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On the history of deformation phosphenes and the idea of internal light generated in the eye for the purpose of vision

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Abstract. *Deformation phosphenes* are light sensations evoked by deformation of the eyeball in total darkness. They were first reported in Western literature by Alcmaeon of Croton in the fifth century B.C. The phenomenon of deformation phosphenes was instrumental in prompting some pre-Socratic philosophers and Plato to conceive the idea that efferent light is emitted from the eye for the purpose of vision and a '*cone of vision*' is formed by interaction with the external light. In the theories of vision this cone of vision played an important role as a signal-transmitting structure and was also used by the Greek opticians as a geometrical construction to explain optical properties of vision.

The impact of the deformation phosphene experiment on the ideas of visual sensation can be followed from Greek antiquity through the period of Roman dominance and Galen's medical teaching on to medieval times and up to the late Renaissance when, based on the anatomy of the eye as illustrated by Felix Platter, the image formation on the retina was correctly described for the first time by Johannes Kepler. In the generations following, deformation phosphenes were still employed as an important argument in defence of the theories of vision. However, the idea of physical light generated by eyeball deformation was rejected with increasing frequency during the 17th and 18th centuries. The literature on this topic is discussed, comprising the contributions of the Arabic philosophers and physicians of the 9th and 10th centuries A.D., the Franciscan and Dominican philosophers of the 13th century, Nicolaus Cusanus of the 15th century, several anatomists of the 16th and 17th centuries, Kepler, Plempius, Descartes, Boyle, Newton and others. After Kepler, the mechanical interpretation of the deformation phosphene being caused by direct action of the eyeball deformation onto the retina slowly became dominant, and the idea that physical light is generated in the eye disappeared.

The *experimentum crucis* in this matter was performed by *Giovanni Battista Morgagni* (1682–1771) and repeated and extended by *Georg August Langguth* (1711–1782). On the basis of their results, the case for physical light being generated in the eye by deformation was refuted definitively and slowly vanished thereafter from scientific literature. Deformation phosphenes were used in the 19th and 20th centuries as an instructive example of the percepts evoked by inadequate stimulation of a sense organ. J.E. Purkyne in particular contributed to the study of deformation phosphenes, and finally in 1978, F. Tyler devoted a careful study to the differences between monocular and binocular deformation phosphenes. Finally some remarks on the *neurophysiological* interpretation of deformation phosphenes, based on microelectrode recordings of the activity of single retinal ganglion cells, are added to the historical report.

1. Introduction

When the eyeball is indented in total darkness, within less than 200 milliseconds an oval or quarter-moon shaped spot of light is perceived in the part of the visual field corresponding to the indented region of the retina. In the seconds following, this *phosphene* extends across the whole visual field and alters in structure during further eyeball indentation. It is then seen as irregular large bright spots of light, finely structured moving light grains ('light nebula') and stationary bright stars. Regular geometrical patterns appear only when both eyes are indented simultaneously [1]. When the eyeball deformation is released, part of the retina again lights up for another one or two seconds and curved light lines are seen following the course of the larger retinal vessels (Fig. 1). In the following we will review the history of this phenomenon, which played an important role during the first 2200 years of vision theories and in the development of models to explain normal vision.

2. Pre-Socratic philosophers, Plato and Aristotle

Alcmaeon of Croton (6–5th century B.C.), who was a member of the Pythagoraean sect and one of the founders of Greek medicine, was the first to describe mechanical deformation of the eyeball leading to light sensations. According to Aristotle's pupil *Theophrast of Eresos*, Alcmaeon reported that '*the eye obviously has fire within, for when the eye is struck fire flashes out*' [2, p. 88]. This observation was included in the theory of vision by another Greek physician, *Empedocles* (419–430 B.C.), who became famous for his medical and political success in the Greek colony of Akragas (Agrigente) in Sicily, but was later exiled by his countrymen. According to the fragmentary reports on Empedocles' deliberations, he also developed distinct ideas on the function of the sense organs including vision [3, p. 342; 2, p. 7–24]. He believed the eye to be composed essentially of the 'elements' *water* and *fire*. From the observations of deformation phosphenes and the lighting-up of animal eyes in the dark, he presumably deduced that internal light generated in the eye is used for the purpose of vision and that the visual percept is caused by an interaction of '*external fire*' from the objects regarded and '*internal fire*' generated by the perceiving eye [4]. This interaction takes place either somewhere within the eye or in the extrapersonal space (Fig. 2a), and follows the general rule of sensory perception postulated by Empedocles and some of the other pre-Socratic philosophers, that perception is only possible when the physiological process in the sense organ is similar to the

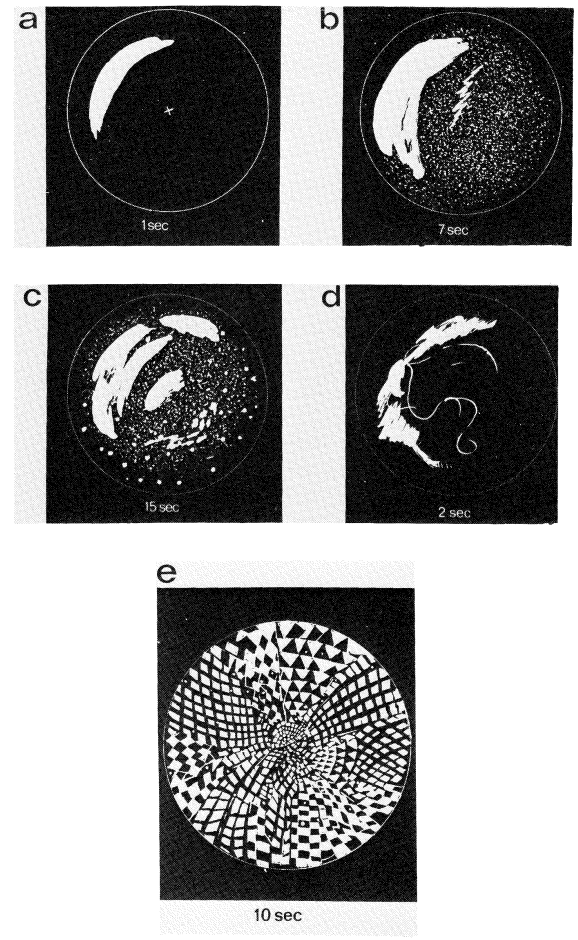

Fig. 1. Development of deformation phosphenes after indentation of the temporal side of the right eyeball at different intervals following indentation (a–c) and after release of eyeball deformation (d), as seen by one of the authors (O.-J. G.). (e) With simultaneous bilateral indentation of both eyeballs on the temporal side of the eye a patterned deformation phosphene is observed, flickering at about 10 Hz. The figure (e) represents the impression after about 10 seconds of indentation.

physical signal in the outer world. Other Greek natural philosophers postulated just the opposite and assumed that perception occurs by *contrast* between signal and sensory process [2].

