Chapter 14
Human Polarization Sensitivity

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Abstract Humans can detect the E-vector of incident polarized light using a subtle, transient visual phenomenon known as Haidinger's brush. The effect is a result of the human macula having the properties of a radial analyser with peak absorption at 460 nm. A number of mechanisms, each capable of generating radial diattenuation, have been proposed: (1) oblique light incident on cone outer segments, (2) form dichroism in the Henle fibre layer (the photoreceptor axons) and (3) a perpendicular arrangement of dichroic carotenoid pigments with respect to the radially oriented Henle fibres. A close correlation between the dichroic ratio of the macula and the optical density spectrum of liposome-bound lutein and zeaxanthin provides strong evidence that macular pigment plays a key role. Corneal birefringence can affect the contrast and perceived angle of the brush, together with the appearance of the phenomenon in circularly polarized light. When the retina is photographed between crossed polarizers, a brush-like pattern is observed; this is a result of the birefringence of the Henle fibre layer and cornea and is distinct from the radial diattenuation that generates Haidinger's brush. A secondary entoptic phenomenon that allows humans to detect the orientation of polarized light was described by Gundo von Boehm. Boehm's brush is only visible when a polarized

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G. Horváth (ed.), *Polarized Light and Polarization Vision in Animal Sciences*,
Springer Series in Vision Research 2, DOI 10.1007/978-3-642-54718-8_14,

light source rotates in the peripheral visual field against a dark background and results from light scattering off axis into the photoreceptors. Both phenomena allow for the detection of polarized light by the unaided human eye; however, there is no evidence to suggest that such capabilities are adaptive.

14.1 Introduction

In 1844, Wilhelm Karl von Haidinger (1795–1871), an Austrian physicist, geologist and mineralogist, discovered that the human eye is able to perceive the linear polarization of light due to an entoptic phenomenon that was later given his name. This discovery of Haidinger's brush preceded, by 100 years, Karl von Frisch's (1949) discovery that honeybees (*Apis mellifera*) are sensitive to the linear polarization of skylight and use it for orientation and navigation. The ability to detect the orientation of the electric field vector (E-vector) of polarized light is surprising as human photoreceptors, like those of all vertebrates, are generally thought to be insensitive to the E-vector orientation of axially incident light (exceptions to this are detailed in Chap. 9). Human polarization sensitivity appears to be a by-product of the dichroic properties of the retinal layers; specifically the macula. To date, there has been no biological function assigned to the human ability to detect the E-vector orientation of polarized light. In 1940, Gundo von Boehm described another entoptic phenomenon that enables the human eye to perceive polarized light. 'Boehm's brush' is most visible when a small polarized light source is viewed against a dark background in the peripheral visual field and is only perceived if the E-vector of the light source is rotating. The literature on human polarization sensitivity has also been reviewed by Lester (1970), Zhevandrov (1995), Fairbairn (2001), Horváth and Varjú (2004, pp. 355–361).

14.2 Haidinger's Brush

If one gazes at a homogenous polarized white light field, a faint pattern can be seen consisting of a small yellowish bowtie or 'brush' with bluish intervening areas (Fig. 14.1). This faint entoptic image referred to as Haidinger's brush subtends approximately 5° and rotates about the fixation point as the E-vector of the incident light is rotated. If the polarized light field remains unchanged, neural adaptation causes the effect to fade within a couple of seconds.

Usually, a little practice is needed to see Haidinger's brush, but the effect can be enhanced and maintained by changing the E-vector angle of the polarized light. Looking at a white polarized light field in which the E-vector alternates between two perpendicular E-vector orientations (e.g. horizontal and then vertical) can make the effect more visible, as the afterimage of one orientation of the brush reinforces the

Fig. 14.1 An illustration of the appearance of Haidinger's brush in response to a vertically polarized light stimulus. The sensation of *blue* (vertically aligned *light blue* 8-shaped figure, the *blue part* of the Haidinger's brush) results from a simultaneous contrast effect and has been generated here by removing *yellow* from regions of an otherwise *yellow-tinted background*. The horizontally aligned *dark yellow* 8-shaped figure is the *yellow part* of the Haidinger's brush

image of the second formed at 90° to the original. Alternatively, the E-vector, or the observers head, can be rotated to continuously refresh the image. Recording the potentials evoked in the visual cortex in response to rotating a linearly polarized blue (465 nm) stimulus, Dodt and Kuba (1990) found that the electrophysiological response they measured disappeared when the E-vector rotation ceased. Similarly, no electrical response was detected in response to the rotation of a green (531 nm) stimulus, consistent with reports that if the blue component of the incident polarized light is filtered out, Haidinger's brush is not observed (Stokes 1850; von Helmholtz 1924).

