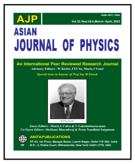

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From waveguides to directional antennas – understanding the optics of retinal photoreceptors

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Dedicated to Prof Jay M Enoch

The Stiles-Crawford effect (i.e., the psychophysical Stiles-Crawford effect of the first kind) has remained somewhat of an enigma in vision science since its discovery 90 years ago. It is often treated as a curiosity, or even a minor effect, but the reality is that at a fundamental level it is so much more. It represents the last optical process in the eye where photon absorption triggers the visual pigments in the cones and rods resulting in neural signals and, ultimately, a visual sensation via the visual cortex. Naturally, most ophthalmic studies focus on the anterior eye, the cornea and lens, that determines how light is focused onto the posterior eye and retina. The latter is typically considered as a screen onto which an image of the outside world is projected. Nonetheless, we can only hope to comprehend vision and the optics of the eye once the detectors, i.e., the photoreceptors and their visual pigments, are included. This has been central to much of Prof Jay M Enoch's work. In my own research, I was initially intrigued by a study on the relationship between the psychophysical Stiles-Crawford effect and the directionality in backscattered light in the pupil plane often referred to as the optical Stiles-Crawford effect. This led me to revisit waveguide models of photoreceptors in what I initially thought would be just a single study. Yet, as a pebble in the shoe, it has kept returning for nearly two decades posing additional questions. Now, we may be at the end of the road in terms of understanding the Stiles-Crawford effect of the first kind, but we are still only in the infancy of comprehending how this vital last optical step in our visual system adapts to changes in relation to age and to disease. Only when comprehending its adaptability and function, can we hope to fully separate optical effects from neural factors to obtain an entirely satisfactory and accurate model of vision.

Keywords: Photoreceptors, Waveguides, Scattering, Leakage, Stiles-Crawford effect, Directionality, Ellipsoid.

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1 Introduction

Almost 200 years ago, E W Brücke reported on the elongated shape of retinal photoreceptors [1]. Yet, its direct impact on vision was first recognized in a vital study by W S Stiles and B H Crawford in 1932/33 who examined the visibility of a pencil of light entering the eye through different parts of the pupil. They recognized that this angular sensitivity is inherent to the retina itself [2]. Both Stiles and Crawford referred it back to the pupil plane using a Gaussian apodization function with a characteristic peak location (x_o, y_o) and directionality parameter, ρ, that has been used frequently since then. Yet, this Gaussian fitting function is empirical, without a physical foundation, and therefore other fitting functions may potentially provide superior outcomes [3,4]. In doing so, it is vital to keep in mind that the effect is due to the optics of the retina and it is therefore not strictly equivalent to a simple pupil apodization [5-7].

B O'Brien proposed a geometrical optics explanation for leakage of light in the ellipsoid between inner and outer segments [8] and performed scaled microwave studies to examine directionality in

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individual waveguides [9]. J M Enoch and G Fry were inspired by this work [10]. Afterwards, Enoch did a postdoctoral stay with Stiles at the National Physical Laboratory (Teddington, UK) where he worked on the trichromator in relation to wavelength and colour matching [11] and the Stiles-Crawford effect of the second kind that describes a hue shift for obliquely incident light at the retina [12]. After returning to the USA, Enoch carried out pioneering microscopy work on retinal tissue and found intriguing mode-like patterns in light transmitted by photoreceptors [13,14]. This work went further than O'Brien's hypothetical model in exploring the wave-nature of light directly by transmission observations. This also happened at a time when manufacturing of high-purity glass waveguides for telecommunications was becoming increasingly important [15] with key contributions on the cladding and fibre bundles by O'Brien, Van Heel, and others, as well as the revolutionary work on high purity glass fibres by Kao. In a theoretical study, the angular-dependent electromagnetic coupling to isolated cylindrical waveguides was examined by A Snyder and C Pask [16]. In several crucial studies in the 1970'ies Enoch examined the variation in photoreceptor pointing across the retina and, together with A M Laties, found that in the healthy eye they were all pointed towards a common point near the centre of the pupil [17]. Together with S Choi, Enoch examined the Stiles-Crawford effect in relation to myopia [18] and how the directionality, or pointing, could be altered over prolonged time with M Kono and colleagues [19]. This was at the same time as Smallman and colleagues [20] traced the peak of the Stiles-Crawford effect in the pupil after cataract removal. This led to several objective studies examining photoreceptor pointing in the optical Stiles-Crawford effect which, for a time, was believed to provide a related measure of directionality [21-26].