A generation after Empedocles, *Democritus of Abdera* (460–370 B.C.),

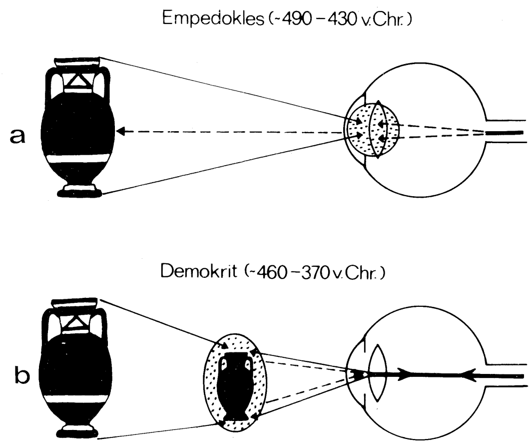

Fig. 2. (a) Interaction-theory of Empedocles: Efferent light is generated in the eye, leaves it, touches the object and is reflected back to the eye for the purpose of vision. (b) Democritus modified this interaction theory: Efferent light interacts with the signals from the objects somewhere in the extrapersonal space between object and eye, where small impressions of the object are generated in the air [74].

who together with his teacher *Leukippos* founded Greek materialistic philosophy, developed more explicit thoughts on the interaction of efferent and afferent visual signal flow. He believed that the process of visual perception uses small impressions, called in Greek '*typoi*', which are generated in the air by fine material images ('*ediola*') composed of atoms, travelling from the objects towards the eye and interacting with internal light evoked in and leaving the eye of the perceiving subject (Fig. 2b). Thus, Democritus assumed that perception occurs only when an extrapersonal interaction of efferent and afferent light has taken place [2].

Although *Plato* (Athens, 427–347 B.C.) disliked the materialistic philosophy of Democritus, he seriously considered models of vision along the same lines and developed a more specific theory of vision (Fig. 3) in his most important book on natural philosophy, '*Timaeus*' [5, 45b–d]. He assumed that 'visual rays' are emitted from the eye and form by interaction with the external light a signal-transmitting structure, the '*body of vision*' or '*cone of vision*', as it was later called by *Euclid* and *Ptolemy* [6]. This body of vision was believed to touch the objects and to be moved by this interaction. The movement is reflected back to the eye, which receives and transmits it to the brain, inducing mechanisms of visual cognition. In this model of vision, which was later called '*synaugia*', perception by touch became the dominant principle in the models for sensory perception.

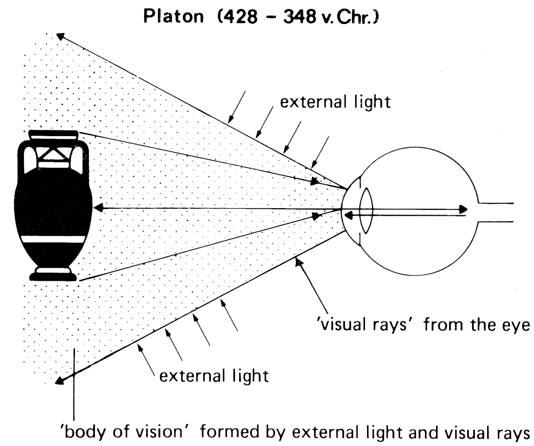

Fig. 3. Plato's interaction theory: Efferent visual rays are emitted from the eye and interact with the external light to form the 'body of vision'. This body of vision touches the objects. The results of this interaction are reflected back to the eye [74].

Several generations later, *Chrysippos* (277–204 B.C.), one of the leading philosophers of the early Stoa [7], on the basis of Plato's theory, proposed the existence of a spatially organized visual cone, having its base at the objects, its pinnacle in the eye [8, 9]. Chrysippos assumed that perception is always dependent on active movement directed towards the objects. Only such an intentionally controlled movement releases '*pneuma*' from the sense organs. The idea of a visual cone composed of internal light (*visual pneuma*, later called in Latin '*Spiritus visibilis*') dominated the theories of vision during Greek and Roman antiquity from the time of Plato to that of *Galen* (129–199 A.D.). *Aristotle* (384–322 B.C.) and his pupil *Theophrastus of Eresos* (372–287 B.C.) were not particularly impressed by the interaction theory and believed that vision, as perception in general, is mainly a passive process. In '*De sensu et sensato*' Aristotle rejected the idea of physical light generated within the eye and leaving the eye for the purpose of vision. He was familiar with the phenomenon of deformation phosphenes, but explained them as 'self-reflection' within the eye, caused by its '*smoothness and its natural illuminating power*', which could be evoked by eyeball deformation in complete darkness [4, 437a–b]. From the accounts of soldiers, Aristotle also knew that injury to the eye produced the impression of a burning lamp being blown out, followed by darkness [4, 438b]. This description leaves open the possibility that Aristotle recognized that an eyeball injury leads to a short transient increase in light sensation before the 'darkness', just as an oil flame, when blown out, flares up before disappearing.

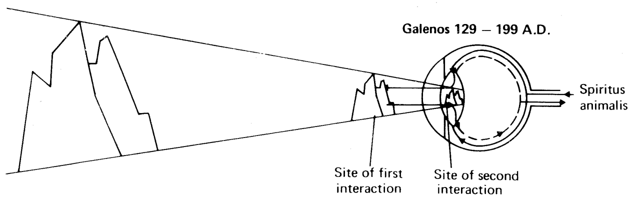

Fig. 4. The eclectic modification of the interaction theory by Galen [75]: The spiritus animalis (pneuma) generated in the brain reaches the eye and leaves it again, altering the air in front of the eye. By this mechanism the image of the object is diminished (first interaction). This reduced image reaches the crystalline body (lens), which is sensitized by the pneuma. There a second interaction occurs, which is then transmitted back to the optic nerve and from there to the brain [13].

A position similar to that of Aristotle was taken by the *Epicureans*. In his '*Letter to Herodotus*' [10] the founder of this Athenean school of philosophy, *Epicurus* (341–270 B.C.), wrote that perception is a passive process in its initial stage, followed by an active recognition mechanism ('*prolepsis*'), which depends on the subject's experience, but operates only *within the organism* and not outside of it. Thus the Epicureans rejected the idea of efferent pneuma leaving the eye for the purpose of vision.

As mentioned above, the idea of Plato's '*synaugia*' was accepted by the great Greek mathematician *Euclid* (end of 3rd century B.C.) and the astronomer *Claudius Ptolemy* (2nd century A.D.), but from their reports it is not clear whether they thought that the efferent pneuma represented more than just a geometrical construction of the '*cone of vision*' [6]. The ancient theories of vision, excluding those of the classical theory of optics, were summarized and discussed by *Galen*, who thought that the illuminating pneuma originates in the brain and reaches the eye via the optic nerves. In '*De usu partium corporis*' he supported an interaction theory similar to that proposed by Plato and Chrysippos. On the other hand, true to his eclectic approach to science, Galen also conceded that vision is possible when only the objects seen emit light directly to the eyes [11, 12, 13] (Fig. 4).