Haidinger's brush has the best contrast when the degree of polarization approaches 100 %, for example looking at a white area on a liquid crystal display (LCD) computer monitor, which employs polarizers as part of the image forming technology. A practiced observer can also detect Haidinger's brush at the zenith of a clear blue sky at sunrise or sunset (or in general, 90° from the sun), where the degree of polarization reaches 75 % (see Chap. 18). For further advice on observing the effect for yourself, consult Fairbairn (2001) or Ovcharenko and Yegorenkov (2002).

14.3 Potential Mechanisms Generating Haidinger's Brush

If one were to image a linearly polarized light field (with homogeneous E-vector orientation) through a linear polarizer in which the transmission axes were oriented radially (a radial analyser) (Fig. 14.2a, b), one would see a dark bowtie-like brush resulting from light attenuation along the meridian perpendicular to the E-vector

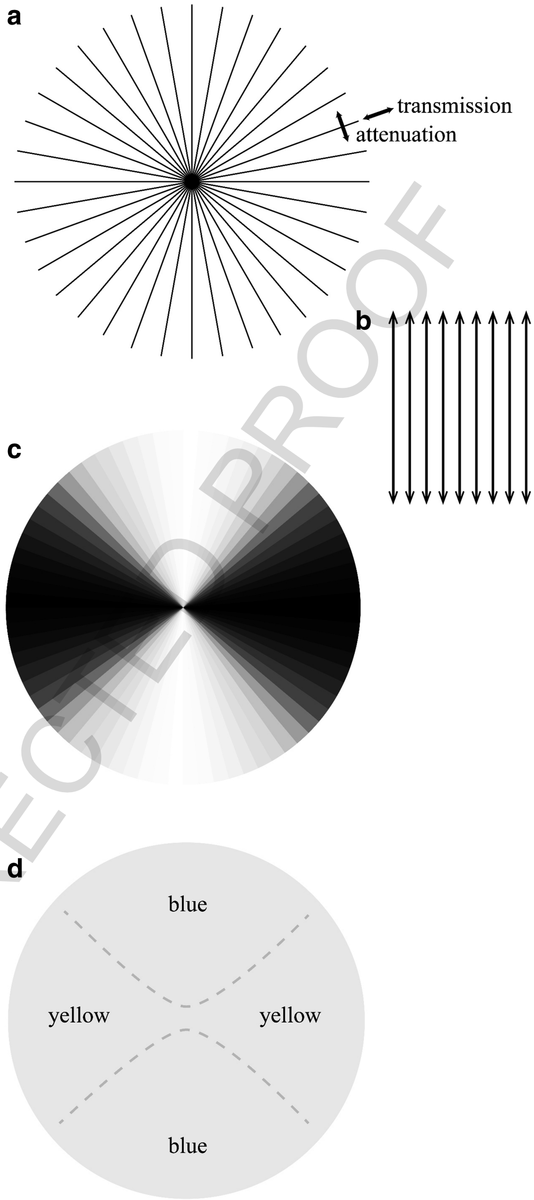

Fig. 14.2 A simple model simulating Haidinger's brush. Looking through a linear polarizer in which the transmission axes are oriented radially (**a**), at a linearly polarized light field with a homogeneous, vertically oriented E-vector (**b**), a darkened bowtie-like pattern of intensity is observed (**c**) as light is preferentially attenuated along the horizontal meridian, perpendicular to the transmission axes of the radial analyser. If the radial analyser selectively attenuates blue light, then areas that appear dark in (**c**) (where blue light has been depleted) would appear yellower than the prevailing incident light field. The resulting percept is shown in (**d**). The blue regions that flank the yellow are understood to be the result of a simultaneous contrast effect produced in response to the yellow bowtie. In this way, a structure in the retina acting as a radial analyser and selectively attenuating short wavelength light could give rise to Haidinger's brush

orientation of the polarized light field (Fig. 14.2c). If this radial analyser preferentially attenuated short wavelengths from the incident white light field, the resulting bowtie (where the blue light had been attenuated) would appear yellow (Figs. 14.1 and 14.2d). The blue-indigo regions that appear perpendicular to the yellow brush have been attributed to a psychophysical simultaneous contrast effect (Stokes 1850) generated by blue-yellow colour opponent processing.