Fig 1. Enjoying an evening with Jay M Enoch and his wife Rebekah A Enoch and friends during the ARVO annual meeting in 2013 (Seattle, USA). Clockwise left-to-right: Leonardo Blanco, Brian Vohnsen, Mirna Vohnsen, Rebekah A Enoch, Jay M Enoch, Susanna Finn, Stacey Choi, Maria Walker, and Nathan Doble.

My first encounter with the Stiles-Crawford effect happened after observing a high degree of directionality in light reflected by retinal cones [27] and coming across a paper on retinal scattering using results for rough surfaces [28] that intrigued me. Having just given lectures to my students at Universidad de Murcia, Spain, on photonics and optical waveguides it was a natural step to see if the psychophysical and optical Stiles-Crawford effects were related [29] and if aberrations could be dampened by the effect [5]. I was invited as speaker at the 2006 ICO meeting in St. Petersburg, Russia, on the topic of near-field optics (a topic I had worked on during and after my doctoral studies in Denmark) and at this occasion also contributed a separate paper on waveguiding, vision and the Stiles-Crawford effects [30]. In the audience, I had two close collaborators of Prof Enoch, namely, Prof Lakshminarayanan and Prof Calvo, then ICO

President, and both Editors of this special 2023 issue of the Asian Journal of Physics. This, together with my recent papers [5,29] likely triggered an invitation to me as speaker for the 75-years celebration of the Stiles-Crawford effect at Frontiers in Optics (FiO, Rochester, 2008). Here, I met for the first time Prof Jay M Enoch. We ended up spending most of the day together both at FiO, and at the following Fall Vision Meeting (FVM, University of Rochester, 2008), discussing the Stiles-Crawford effect. He strongly encouraged me to continue my line of research on this topic and described his own challenges with the understanding of the effect, on the superior performance of the bipartite over the flickering characterization system, and his failed attempts at measuring *in-vivo* waveguide modes of light transmitted by the retina in living eyes of rabbits due to the pulse of the anesthetized animals. I also realized that we share a common passion for the history of optics at a fundamental level [31] and from Viking navigation using polarized light to the understanding of lenses in ancient Egyptian statues [32]. When completing my proceedings manuscript for the FiO meeting over the Christmas of 2008, I had an "eureka" moment when plotting the derivate of the SCE-I effect and recognizing that the SCE-II can be derived as a wavelength derivative of the SCE-I as a function of pupil point and wavelength [3,33]. It was a great pleasure to meet Prof Enoch again during ARVO 2013, see Fig 1.

2 Waveguide models

In this contribution, I will summarize some of the studies done in our laboratory on trying to get deeper into our understanding of the Stiles-Crawford effect using psychophysical and objective methods.

I was intrigued by the merging of a retinal scattering model coming from rough metallic surfaces as an ad-hoc correction to waveguiding when explaining differences in directionality between the psychophysical and optical Stiles-Crawford effects [28]. Retinal scattering is very small in the eye and therefore, very different from that of metals. This led me to look on waveguiding both in the forward and backward directions while including diffraction between the pupil and the photoreceptors. A key novelty was the use of a Gaussian fundamental waveguide mode, which upon propagation remains Gaussian, as this allows for an analytical estimation of the directionality parameter in relation to mode width radius, w, (or waveguide diameter ~$2w$), axial length of the eye, f_{eye}, and effective index of refraction, n_{eye}, at wavelength, λ [29]

$$\rho = 4.29 \times \left(\frac{n_{eye}\, w}{\lambda f_{eye}} \right)^2 \tag{1}$$

The angular dependence of the coupling efficiency for incident light to the waveguide [3,16,29] can explain the dampening of oblique light, whereas differences in allowed modes in the forward and backward directions can explain differences in the directionality parameter of the psychophysical and optical Stiles-Crawford effects, with the latter being narrower than expressed by Eq (1). This also led me to consider the impact of waveguiding on the point-spread function of the eye [5]. Clearly, the retina is not a wavefront sensor, but still an important difference exists between odd- and even-order Zernike modes. Only the latter have an associated wavefront slope at the retina whereby the Stiles-Crawford effect will only dampen even radial orders [5,7].