3. Medieval and Renaissance variations on the idea that light is generated in the eye

The Greek concept of efferent and afferent light interaction as a primary source in visual perception was still under discussion in medieval and Renaissance theories of vision [14]. In the early Middle Ages the Arabian physicians and scientists *Hunain Ibn Ishaq* (808–873 A.D.) and *Al-Kindi* (813–873 A.D.) supported the extrapersonal interaction theory but believed

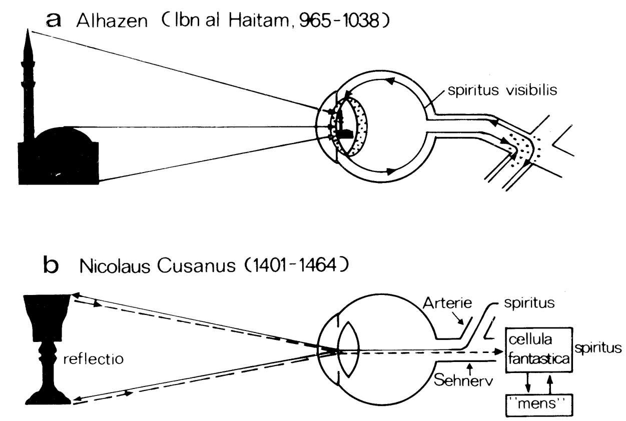

Fig. 5. (a) Alhazen's modification of the interaction theory: Efferent signals, the spiritus visibilis generated in the brain, reach the eye via the optic nerve and interact for the purpose of vision with the images of the objects formed on the crystalline lens at the site of the pupil. The modified spiritus visibilis is then sent back to the optic chiasm and from there to the brain. (b) Nikolaus Cusanus modified the old external interaction theory: The spiritus visibilis leaves the eye only when attention is cast upon certain objects. After interaction with the object, it is reflected back to the eye and transmitted via the optic nerve to the cellula phantastica, where the material spiritus visibilis interacts with the immaterial soul ('*mens*') [74].

that the emission of internal light is strictly dependent on eye movements [15, 16]. In the next generation of Arab scientists, however, *Ibn-al-Haytham* (in Latin *Alhazen*, 965–1040 A.D.) rejected the external interaction theory [17]. He developed some new ideas based on the *Optics* of *Ptolemy* and the anatomy of the eye as described by *Galen* [18, 19]. From the Latin translation of Alhazen's main book on optics, one could infer that he believed the interaction between efferent pneuma and the visual rays from the outside world to take place in the crystalline lens of the eye. He assumed that the *spiritus visibilis* is produced in the brain near the chiasm of the optic nerves and flows in small vessels through the optic nerve to the retina and within the retina to the crystalline lens, where it interacts with the object images formed there by the light of the outside world. Subsequently, the *spiritus visibilis* flows back to the optic nerve and through its channels to the chiasm, where it mixes with the afferent *spiritus visibilis* of the other eye (Fig. 5a). Alhazen was convinced of the necessity of this mechanism for correct binocular fusion. Like Aristotle, he discarded the idea that internal light leaves the eye. He also argued that efferent light inevitably would disturb the process of seeing. Recently G.A. Russell [20] studied the Arabic manuscript of Alhazen's Optics, '*Kitab al-Manazir*' and provided convincing evidence that Alhazen believed light to be refracted twice within the optics of the eye and an image formed at the '*funnel of the optic nerve*', from where the signal is transmitted to the brain. This leads to the supposition that Alhazen assumed an interaction of light and visual pneuma in the optic nerve.

Alhazen's position was supported by *Avicenna* (*Ibn Sina* 980–1037 A.D.) who put forward a simple argument against internal light leaving the eye. If this theory were correct, he wrote, the presence of many observers would improve the perception properties of the air surrounding them, since more visual pneuma would be released into the extrapersonal space. Evidently, this could be refuted empirically and Avicenna therefore rejected Plato's interaction theory [21, 22].

Among the famous philosophers of the 13th century, *Robert Grosseteste* (ca. 1168–1253), Chancellor of the University of Oxford and later Bishop of Lincoln, supported the idea of internal light leaving the eye for the purpose of vision. Grosseteste wrote: '*One should not assume that the emission of rays from the eye is only apparent and without reality. This is the opinion of those, who know parts, but do not consider the whole. One should understand that the visual species emitted from the eye is a substance which illuminates similarly as the sun. These emitted rays complete the act of vision when they join those from the objects of the extrapersonal space*' [23, p. 72–73]. He considered light to be the elementary substance of the world and consequently to have a metaphysical function far beyond vision.

The most important follower of Robert Grosseteste within the next generation of Oxford Franciscans was *Roger Bacon* (1214–1292). He was not only interested in scientific experimentation but was also well-read in Greek and Arabic medical texts. He rejected Alhazen's model of vision, the concept of higher activity with a physiological mechanism inside the eye, but emphasized the Platonic teaching of pneuma and that a special vital 'species' i.e., a signal, is emitted by the eyes and reaches the objects of vision [24]. He believed that '*The species of the things of the world are not suited to act immediately and fully on sight because of the nobility of the latter. Therefore these species must be aided and excited by the species of the eye, which proceeds through the locale of the visual pyramid, altering and ennobling the medium and rendering it commensurate with sight; and thus it prepares for the approach of the species of the visible object* [*itself*]*, so that it is altogether conformable and commensurate with the nobility of the animated body, i.e., the eye.*' [24, p. 52].

Albertus Magnus (1197–1280), the great teacher of the Dominican order, also reported that light is seen during eyeball deformation, but rejected the idea of light leaving the eye. This was not the only scientific dissent regarding the function of sense organs between the English Franciscans and the

continental Dominicans of that time. Albert wrote: '. . . *A certain sensation appears in the eyes in darkness, either when they are compressed from outside or suddenly beaten: then a lightening fire is generated in the eye and it would not light up inside if it would not be inside*' (25, Quaestio XX, ad. 11). As a possible interpretation of the deformation phosphenes Albert discussed: '. . . *that the cause is the transluminance* [claritas] *of the spiritus visibilis, which extends in itself by the bending or beating* [of the eye]. *Therefore a luminous variation appears in the rear of the eye* . . .' [25, Quaestio, XX, ad. 11].

Albert conjectured furthermore that the *spiritus visibilis* interacts with the form of the visual images *inside the eye*, most probably at the site of the crystalline lens (Fig. 5a). Only in the case of some nocturnal animals, such as cats and wolves, did he still believe that light is generated inside the eye and might leave it for the purpose of vision [25, Quaestio XIX].