The possibility that a radial analyser located within the retina is generating Haidinger's brush was first proposed by Maxwell (1850), and radial dichroism has now been demonstrated by both microdensitometry experiments on excised retinas (Snodderly et al. 1984) and psychophysical tests (De Vries et al. 1953; Naylor and Stanworth 1954; Bone 1980; Bone et al. 1992). A close correlation between the optical density spectrum of the macular pigment and the dichroic ratio of the macula as a function of wavelength has provided strong support for the involvement of the macular pigment in generating this dichroism (Bone et al. 1992). Macular pigment is localized in the Henle fibre layer of the retina, which contains numerous, closely packed, cone photoreceptor axons that extend radially from the fovea towards synapses in the displaced outer plexiform layer (Figs. 14.3 and 14.4). Although other models have also been proposed (Summers et al. 1970; Hochheimer and Kues 1982; Le Floch et al. 2010), an interaction between the macular pigment and this radially symmetric fibre framework is the leading hypothesis explaining the origin of radial dichroism in the retina. However, the exact nature of this interaction is subject to debate. A number of authors (e.g. von Helmholtz 1924; De Vries et al. 1953; Naylor and Stanworth 1954; Bone 1980) have attributed Haidinger's brush to a tangential arrangement of dichroic macular pigment molecules, oriented on average, perpendicular to the Henle fibre membranes. Alternatively, the macular pigment molecules could be randomly oriented within a geometrical arrangement of Henle fibres capable of generating form dichroism (Hemenger 1982). In what remains of this section we review the proposed hypotheses in more detail.

Macular pigment is composed of the carotenoids lutein, zeaxanthin and meso-zeaxanthin (Bone et al. 1985, 1993; Schalch et al. 2009), which are extensively conjugated along their polyene chains and absorb strongly if the incident light is polarized parallel to the long axis of the molecule (Bone and Landrum 1983, 1984). If the long axes of the carotenoid pigment molecules were aligned tangentially to concentric circles centred on the fovea (Fig. 14.3), the result would be a radial analyser. Bone et al. (1992) calculated that an average molecular orientation of 54.7° or less with respect to the normal to the surface of the Henle fibres would be sufficient to generate Haidinger's brush in the correct orientation. If the carotenoids adopted a membrane spanning configuration in the lipid bilayers of the Henle fibres, this could generate the radial dichroism necessary to explain Haidinger's brush (Bone and Landrum 1984). This configuration is certainly plausible; however, as carotenoids can adopt a range of orientations within lipid bilayers (Gruszecki and Strzalka 2005), the specific orientations of the various carotenoid components of the macular pigment within the Henle fibre membranes remain uncertain. Recently, specific macular binding proteins for lutein and zeaxanthin have been identified (Bhosale et al. 2004; Li et al. 2011) and may provide another mechanism for the tangential alignment of the dichroic macular pigments.

An alternative model, proposed by Hemenger (1982), does not require the directional organization of the macular pigment molecules, but rather of the