To probe the impact of slope directly for coherent light, we used annular apertures in Maxwellian view and found that the psychophysical directionality parameter could effectively be cancelled as shown in Fig 2. The slope of the wavefront at the retina within each speckle depends on the effective centre-of-mass of the pupil aperture, which for an annular aperture coincides with the middle of the pupil, whereas for a semi-circular pupil it is offset by less than the pupil radius. In an e-mail exchange in 2013 with Prof G Westheimer, a former colleague of Prof J M Enoch, he kindly commented "one of my all-time favorites in the SC literature" when referring to this figure in our coherence-related study [34]. Our study was a novel take on the integrated Stiles-Crawford effect with coherent light. A related study by B Drum [35] had analyzed it with low-coherence light, whereas the main novelty in our study was the use of a highly coherent laser source that directly showed the impact of any wavefront tilt [35].

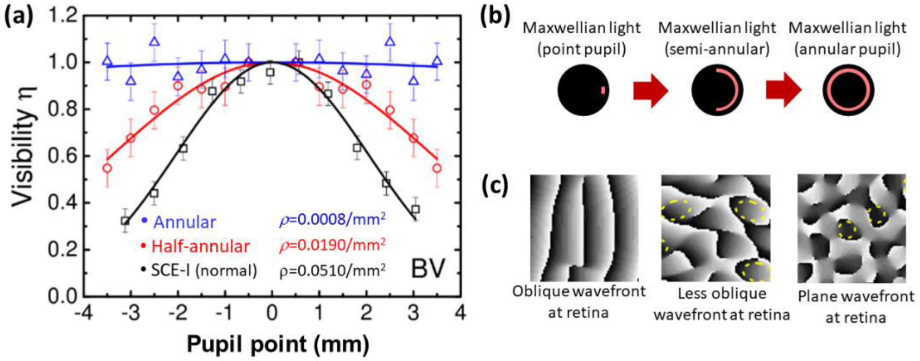

Fig 2. (a) Psychophysically determined Stiles-Crawford visibility function in Maxwellian view with annular pupils (blue), semi-annular pupils (red) and with a traditional pupil-point entry (black) in the author's right eye using a 632.8 nm wavelength HeNe laser as source. In (b) the corresponding point, semi-annular, and annular pupil view, and in (c) the corresponding tilt of the wavefront in the retinal plane, with bright speckles indicated with yellow-dashed circles. The figure has been reproduced with modifications from Ref [34].

The waveguiding model can also be altered to include absorption [36]. We used such ideas to create a waveguide-based retinal phantom in photoresist [37] that could potentially be added to retinal implants to reduce their sensitivity to scattering of light as shown in Fig 3. With this, the waveguide-assisted implants would mostly capture direct imaging light transmitted through the centre of the pupil.

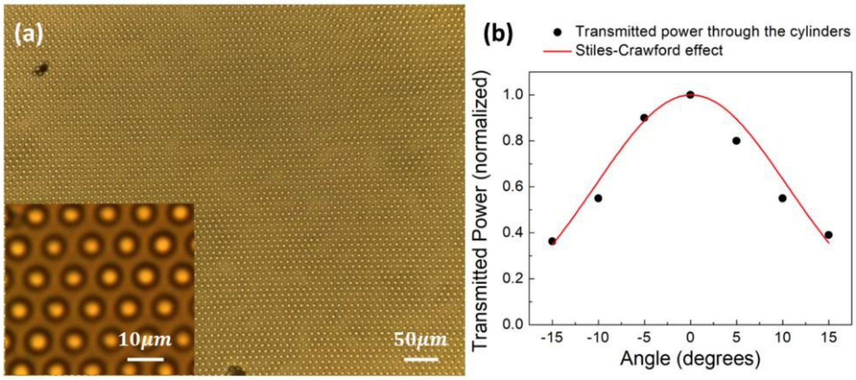

Fig 3. (a) A photoresist retinal phantom with a parallel array of waveguides that (b) functions as an angular filter for oblique light with a directionality parameter that depends on the film thickness as determined by the light within the core of each waveguide. Adapted with permission from Ref [37] © The Optical Society.