The Parisian *Jean Buridan* (1295–1358), one of the leading nominalistic and aristotelian philosophers of his time, while commenting on Aristotle's book in his '*Quaestiones super librum de sensu et sensato*', mentioned that the appearance of phosphenes does not support the idea of efferent light and the Platonic interaction theory. He argued, as Alhazen, that light generated in the eye would be permanently visible for the observer and would therefore interfere with normal vision. Buridan wrote on deformation phosphenes: '. . . *but when the eye is struck it* [*the light*] *is bent inward and thus one part reflects light into another part* [*of the eye*] *and vice versa; therefore one part perceives 'lux' through 'lumen' reflected by the other part*' [14, p. 135].

Despite the strong arguments against emission of internal light, this hypothesis still had supporters during the 15th century. *Nicolaus Cusanus* (1401–1464), for example, a philosopher, mathematician and church politician of great repute, presented a variant of the old interaction theory in his books '*Compendium*' [26] and '*Liber de mente*' and a generalization thereof for the other senses: '*Because the spiritus is an instrument of the senses, the eyes, the nose and the other sense organs can be considered to be windows through which the spiritus has its exit for the purpose of perception*' [27, p. 257].

Cusanus believed that two arteries transport a highly movable type of *spiritus visibilis* to the eye, which then leaves the eye and hits the objects in the extrapersonal space. Thereafter the spiritus visibilis is reflected back to the eye and, after some refinement, reaches the *cellula phantastica* of the brain via the optic nerve. *Cellula phantastica* was the name for the lateral ventricles of the brain, the place where Cusanus believed the immaterial soul '*mens*' to be aroused by an exchange of information (*phantasma*) with the very fine, but material *spiritus visibilis* from the eye. The result of this exchange is transmitted to the third cerebral ventricle in the middle part of the brain, the *cellula rationis*, thought to be the seat of the immaterial, rational argumentation and insight. In accordance with ancient Stoic teaching, Cusanus supported the idea that the generation of *spiritus visibilis* has something to do with motor acts, i.e., the emission of the spiritus visibilis depends on *spatially selective attention* being directed towards the object one wishes to see (Fig. 5b).

4. Further modifications of Alcmaeon's and Plato's hypothesis on deformation phosphenes and the development of a new theory of vision based on Renaissance anatomy

Towards the second half of the 16th and the first half of the 17th centuries, the field of anatomy advanced considerably and the body of information on the structure of the sense organs gained in empirical foundation. Improved knowledge of eye structures also led to gradual changes in their functional interpretation. The anatomist *Girolamo* (*Hieronymus*) *Fabricius ab Aquapendente* (1537–1619), who taught at the University of Padova, gave a fairly correct description of the anatomy of the eye in his tractate '*De actione oculorum*' and rejected the idea of light emitted from the eye. He took the cone of vision only as a *geometrical construction* to explain why vision with one eye is restricted to a certain part of the extrapersonal space. He considered the retina to be the light-sensitive structure, but finally opted for the old dogma that the crystalline lens is where the image is transformed into a physiological process [28, p. 203ff; 29].

The great clinician and anatomist from the University of Basel, *Felix Platter* (*Plater*, 1536–1614), deeply impressed by the 'new anatomy' of *Andreas Vesalius*, described the anatomy of the eye somewhat more realistically than Fabricius, depicted the lens in its proper position and drew the curvature of its surfaces correctly [30, 31]. Platter's anatomy of the eye was adapted by *Caspar Bauhin* (1560–1624), who in 1589 became professor of anatomy at the University of Basel, but in Bauhin's books '*De corporis humani fabrica, libri IV*' [32] and '*Theatrum anatomicum*' [33, p. 706ff, Tab XIX] the Galenic tradition, that the crystal lens is the sensitive organ for vision, was still supported. The older Felix Platter, however, was more progressive and attributed this function to the retina, but he still did not understand the image formation on the retina correctly.

Based on the anatomical findings and speculations of Platter, the famous Suebian astronomer *Johannes Kepler* (1571–1630) was finally able to reject the age-old concept that the transductive mechanisms between external light

and physiological processes are located in the crystal lens of the eye. In his book '*Paralipomena ad Vittelonem...*' in 1604 Kepler, applying the laws of refraction by optical surfaces, proposed that an *inverted image* of the object is cast onto the inner surface of the retina and assumed that this structure is also responsible for the transduction of external light into a physiological process, which is then transmitted by the optic nerve to the brain [34, 35]. Kepler also deliberated over a new explanation for deformation phosphenes. He maintained that the *mechanical irritation of the iris* by eyeball deformation induces sparks which stimulate the retina. Thus, he still believed that 'physical' light is generated in the eye during the perception of deformation phosphenes, but as the source of this light he selected a structure in the eye not directly involved in the process of vision. His arguments for light generation in the iris by eyeball deformation were rather indirect: '*the light can impossibly have its seat in the moistures of the eye* [i.e., crystal lens and vitreous body], *because then it would disturb the process of vision*' [35, 36, 37].

Kepler's contemporary, the Jesuit Father *Christoph Scheiner* (1579–1650), followed the idea that during the perception of deformation phosphenes physical light is generated in the eye, but he believed it to be produced in the crystal lens and normally too weak to be seen. Only when the mechanical stimulation releases a large amount of this internal light, as in the case of deformation phosphenes, can it be seen. Scheiner performed several important experiments in visual psychophysics and also gave a detailed description of deformation phosphenes, observing the correlation between the position of the phosphene in the visual field and the site of the retina indented: '*The appearance* [of the phosphene] *is round. But if the pressure is stronger the perceived light extends and finally takes an elliptic form. One always perceives it on the opposite side* [in the visual field] *to where the eye is deformed. The spark is mainly to be seen in the darkness, independent of whether the eyelids are closed or open. But one perceives it even by day and with open eyes, especially near the angle of eye. The whole appearance consists of a gleaming border, it is then in the middle dark and nearly black*' [38, p. 238].

Accordingly, Scheiner contributed three new ideas to the traditional description of deformation phosphenes:

a) deformation phosphenes depend on the amount of pressure exerted onto the eye;
b) phosphenes evoked in darkness differ from those seen in light;
c) the initial phosphene is perceived opposite the site of deformation, an observation corroborating Kepler's concept of functional reversion of the retina.

Scheiner believed that the internal light illuminates the crystal lens and
the age-old concept that the transductive mechanisms between external light

this illumination is reflected to and perceived by the retina. Like Kepler, he assumed that the phosphenes are a kind of *real light* and are caused by mechanical processes within the eye. In the opinion of both, however, intraocular light was a curiosity rather than anything of great importance to the process of normal vision.