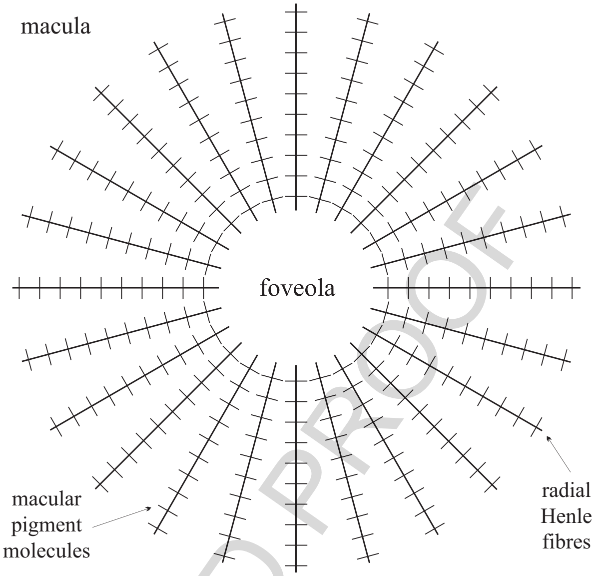

Fig. 14.3 Schematic representation of the hypothesized tangential arrangement of the macular pigment molecules bound to the radially oriented Henle fibres in the human macula [adapted from Fig. 32.3 of Horváth and Varjú (2004, p. 358)]

medium in which they are located. Form dichroism results from repeated blocks of absorbing and non-absorbing materials with a spatial frequency comparable to the wavelength of light. This could be the case in the Henle fibre layer, with pigment molecules randomly oriented between the radially arranged photoreceptor axons. Hemenger (1982) stopped short of a full model of form dichroism demonstrating only that attenuation could be increased in the local environment of a single fibre. Detractors of this hypothesis have indicated that it requires carotenoids to be present in an aqueous phase between the Henle fibres, the spectroscopic signature of which is not consistent with psychophysical measurements of dichroic ratio (Bone and Landrum 1984). Summers et al. (1970) developed a related theory that Haidinger's brush is an interference figure resulting from the illumination of an anisotropic absorbing crystal with strongly convergent polarized light. They proposed that the regular arrangement of fibrils gives rise to form birefringence, and the presence of macular pigment adds absorption to the system. A distinctive feature of this hypothesis is that it does not involve the circular symmetry of the Henle fibre layer, but rather looks to the many parallel fibres that traverse the region between the fovea and the optic disc (the retinal nerve fibre layer; Fig. 14.4b) as the potential birefringent crystal producing Haidinger's brush. Attributing polarization sensitivity to this structure is problematic as this would produce an effect that is not centred at the fixation point, which is inconsistent with all reports that Haidinger's brush is localized in the centre of the visual field (Maxwell 1850).

It has also been suggested that Haidinger's brush is produced by light impinging on the outer segments of foveal photoreceptors slightly off axis, as it is well established that photoreceptor outer segments are dichroic when illuminated transversely (Denton 1959; Liebman et al. 1974). Gribakin and Govardovskii (1975)