Over the years, I became increasingly concerned with the, at times, non-critical use of waveguiding nomenclature in the community when evaluating photoreceptor optics and their visibility in retinal images (dark cones, circular apertures, perfect guiding). These concerns may be summarized as follows:

- What happens to the nonguided light?
- Why are cones directional (even at the fovea) whereas rods are not?
- Most waveguide models examine transmitted light, not absorbed light and vision.

- How can single waveguide optics be valid for densely packed irregular photoreceptors?
- Obliquely guided rays have higher absorption, not lower, due to the increased angle and optical path in the outer segments, potentially inverting the Stiles-Crawford effect.
- Is it the ray angle or wavevector that matters most for the effective visibility?

My thoughts on these questions drove me further into this area of research and followed naturally on from the encouraging advice given to me by Enoch in 2008.

3 Leakage models

In late 2013, I authored a manuscript on the view of antennas as photoreceptors based on the question: "How would individual visual pigments in the lipid bilayers of outer segment discs or infoldings ideally like to capture light?". Based on optical reciprocity, the capturing lopes of densely packed discs or infoldings would be the same as the emission lopes of phased and stacked circular apertures [38] as shown in Fig 4. This idea stems from the early paper by di Francia that photoreceptors are optical antennas [39]. It also links back to the findings on alignment by Laties and Enoch [17] as the photoreceptor cells would obviously capture most photons when oriented so that light can traverse the entire outer segment length thereby increasing the likelihood of absorption. The approximately square grid of visual pigments within each layer approximately fills up the disc and membrane invaginations with an approximately circular cross section representing the inner diameter of the outer segments. Each of these micron-sized discs are ideally coaxially aligned with their surface normal pointed towards the peak location (x_o, y_o) of the Stiles-Crawford function at the pupil as identified by Laties and Enoch. If only few layers contribute to the visual sensation, representative of dim light, then the uppermost layers would be mostly responsible for the directionality, and when fully bleached each of these circular receivers/emitters would contribute thereby narrowing the effective directionality as expressed in the optical Stiles-Crawford effect [38].

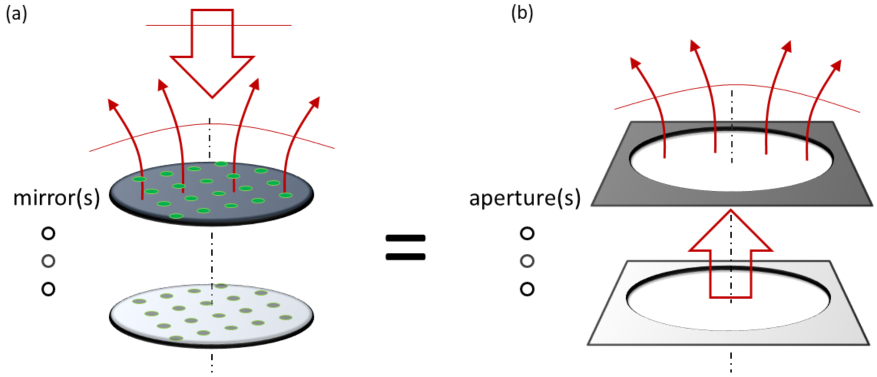

Fig 4. Equivalence between (a) light reflected off a circular mirror, or a phase-stacked array of semi-transparent mirrors representative of each outer segment membrane invagination with visual pigments. and (b) diffraction through a phase-stacked array of semi-transparent circular apertures leading to diffraction towards the eye pupil.

The circular geometry means that the pupil field is expressed by the Airy disc function (if only a single aperture is contributing) and a modified Airy disc function with the entire phased outer segment contributing. This gives a physical optics explanation to the Stiles-Crawford visibility function η which instead of Gaussian is expressed by the Airy disc function

$$\eta = 10^{-\rho r^2} \rightarrow \eta = \left[\frac{2J_1(\alpha r)}{\alpha r}\right]^2 \tag{2}$$

The scaling factor α relates to the directionality parameter. The Airy disc in Eq (2) has oscillations, but these fall outside of the area of the dilated pupil with the collective contributions across the outer segments. As shown in Fig 5, the Gaussian (SCEfit) and the Airy disc function (BESSELfit) for the author's right eye are largely identical, but the latter has a solid physical optics basis.