Kepler's description of image formation in the eye only gained slow acceptance among the anatomists of his time, despite the fact that he based his theory on the anatomical figures of Felix Platter and had collaborated with the anatomist *Johannes Jessen* (1566–1621) of Prague during his years as Habsburg court astronomer and astrologer of *Wallenstein*. In 1632, for example, the Dutch anatomist and physician *Plempius* (Plemp) published a book '*Ophthalmographia*', in which he mentioned Kepler's '*Dioptrice*' but was hesitant to introduce the '*teaching of the mathematicians*' into medicine. He attributed the idea of the retina being the organ of light sensation to Fabricius ab Aquapendente [39], but most likely did not understand the constructions of the dioptrics of the eye published a quarter of a century before by Johannes Kepler. *Vopiscus Fortunatus Plempius* (1601–1671) is known to posterity as a correspondence partner of Descartes on the matter of perception and on Harvey's concept of blood circulation. He was trained in Leyden, Padova and Bologna and taught from 1633 as professor at the Faculty of Medicine at Loewen. Plempius was a convinced Aristotelian, opposed heavily to the spread of Cartesian ideas at the university [40]. In his '*Ophthalmographia*' he devoted a full chapter to phosphenes. Under the heading '*What is the cause for our incidental perception of flashes or moving sparks in the eyes*?' he described phosphenes visible when the eye is pressed or rubbed [39, p. 237–240]. He also mentioned phosphenes seen during fast saccadic eye movements in the dark and was well acquainted with the traditional ideas on phosphene generation. He rejected Scheiner's hypothesis that physical light is generated inside the eye and assumed that the light sensations caused by eyeball deformation are evoked by a change in the flow of the spiritus visibilis in the eye: Due to the mechanically increased speed of the spiritus the latter is 'inflamed'. He believed that the same phenomenon also occurred by a chemical process caused by additional gases ('*vapores*') mixed to the spiritus by the mechanical forces during eyeball deformation. Thus Plempius favoured a mechano-chemical hypothesis of phosphene generation. He emphasized that this internal '*ignition*' is relatively mild. Therefore phosphenes are not seen when the deformed eye looks simultaneously at a bright external light, which is then believed to mask the '*glare of the spiritus*' in a similar manner as the light of the sun masks the light of the stars during the daytime.

Kepler's idea on the dioptrics of the eye and vision in general undoubtedly

had some impact on *René Descartes* (1596–1650). In his books '*Dioptrique*' [41] and '*Tractatus de homine*' [42] Descartes accepted Kepler's construction of the inverted retinal image. He believed that light acting on the retina exerts a direct mechanical influence on the optic nerve, being transmitted according to the laws of mechanics by means of small fibers located inside the tubular nerve channels to the central projection regions of the optic nerve. As *Leonardo da Vinci* (1452–1519) a century before [43, Codex D, folio 5 recto], he assumed the latter to be located along the walls of the lateral ventricles of the brain and explained the deformation phosphenes according to this mechanical model:

'. . . *remember those whose eyes will be beaten. They believed to see light flashes, although their eyelids are closed or they are in a dark room. Therefore the origin of this sensation can only be the power or the blow on the eye, which moves the small fibers of the optic nerves equally as light does*' [41, p. 31].

With these remarks Descartes clearly rejected, as Plempius at that time, the idea that *physical light* was generated within the eye. A similar position was taken by the English chemist *Robert Boyle* (1627–1691), who described deformation phosphenes in his book '*Experiments and considerations touching colours*' [44]. He also believed that external light acts on the retina by means of mechanical interaction:

'*But I will rather observe that not only when a man receives a great stroke upon his eye or a very great one upon some other part of his head, he is wont to see, as it were, flashes of lightning, and little vivid, but vanishing flames, though perhaps his eyes be shut; but the like apparitions may happen, when the motion proceeds not from something without, but from something within the body, provided the unwanted fumes that wander up and down in the head, or the propagated concussion of any internal part in the body, to cause about the inward extremities of the optic nerve, such a motion as is wont to be there produced, when the stroke of the light upon the retina makes us conclude, that we see either light or such and such a colour*' [44, p. 671–672].

It is not clear what Boyle meant precisely by '*fumes*', but it is evident that he followed, in general, the mechanistic concepts of Plempius and Descartes and did not support the old hypothesis of physical light evoked by mechanical eyeball irritation. As another example of visual sensations evoked by mechanical irritation of the eye, Boyle mentioned phosphenes seen during a fit of coughing.

Similarly, the Cartesians of the generation following Descartes usually explained the deformation phosphenes by mechanical irritation of the retina. *Johannes Clauberg* (1622–1665), for example, who was the most active promotor of Cartesian thought in Germany and as professor of philosophy taught at the University of Duisburg during the last decade of his life (45), assumed that the light perceived on mechanical irritation or injury of the eye is caused by a mechanical activation of the *spiritus visibilis* inside the retina, which is then transmitted into the brain. There, he believed, the essential mechanisms of perception occur. Since Clauberg was a strict *occasionalist* who postulated *psychophysical parallelism* without any causal connections between body and soul ('*mens*'), he believed that the unusual activation of spiritus visibilis by eyeball deformation is automatically paralleled by a corresponding light sensation of the immaterial soul. He compared the activation of the spiritus visibilis in the eye by mechanical irritation with the similar 'turbulence' of the spiritus occurring inside the brain during the state of vertigo [46, p. 196].

The French Cartesian *Nicolas Malebranche* (1638–1715) discussed deformation phosphenes, applying a strict occasionalistic interpretation: '*Due to the pressure exerted onto the eye, one perceives light, despite no illuminated body being present. This is caused by the pressure exerted by the finger onto the eye and therefore also onto the brain . . . The light one perceives, is a property of mental activity and as a consequence is only found in this sphere. . .*' [47, p. 94–95]. Malebranche pointed out that the light is not seen at the site where the eyeball is indented, but in the extrapersonal space opposite. He explained this by the assumption that '*the pressure of the finger on the left* [indented] *side of the eyeball has the same effect as an illuminated body seen on the right side . . .*' [47, p. 95]. Malebranche applied Kepler's idea of the inverted retinal image to explain the localisation of the deformation phosphenes, whereby his arguments were deduced from the '*divine laws*', '*which were arranged by God to save in his design* (*of the organism*) *complete unity*' [47, p. 95].

Thomas Bartholinus (1616–1680), professor of anatomy at the University of Copenhagen, wrote a comprehensive monograph on the importance of light in men and animals [48]. He discussed extensively older reports on light believed to be emitted from the eyes of men, especially those of great political repute, such as the Roman emperors *Augustus* or *Tiberius*, and described meticulously ways of eliciting deformation phosphenes: '*It is true without doubt that when the eyes are pressed near the angle of the orbit that even in total darkness, whenever the indenting finger moves, a real light lights up. It disappears when the eyelids are moved away and reappears when the eyelids are pressed* [towards the eyeball]. *I can confirm from my own experience that everybody can perceive this light in his eyes when he follows this procedure. It is certain that by slight compression* [of the eyes] *only mild light is evoked. Yet the stronger one presses, the stronger the fist is moved to the eyes, the stronger light scintillations appear, in the same manner as sparks are evoked when flintstones are struck against each other. . .*' [48, p. 109]. Bartholinus, however, still believed that some animal eyes, like those of cats, can emit real light in the dark for the purpose of vision [48, p. 249–250].