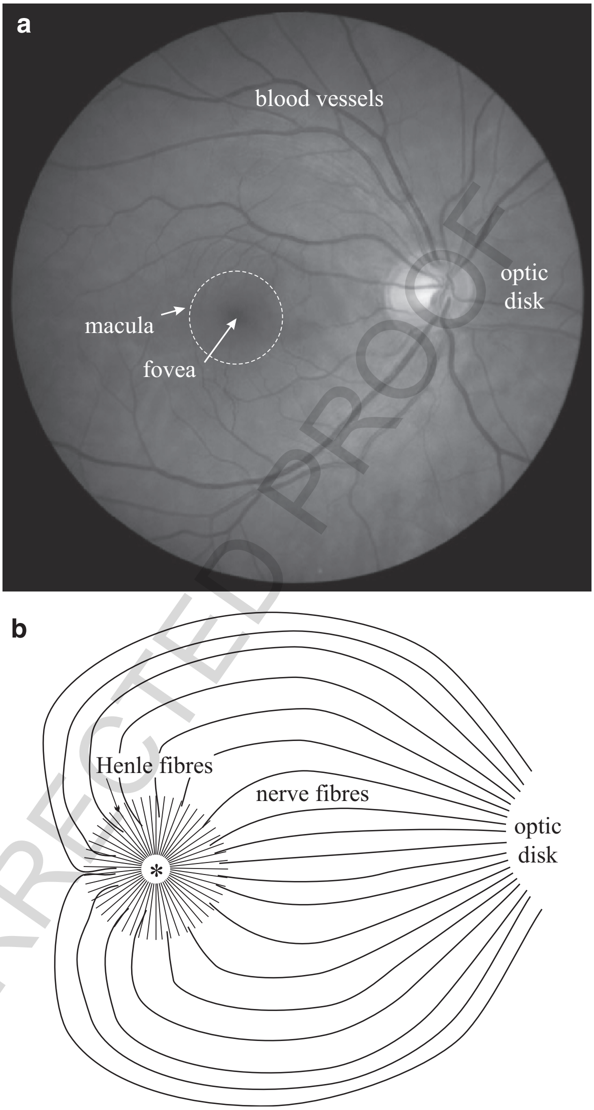

Fig. 14.4 (**a**) Photograph of a human retina with the fovea, optic disc (blind spot) and blood vessels [after Fig. 32.2a of Horváth and Varjú (2004, p. 357)]. (**b**) Schematic drawing of the retinal nerve fibre axon arrangement at the fovea (marked by an *asterisk*), which is nearly devoid of nerve fibres, includes the central 0.35 mm of the fovea (1.2° of the visual field), located 4 mm temporally and 0.8 mm inferior to the centre of the optic disc. The macula lutea (Latin for *yellow spot*) is a portion of the retina centred on the fovea containing the carotenoid pigments lutein, zeaxanthin and meso-zeaxanthin [after Fig. 32.1b of Horváth and Varjú (2004, p 356)]

suggested that any slight tilt in the cone array would provide a mechanism for detecting polarization. However, the Stiles–Crawford effect (Stiles and Crawford 1933) together with micrographic evidence (Laties et al. 1968; Fuld et al. 1979) indicates that photoreceptors in the human retina align towards the centre of the pupil to maximize photon catch; thus a systematically tilted photoreceptor array in the human eye is unlikely. Furthermore, the off axis light hypothesis could not readily explain the blue and yellow colours of the brushes. Alternatively, there may be a significant amount of non-image-forming light incident obliquely on the foveal photoreceptor array. Polarized light differentially scattered by the Henle fibre layer could traverse the outer segments obliquely to produce brush-like effects (Weale 1976). Le Floch et al. (2010) proposed that differential attenuation arises through differential reflection of oblique polarized light from the surface of short-wavelength-sensitive cones, which have a lower density in the fovea, and therefore, it is claimed, have a greater exposure to oblique light. However, the existence of sufficient oblique light to generate this phenomenon in the retina remains speculative, and the sensitivity spectrum of macular dichroism (Bone et al. 1992) does not match the spectral sensitivity of human short-wavelength-sensitive cone photoreceptors, as would be expected if this hypothesis were the true explanation.

14.4 Corneal Birefringence, Circular Polarization and Haidinger's Brush

Shurcliff (1955) observed that circularly polarized light can also produce a brush, such that an observer can determine the handedness of circular polarization. Right-handed circularly polarized light reportedly produces a brush at approximately +45°, and left-handed circularly polarized light produces a brush at −45°. These fixed brushes have been referred to as 'Shurcliff's brushes', but this is potentially misleading as they have the same origins as Haidinger's brush. The effect can be simply explained by the presence of the birefringent cornea, acting as a quarter waveplate. Circularly polarized light incident on such a structure emerges linearly polarized at ±45° to the optical axis of the waveplate, and Haidinger's brush is perceived as before. In practice, the orientation of the optical axes and the retardation that the cornea introduces vary across the population. Knighton and Huang (2002) found that 80 % of subjects they measured had corneal retardance values in the range 0.03λ to 0.12λ for measurements taken at $\lambda = 585$ nm. Furthermore, the orientation of the fast and slow axes of the cornea varied by tens of degrees between individuals (Knighton and Huang 2002). Rigorous measurements of the angle at which a brush induced by circularly polarized light is perceived have not yet been undertaken, but the inter-individual variability in corneal parameters means that a brush fixed at exactly 45°, as would be produced by a quarter waveplate with fast and slow axes aligned horizontally and vertically, is more likely to be the exception than the rule.

