	591 ± 47	1614 ± 147	635 ± 60	551 ± 48	1134 ± 160	905 ± 247
	Arterioles and venules	358 ± 26	946 ± 98	451 ± 57	616 ± 43	320 ± 34	538 ± 114
Collimated	Capillaries	52 ± 34	70 ± 20	100 ± 16	85 ± 7	86 ± 7	78 ± 8

In trials measuring reaction time, which alternated with the image persistence trials, the subject was instructed to press a key the moment the light source stopped moving. Corrected values of persistence were obtained by subtracting the average of the five uncorrected persistence trials and the average of the five reaction time trials (range = 171–352 msec). As there were 10 such five by five trial sets, the mean values for the different subjects are based on a sample size of 10. Since all five subjects reported the disappearance of the arrested capillary shadows to be immediate, this method may overestimate image persistence. All values are reported in msec; the mean ± 1 SEM are shown.

thought to prevent image disappearance and optimize vision during fixation (21, 23) would also be insufficient to maintain the percept of capillary shadows. Our results demonstrate this in two ways: (*i*) by the need to move the light source at velocities far exceeding normal drift rates for visibility (Fig. 3) and (*ii*) by the failure to see the entoptic images when subjects observed the light source with their heads free to move.

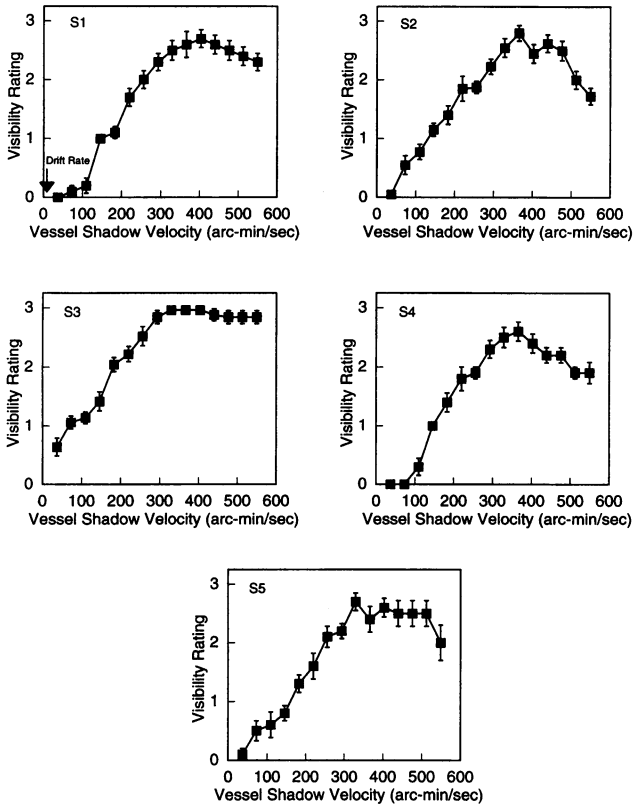

FIG. 3. Visibility of foveal capillary shadows as a function of the velocity of their movement across the retina. Data were collected in randomized trials in which subjects were allowed to view the entoptic image for 2 sec at a particular velocity of the light source. The quality of the entoptic image was then rated on a four-point scale, with 0 corresponding to absence of any shadow perception and 3 to an optimal image. Fifteen velocities were presented in random order in each of 10 trials. The results were then averaged. The mean visibility rating (±1 SEM) for each of the five subjects is plotted against the calculated shadow velocity in minutes of arc/sec. For this purpose, we assumed a point source in the plane of the eye's exit pupil 20.5 mm from the retina (Gullstrand's schematic eye). We further assumed that the capillaries are 300 μm from the outer segments of the cones (14, 15). Knowing that the light source moved over a 6-mm path, we could calculate the velocity of the shadow movement. The arrow indicates the mean velocity of drift movements for the human eye during fixation (taken from ref. 11). Optimal velocities for maintaining the entoptic image were about 60 times the average velocity of such slow eye movements with the head fixed and several times greater than image velocities measured with the head free to move (1, 17, 22).

Why then do similar exoptic images remain visible while the entoptic images of vascular shadows disappear nearly instantly in the absence of motion? The answer is presumably that the eye movements normally change the position of the retinal images derived from exoptic objects by a large enough amount to sustain perception for periods substantially greater than the disappearance times we report (a phenomenon that probably depends on the number of novel photoreceptors that are stimulated per unit time). The close and constant relationship of retinal vessels to the underlying receptors allows only a fraction of this change for entoptic vascular shadows, thereby limiting the ability of normal eye or head (or object) movements to sustain their perception. This relationship may also explain the longer persistence time of the entoptic images of larger vessels (since the arteries and veins are farther from the retina than the capillaries, their shadows move greater distances).

In summary, entoptic images of central retinal capillaries vanish less than 0.1 sec after cessation of shadow movements. Eye movements do not provide sufficiently rapid translocation of vascular shadows to maintain perception of these images. These observations show that vision entails an active mechanism that can erase visual images at a surprisingly high frequency (>10 Hz). By the same token, sustaining vision in these circumstances requires the stimulation of novel sets of photoreceptors at a much higher rate than can be provided by eye movements. Thus, these conclusions point to a rapid mechanism of image creation and erasure as the foundation of normal visual processing (see also refs. 24 and 25).

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