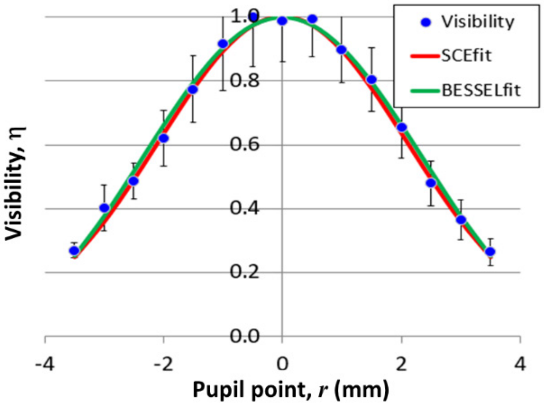

Fig 5. Stiles-Crawford effect visibility data (blue dots) for the author's right eye fitted to a Gaussian Stiles-Crawford function as in Eq (1), in red, and to a scaled Airy disc function as in Eq (2), in green, when adjusting the alpha parameter to the best fit with $\alpha \cong \sqrt{\rho \times ln(10)}$.

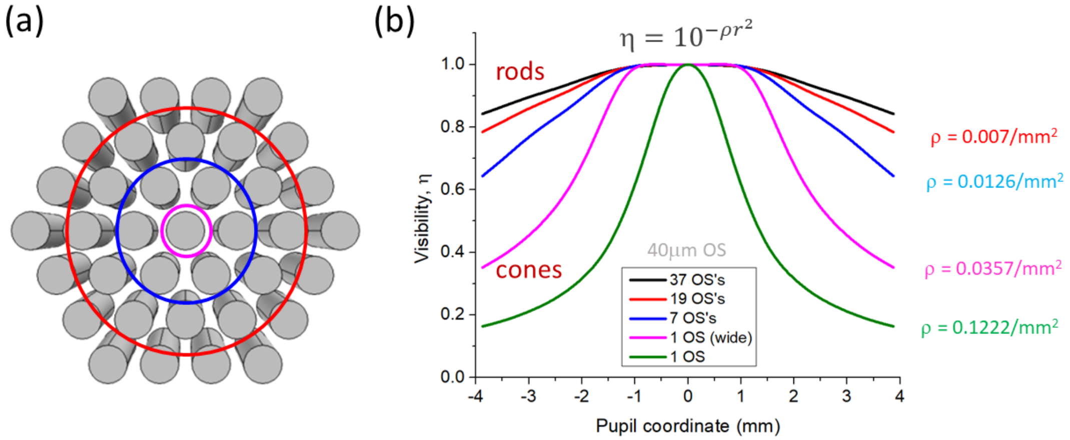

Fig 6. Geometrical light leakage model (a) between adjacent cells and (b) corresponding effective Stiles-Crawford visibility plots when a different number of identical outer segments (OS) contribute to the visual sensation produced in Maxwellian view. The more outer segments illuminated by the incident planar wave, the flatter the curve becomes when the adjacent outer segments all contain the same type of visual pigments (which is the case of the rods, black curve) whereas cones grouped into cone types, or mostly individual in the case of S-cones, a characteristic directionality remains (green and magenta curves).

As a result, my understanding of the Stiles-Crawford effect of the first kind has evolved from that of waveguiding [5,29] to leakage [6,38] as already proposed by O'Brien [8] thereby explaining why foveal cones are directional whereas rods are not, and solving the problem of what happens to the nonguided light. This is also in good correspondence to recent animal studies showing leakage at the ellipsoid [40].

This shows that directionality of photoreceptors is mostly due to leakage and lensing by the high-index mitochondria in the ellipsoid rather than waveguiding. This scattering can still produce mode-like patterns [38]. The leakage also adds to the second Stiles-Crawford effect as blue light leaking out of S-cones is likely to enter neighbouring M- or L-cones (causing positive hue shift) and red light leaking out of L-cones is likely to enter neighbouring S- or M- cones (causing negative hue shift). This is in addition to the sensitivity changes across the spectral bandwidth of the source [3,33]. In turn, if light leaks out of peripheral rods it is likely to be captured by neighbouring rods containing identical rhodopsin proteins and, therefore, the directionality response is flattened as seen in Fig 6 [6].