In the second half of the 17th century in his book '*Ophthalmographia*' [49] the English physician and ophthalmologist *William Briggs* (1642–1704) continued to defend the old idea of 'real' internal light generated in the eyeball by deformation. He believed that the *spiritus visibilis* acts within the retina, begins to gleam when the eyeball is deformed and stimulates the retina in a way similar to natural light projected from the oustide world. With this hypothesis Briggs contradicted Kepler and Scheiner, as he could not understand how a liquid structure such as the lens could generate light when pressure acted on it.

Towards the end of the 17th century the mechanical model of deformation phosphenes became clearly dominant. *Isaac Newton* (1643–1727) also rejected the idea that physical light is generated by eyeball deformation. In book 3, part I of his '*Opticks*' he wrote in <u>*Quaerie*</u> 16:

> '*When a man in the dark presses either corner of his eye with his finger, and turns his eye away from his finger, he will see a circle of colours like those in the feather of a peacock's tail. If the eye and the finger remain quiet these colours vanish in a second minute of time, but if the finger be moved with a quavering motion they appear again. Do not these colours arise from such motions, excited in the bottom of the eye by the pressure and motion of the finger, as, at other times are excited there by light for causing vision? And do not these motions once excited continue about a second of time before they cease? And when a man by a stroke upon his eyes sees a flash of light, are not the like motions excited in the retina by the stroke? . . . And considering the lastingness of the motions excited in the bottom of the eye by light, are they not of a vibrating nature*?' [50, p. 347].

Accordingly Newton's explanation of deformation phosphenes avoided the hypothesis of gleaming animal spirits. He preferred to defend the direct transduction from mechanical vibration of the retina into sensation rather than to follow Brigg's speculations.

5. The experimental refutation of the idea that physical light is generated in the deformed eye

It is evident that with Kepler's concept of the inverted image which is transformed in the retina into a physiological process, a theory of vision no longer required the hypothesis of light generated in the eye. Nevertheless, the deformation phosphenes remained an interesting phenomenon for those discussing the elementary mechanisms of vision. The phosphene was still interpreted as a kind of 'activated' internal light and thus became a link between new theories of vision in the 17th century and the traditional interpretations. The reason for this was the limited use of Kepler's theory of vision by himself, by Scheiner and by Briggs. A consistent application of Kepler's image formation theory was performed by Descartes and his successors and by Newton. Their concept of a mechanical process underlying all sensation, applied to the theory of vision, became a plausible explanation for the phosphene, replacing the older theories.

The final *experimental* refutation of the age-old postulate that physical light is generated in the eye by eyeball deformation or blows to the eyeball did not come about until the beginning of the 18th century. It was *Giovanni Battista Morgagni* (1682–1771), one of the leading Italian anatomists of his time, who furnished the experimental evidence to directly reject the generation of physical light within the deformed eye. In his '*Adversaria anatomica omnia*' [51] he devoted one chapter to ophthalmology in which he also discussed the deformation phosphenes. He sided with William Briggs against Christoph Scheiner and pointed out that pressure exerted on the cornea and transmitted directly to the crystal lens could not be the cause of any light sensation. Similarly, he opposed Kepler's view that the iris could generate light. Morgagni also observed that deformation of the eyeball on two sides leads to two phosphenes:

> *As I observed repeatedly it is certain that no light appears when the cornea is pressed. When, however, the region near the cornea is deformed, light appears immediately in the shape of half an annulus. Deformation a little further away produces a light annulus. If during the same time two regions of the eyeball are deformed, two light rings appear immediately. When, however, the pressure is exerted not only with the finger tips but with the whole finger, the light takes on an elliptic form. Applying instead of the finger a much smaller round body, such as the head of a needle, the light ring is much smaller. It always appears on the side* [of the visual field] *opposite that indented*' [51, p. 92].

Morgagni believed that the phosphenes are caused by '*stretch of the fibers of the tunica retiformis*' [i.e., the retina] and assumed that by these '*vibrations, the animal spirit is affected as it is by the rays of light.*' Finally with the help of an assistant he performed a simple and elegant experiment in a dark room, demonstrating that no light is generated by mechanical irritation of the eyeball. When Morgagni deformed his eye with his finger and perceived bright phosphenes, the other person was asked to see whether light leaves Morgagni's eye, but '*even when he observed extremely carefully and very bright light appeared to me* [Morgagni], *he could never observe any light by himself*' [51, p. 93]. From the outcome of this expeirment and his previous experimental observations, Morgagni concluded that deformation in excised eyes did not produce any light and that the phosphenes are entirely *subjective*. As an explanation for their existence he assumed a *mechanical irritation of the spiritus visibilis*. Morgagni performed his deformation phosphene experiments not only out of theoretical interest but also with practical goals in mind. He believed that the apparition of the light cycle caused by eyeball deformation in the dark can be taken as an indication of normal retinal function. Thus he argued that a pressure phosphene seen by patients suffering from cataract of the lens is a positive prognostic criterion for the ophthalmic surgeon: when he removes the opaque crystal lens, the patient's chances of regaining his vision are fairly good [51, p. 94].

Morgagni's publication came into the hands of *Georg August Langguth* (1711–1782), a German physician working at that time at the famous *University of Wittenberg*. He had taught anatomy and botany there since 1742 and held a chair in both since 1747. His bibliography contains nearly 70 papers, dealing mainly with surgical topics. His dissertation '*De luce ex pressione oculi*' [52] was published in 1742 when he became a member of the medical faculty.* This paper seems to be Langguth's only contribution to sensory physiology.

In the introduction to his essay, Langguth wrote that he perceived the phosphene for the first time by chance, but before setting up his experiments, he was evidently also acquainted with Morgagni's description of the phosphenes in '*Adversaria anatomica omnia*'. Langguth performed his experiments in an absolutely dark room and deformed his eyeball with a finger or an ivory ball the size of a pea mounted on a small stick. He described how the phosphene '*always appears opposite the deformation site*' [52, p. IV]. To find out whether physical light is generated in the eyeball by the deformation, he observed his deformed eye in a mirror in the dark and tried to see whether in addition to the phosphene he could discover light appearing at

* One copy of Langguths '*De luce ex pressione oculi*' is extant at the Herzog August Bibliothek, Wolfenbüttel.

the spot where he believed he should see his pupil. Finally he repeated Morgagni's experiment:

'*A friend, who became curious about these phenomena . . . visited me in the dark room. I briefly explained to him what I was doing. The doors were closed and I asked him to observe my eyes very closely. While I was perceiving the small lights* [i.e., the deformation phosphenes] *he was not able to observe any small flashes or oscillating lights. Thereafter he performed the same experiment by himself according to the same rules, experimental procedure and design. He was asked to confirm whether light appears to him immediately by pressure on the eye. I, however, could not discover any light leaving his eyes. Later I performed this experiment repeatedly, always with the same result; in the middle of the night or when I was lying horizontally, early in the morning when I awoke from sleep before sunrise. Even when I covered one eye for the whole day and occluded* [during the experiment] *the other eye with the hand, the described pressure on the eye led to the same effect. Similarly, when I opened one eye, observed the normally illuminated objects, closed the other eye and pressed on it, the same light sensations appeared, but somewhat weaker*' [52, p. VI].*

Langguth explained his observations by a rather traditional model of vision: the image of the object affects the retina and alters immediately the spiritus animalis. This alteration is transmitted to the brain by the spiritus flow and activates the immaterial mind within the brain, which directs its attention to the object. The action of the spiritus animalis in the retina is governed by certain chemical processes. He applied the same idea to explain the appearance of the deformation phosphenes:

'*The particles at hand* [of the animal spirit] *are gathered together and somehow mingled with the liquid, oily, most subtle fluids. The eyelid is held very slightly away from the eyeball by mechanical pressure, when the eyelids are firmly closed and a vacuum is generated. This causes the flash of light to appear*' [52, p. XIII].

Langguth's physico-chemical hypothesis of the deformation phosphenes is not very clear. Apparently he thought that mechanical pressure would lead to an *interaction of the retina and the vitreous body* at their contiguous surfaces. This would change some properties of the vitreous body, which are transmitted to the *spiritus animalis* in the retina.

* German translation of Langguth's '*dissertatio*' in Hagner 1987, p. 132–142.

Morgagni's and Langguth's observations and explanations could be considered a modification of Plempius' and Decartes' mechanical theory on pressure phosphenes, although both did not mention either of them. Langguth only referred to those authors whose names he had read in Morgagni's book. Somewhat unjustly he criticized the theory of Kepler, Scheiner and Briggs, mentioned above, and was convinced that their explanations of the pressure phosphenes had not advanced the comprehension of this phenomenon [52, p. XIV]. On the other hand, he developed a stringent mechano-chemical theory, whereby he was aware of the fact that his theoretical assumptions were rather speculative.

In a quite amicable manner Morgagni mentioned Langguth's experiments in his major opus '*De sedibus et causis morborum*' [53, 54]:

'*My profound wish was to read the thoughts of the most admirable Mr. Georg August Langguth. In his dissertation on the light apparition, he not only affirmed my statements but also confirmed them with his own experiments. Accordingly, when one would explain in particular and not in general that which we both observed in the same question and especially that which he performed with a friend, one would easily recognize which of the two premises are most suitable*' [54, p. 598].

Comparing Langguth's and Morgagni's studies on the deformation phosphenes, one empirical step forward has been made in the report of the former: He refers to the fact that in principle, pressure phosphenes do not change during the course of dark adaptation. We repeated these dark adaptation experiments and could confirm Langguth's observation: The pressure phosphenes appear to be about the same, whether in a photopic-adapted retina within the first minute after the light is turned off or under scotopic adaptation conditions after the subject has remained for one hour in a totally dark room [55].

6. The discussion of deformation phosphenes in the physiological literature of the 18th, 19th and early 20th centuries

Morgagni's and Langguth's explanation of the deformation phosphenes and their rejection of the idea of physical light generated in the eye were accepted by the physiologists of following generations. Soon their names no longer appeared in the textbooks, only their experiments and results. *Herman Boerhaave* (1668–1738), the eminent clinician from the University of Leyden, mentioned the deformation phosphenes in his textbooks on vision and the disease of the eye [56]. He described phosphenes on different occasions, attributed them to mechanical irritation of the optic nerve, and observed light sensations not only when the eye was directly indented but also affected by other mechanical forces: '*Whenever we sneeze in darkness or cough, we can perceive light sparks, and the same is true when someone hits against our head or the eye . . . This is no real light but only a change in the shape of the eye together with the compression of the optic nerve or the retina, and these changes produce the same sensation of light, which normally are evoked by the refracted light beams. Whenever the optic nerve is moved as it is moved by the light, independent of which cause moves it, the same impression of light is evoked . . .*' [56, p. 121]. Boerhaave mentioned that when infections or other diseases affect the eye, light sensations are particularly easy to evoke by pressure on the eye in total darkness. He considered this phenomenon as a bad sign for the prognosis of the disease, indicating the danger of total blindness. Boerhaave rejected the traditional idea that cats, horses or other animals emit light from their eyes in the dark for the purpose of vision. It was evident to him that in total darkness the only advantage these animals had over man was that their pupils could dilate more so that the retina could catch more light from the surroundings [56, p. 193].

Boerhaaves pupil, the Swiss-born *Albrecht von Haller* (1708–1777), professor of anatomy and physiology at the University of Göttingen, who became famous in the neurosciences because of his intensive discussion on the sensibility (*sensibilitas*) of the nerve and the irritability (*irritabilitas*) of the muscles, devoted a small chapter of his eight-volume Physiology Handbook to the phosphenes [57]. He followed Boerhaave in emphasizing the effect of mechanical pressure exerted on the retina by eyeball deformation and conjectured that physical light also causes mechanical pressure on the retina. Therefore the same percept, namely light is evoked: '*It is . . . a useful dogma that our soul cannot discriminate equal percepts and attributes the* [perceptual] *consequences of an unknown cause to another, better known cause, as soon as the effects are identical. Therefore the pressure on the retina, which is generated by external light, seems to us more familiar than the pressure caused by a hard, non-luminous object. Since pressure is pressure the soul believes* [when perceiving deformation phosphenes] *that light is acting on the retina . . .*' [57, p. 1041]. Haller mentioned the experiments of Morgagni and Langguth and supported the idea that no physical light is generated when the eyeball is deformed [57].

As an example of the discussion on phosphenes in the textbooks of physiology of the early 19th century, we wish to mention *Johann Heinrich Ferdinand Autenrieth*'s '*Handbuch der empirischen Physiologie*' [58]. Autenrieth (1772–1835) taught as professor of medicine at the University of

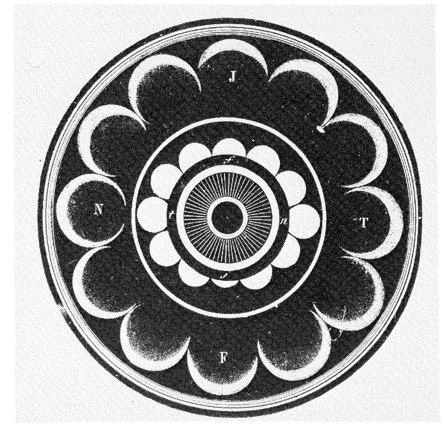

Fig. 6. Serre d'Uzèz published this figure in his '*Essai sur les phosphenes*' [59]. This illustration demonstrates the quarter-moon phosphene which appears at the contralateral side to the indentation site. Serre d'Uzez summarized his observations schematically: The central part of the figure represents the pupil and the iris, the filled circles the site of indentation, the size of these filled circles the strength of local eyeball deformation, and the quarter-moons the phosphene seen in the visual field opposite the respective indentation site.