The salience of Haidinger's brush is also expected to vary with orientation of the incident E-vector as a result of the birefringence of the cornea. Modelling the birefringent cornea and radially dichroic retina, Misson (2003) and Rothmayer et al. (2007) predicted an angle- and retardation-dependent contrast fluctuation with minimum contrast associated with linearly polarized light incident at 45° to the optical axes of the cornea, which introduces a retardation of a quarter of a wavelength. This is the reverse scenario to that described above: linearly polarized light is now converted to circularly polarized light and Haidinger's brush is abolished. Rothmayer et al. (2007) also predicted an increasingly nonlinear relationship between the E-vector angle of incident polarized light and the perceived angle of the brush as the retardation of the cornea approaches a quarter of a wavelength. As a result, some observers may describe the brush 'jumping' or 'switching' as the incident E-vector rotates relative to the eye. The optical properties of the human cornea are still under investigation, with some authors reporting that it is best described as a curved dome of biaxial material (Knighton et al. 2008). If this is the case then the retardation and orientation of the optical axes will vary with position. To date, theoretical models of the dynamics of Haidinger's brush have not incorporated these more advanced models of corneal birefringence. von Helmholtz (1924) reported that when viewing linearly polarized light at various orientations, the width of Haidinger's brush changed. If the yellow brush was formed horizontally, it was narrower at its centre than when the yellow brush was vertical. Hochheimer and Kues (1982) speculated that this effect may also be due to the birefringence of the cornea.

14.5 Imaging Retinal Polarization Patterns: The Macular Cross

If the primate retina is photographed with the cornea removed and crossed linear polarizers in the stimulating and recording light paths, a 4–5° Maltese cross pattern can be observed overlying the macula, centred on the fovea (Hochheimer 1978). The macular cross pattern is produced when the illuminating polarized light is in the range 400–700 nm, but disappears for wavelengths longer than this (Hochheimer and Kues 1982). The formation of this cross pattern is due to a periodic refractive index variation between the Henle fibres and the Müller cells, which are in close apposition to them. This radial refractive index modulation produces uniaxial form birefringence with the slow optic axis directed along the length of the fibres (Brink and van Blokland 1988; Elsner et al. 2008). Macular birefringence is solely responsible for the cross pattern, but if the macula is imaged in the same way (with polarizers in the stimulating and recording light paths) but now through the birefringent cornea, then a brush-like pattern is obtained (Delori et al. 1979). The cross pattern is recovered when the E-vector of the incident light is aligned with either the slow or the fast axis of the cornea. The similar appearance of the macular cross to the entoptic phenomenon of Haidinger's brush has led to some confusion between (a) the radial birefringence and additional linear polarizer, which gives rise to the cross and (b) the radial dichroism that gives rise to the perception of Haidinger's brush.

Hochheimer and Kues (1982) tested several healthy human subjects and several patients with diseased retinae to establish whether they could see Haidinger's brush. All those who could see Haidinger's brush had an easily discernible macular cross, and those who could not see Haidinger's brush did not display any such retinal polarization pattern. If both effects are dependent on the radial arrangement of the Henle fibre layer (albeit with different physical origins), this correlation is to be expected. More recently, scanning laser polarimetry of the macular cross has been employed to identify the location of the fovea in babies and young subjects (Van Nasdale et al. 2009).

14.6 Boehm's Brush

There is another entoptic phenomenon that provides a means for the perception of polarized light, the so-called "Boehm's brush", which is named after the German scientist Gundo von Boehm who first reported the effect in 1940. He described a visible rotating brush pattern of increased intensity that has its long axis oriented perpendicularly to the E-vector of a small (1–2°), rotating (1-2 Hz), linearly polarized light source, viewed in the peripheral visual field (15–20° parafoveally) against a dark background. Boehm's brush does not appear within the light source that causes it, but is perceived as a pattern of glare on either side of the image of the light source on the retina (Fig. 14.5). von Boehm (1940a, b) performed a range of tests to characterize the phenomenon and showed that the effect disappears instantly when rotation of the polarized light source stops. If the rotation is too fast, the ends of the observed brush lag behind creating a spiral-like effect. Under optimal viewing conditions, Boehm's brush may subtend an arc of up to 12° and, unlike Haidinger's brush, is perceived to be the same colour as the light source. The phenomenon is also visible when the light source is elliptically polarized, but becomes invisible as linearly polarized light becomes more circular (disappearing when ellipticity is above 0.8). It is equally salient in both right and left handed elliptically polarized conditions. Furthermore, von Boehm (1940a, b) showed that it is visible to people of all ages, as well as aphakics (people lacking lenses) and those suffering from various forms of colour blindness.