Although the antenna approach is attractive from an optics perspective [38], and in understanding adaptation and phototropism of the cones and rods to changed illumination conditions after visual pigment renewal [19,20], a conceptually simpler visualization approach is often desirable. The fraction of light absorbed is determined by Beer-Lambert's law which to a first approximation means that visibility is determined by length. In 3-D, this translates into a volumetric absorption model that calculated the volume of light overlapping with the visual pigments. This model provides excellent agreement with direct measurements of the integrated Stiles-Crawford effect through a flickering pupil and shows that visibility drops off nearly an-order-of-magnitude faster than predicted by Eq (1). The best fitting curve is that of a power law [7].

4 Measuring the Stiles-Crawford effect

To analyse the psychophysical Stiles-Crawford effect of the first kind either flickering or bipartite fields can be used as I also had discussed with Prof Enoch back in 2008. In our earliest approaches bipartite systems with liquid-crystal bandpass filters for wavelength tuning, liquid-crystal attenuators for brightness adjustment, and tuneable lenses for defocus correction were used [41,42]. We subsequently developed a uniaxial system with a digital micromirror device (DMD) to effectively scan across the pupil and allow tunability of brightness via the very high kHz duty cycle [43]. The latter system has been used to analyse the impact of axial length for myopes confirming a reduction in the characteristic directionality parameter, ρ_M, with increased axial length Δz beyond that of an emmetropic eye

$$\rho_M \approx (1 - 2\,\Delta z / f_{eye})\rho \tag{3}$$

Such geometrical scaling ideas impacted my thinking on myopia onset and the need for being outdoors. Only with a small outdoor pupil <3 mm will aberrations be small and, importantly, leakage and crosstalk across the retinal photoreceptors can be effectively avoided in the critical school years where the photoreceptor density and retina still undergo changes as its structure approaches to that of the adult eye [44].

Measuring the Stiles-Crawford effect of the first kind is challenged by variations in data capture and the need for subjects to remain stable for prolonged time using a bite bar, head and/or chinrest. Recently, Bang *et al* reported that the Stiles-Crawford pupil peak location is highly correlated with the visual axis [45] in good agreement with expectations based on the histology work by Laties and Enoch [17]. Yet, it is very relevant to investigate options of altering the outer segment pointing due to the continued renewal of visual pigments, and to explore the possibility of improved diagnostic capabilities for diseases that directly affect photoreceptor integrity and pointing [21-26,46]. Ultimately, the directionality still needs to be assessed with psychophysical means in possible combination with electroretinography.

For the geometrical absorption model, we developed a technique to measure the impact of the integrated psychophysical Stiles-Crawford effect of the first kind in direct vision, rather than with Maxwellian light, using a motorized flickering pupil that alternates between a small reference and a larger-and-larger test pupil [6,7]. This analysis shows a much stronger truncation than predicted by a Gaussian Stiles-Crawford function which can be explained by the fact that only for a small pupil will light remain confined within the full length of the outer segments [44]. This matters for further improvements of lenses and implants without relying on an additional retinal adaptation to changes in illumination. It can also be a factor for future virtual reality and augmented reality that adapts in the best possible way to the optics of the eye.

5 Conclusions and outlook

Jay M Enoch's work on photoreceptor optics, in natural succession to W S Stiles, B H Crawford and B O'Brien, has inspired a wealth of studies over the past 60+ years. Enoch understood early on the vital role of photoreceptor directionality. He did this with utmost care and insight while recognizing the need for advancements in vision science, in cellular imaging, and in optical theory. Such diverse knowledge is vital to comprehend vision in the healthy eye and in eyes affected by disease, since the photoreceptors and eye are to some degree adaptable to changes. Since the 1990'ies ultrahigh resolution adaptive-optics imaging and vision testing has become a reality [47] and, together with optoretinograms [48], the probing of photoreceptor optomechanics at unprecedented spatial and temporal resolution has become a reality. Such progress owes a great deal to the pioneering work by Jay M Enoch for knowing which questions to ask, and how to resolve them.

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