von Boehm (1940a, b) proposed that scattering within the retina gives rise to the phenomenon, which explains why the rotating brush pattern is oriented perpendicular to the orientation of the E-vector. When the light source is polarized, light interacting with the non-photosensitive layers of the retina will be preferentially scattered along an axis that is perpendicular to the E-vector orientation of the incoming light. Scattering should be strongest near the axis of the beam and decreases sharply with increasing angular distance. In support of his scattering hypothesis, Boehm (1940a, b) showed that the brush effect is weaker (narrower and shorter) at longer wavelengths. This would be expected if the brush is generated by a Rayleigh scattering process, which has a $1/\lambda^4$ dependence. He also showed that the brush takes on the same colour as the polarized light source, also consistent with the proposed scattering mechanism.

14.7 Applications of Human Polarization Sensitivity

Whilst human polarization sensitivity is not understood to have any direct behavioural significance, efforts have been made to make practical use of the phenomenon. A simple test based on a rotating polarized light field was developed to assess the potential clinical relevance of polarization sensitivity. The test consisted of a small light fitted with a blue filter and a rotating linear polarizer. Subjects were asked to identify the direction that the brush was rotating. Healthy

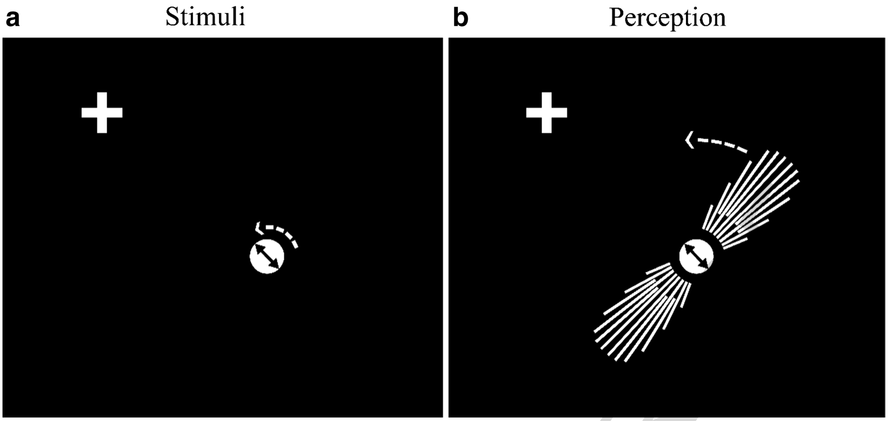

Fig. 14.5 Schematic representation of the conditions necessary to elicit the Boehm's brush phenomenon (**a**), and how it is perceived (**b**) relative to a linearly polarized light source (*circle with arrow inside*). The cross is the point of fixation. The *circle with arrow inside* represents a small (1–2°) linearly polarized light source rotating in the direction of the *broken arrow above the circle*, and positioned in the peripheral field of view. The rotating brush-like pattern in **b** has its long axis perpendicular to the E-vector of the rotating polarized light source

subjects and subjects with known existing eye diseases were tested (Schmidt 1938; Goldschmidt 1950; Forster 1954; Naylor and Stanworth 1955; Sloan and Naquin 1955). These studies revealed that perception of Haidinger's brush is normal in humans without visual defects. An inability to perceive Haidinger's brush is associated with disturbance of the macula and its surrounding structure, but this has proven to be of little use for differential diagnostic assessment. Recent studies have suggested that the human ability to perceive Haidinger's brush could be used to directly observe the optical activity of chiral molecules, the Faraday effect and the outcome of quantum entanglement experiments (Sekatski et al. 2009; Ropars et al. 2012a). Ropars et al. (2012b) suggested that the alleged sky-polarimetric Viking navigation could have been based on the perception of Haidinger's brush (see Chap. 25). Boehm's brush has been used to investigate intraocular scatter. Vos and Bouman (1964), for example, used the phenomenon to show that scatter from the retina itself accounts for between 12 and 40 % of the total scattered light inside the eye. Weale (1976) used Boehm's brush as a tool to investigate spectral aspects of the Stiles–Crawford effect.

A greater understanding of the structures and mechanisms giving rise to polarization sensitivity has the potential to generate future applications in biomedical science. It is also useful to note that the human ability to detect E-vector orientation is a great way to introduce the uninitiated to the study of polarized light!

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