Tübingen and was one of the protagonists of empirical medicine during the outgoing period of enlightenment and the beginning of romanticism in Germany. In his handbook chapter on vision he also described phosphenes and analysed the light and dark ('*black-bluish*') components of the deformation phosphenes, arguing that the bright parts are caused by retinal excitation, while the dark parts indicate retinal suppression ('*Lähmung*'). Without mentioning Morgagni and Langguth he reported the results of their experiments as proof that no physical light is generated during eyeball deformation [58, Vol. II, p. 191].

The name '*phosphene*' was first coined in 1838 by the French physician *Savigny* [13], and the first extensive review on deformation phosphenes was published in 1853 by the French physiologist *Serre d'Uzèz* [59]. He had also performed detailed experiments on pressure phosphenes in which the relationship between site and strength of eyeball deformation, on the one hand, was carefully determined and on the other, the shape and localization of the phosphene in the visual field. In Fig. 6 his findings are summarized.

One of the leading sensory physiologists of the first half of the 19th century, the Bohemian *Jan Evangelista Pŭrkyne* (1787–1864), professor of physiology at the Prussian University of Breslau (now Wroclaw, Poland) and later at the University of Prague, also conducted extensive investigations on deformation phosphenes [60]. The first study of Pŭrkyne on the

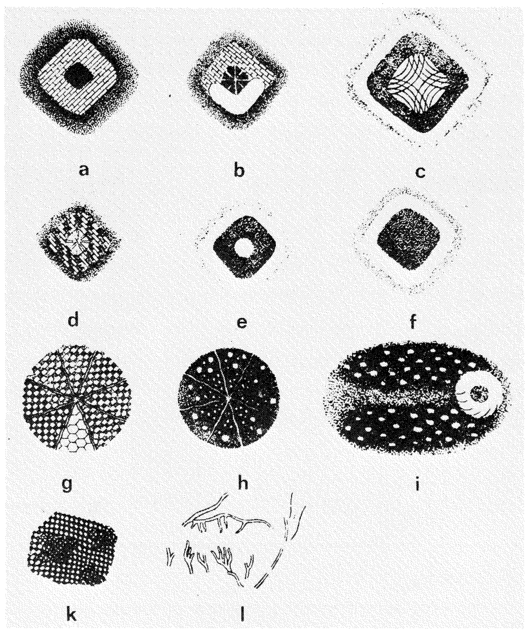

Fig. 7. Selection of deformation phosphenes as observed by J.E. Půrkyne [61, 68]. For further explanation see text.

'*Druckfigur des Auges*', as he called them, was published in his doctoral thesis [61]. He described the subjective light sensations evoked by deformation of the eyeball on the side of the cornea. Immediately after the onset of pressure he observed a *ring of light* consisting of small light or dark squares and a round dark hole in the middle. When the pressure was maintained, the hole became filled with bright lines and the size of the ring increased (Fig. 7a–d). Within a few seconds the phenomenon was transformed into a larger ring of light, whereby a luminous central structure became visible (Fig. 7e). As soon as the deforming pressure was released, the central structure disappeared, but the ring was still visible for a few seconds (Fig. 7f). Půrkyne noted the variability of the '*Druckfigur*' when he repeated the experiment. In some cases he also observed *patterned visual structures* as shown in Fig. 7g and k and light nebula superimposed by bright stars (Fig. 7h). When the pressure was relieved, he noted fragments of the figure of retinal vessels (Fig. 7l).

In addition to the deformation phosphenes Půrkyne also observed short phosphenes during large saccades:

'*If I cover the eye well and move it fast and with some force towards the outer corners of the orbit, a large luminous ring appears on the outer side of the dark field of vision*' [61, p. 26] (Fig. 7i). He concluded that this light is caused by the sudden stretch of the optic nerve, which produces '*in the substance of the nerve electrical antagonistic processes causing the development of light . . .*' [61, p. 27].

In his second book on vision in 1825 Půrkyne extended these studies. He described how he could observe weakly illuminated phosphenes of al elliptic shape in a totally dark room when he pressed his eyelids tightly together and then suddenly relaxed them. In contrast to most reports, Půrkyne, who was an extremely careful and skilled observer, repeatedly saw *patterned phosphenes* during the deformation of one eye (Fig. 7g and k). Such patterned phosphenes normally are only visible when both eyeballs are deformed simultaneously [l]: A few seconds after binocular eyeball deformation, in addition to the phenomena known from monocular deformation, the patterned phosphene appears. Square-shaped or rhomboid structures in a regular formation and increasing in size from the center of the field of vision to the periphery appear to flicker at about 10 Hz. In between these flickering patterns very bright non-flickering small stars of a slight bluish colour appear together with some small dark bands extending from the center of the visual field radially to the periphery. These binocular deformation phosphenes are shown in Fig. 1e as they appeared to one of the authors (O.-J. G.). We explored this phenomenon in many subjects, most of them inexperienced and uninformed with regard to phosphenes. In all subjects periodic geometrical patterns as shown in Fig. 1e were described but the details of the light-dark patterns varied from subject to subject [62].

We became curious of course as to why Půrkyne's reports should deviate from those of most subjects, in which pattern phosphenes only appeared during *binocular* eyeball deformation. The hypothesis was put forward that Půrkyne had an amblyopic eye and poor binocular integration [60]. Indeed we could find some biographic evidence that this was the case [63]. Půrkyne was therefore very cautious in describing binocular phenomena of vision.

Despite the fact that all physiologists towards the end of the 18th century were in agreement that eyeball deformation only evokes subjective light and not physical light, the belief that efferent light from the eye could illuminate the extrapersonal space lived on in the public mind as well as in the conceptions of some medical doctors. In 1834 Johannes Müller reported on such a case, which was analysed by a *Hofrath Seiler*, specialist in forensic medicine: '*The question whether the human eye can see in the dark due to emission of subjective light was analysed in a forensic medical examination. A dignified priest had been robbed on a dark night by two men and his right eye* *hit by a stone. "In the same moment light similar to electrical glare or the illumination caused by summer lightning was emitted from his eyes. He could therefore distinctly recognize the culprit." Hofrath Seiler, who was asked to decide on the question, did not directly support this statement, since analogous cases were lacking. However he considered it as a possible argument, because some men and animals can see in the dark (which only proves that they have a sensitive retina). He mentioned by name Kaspar Hauser, who could see at dawn much better than in the daylight. Furthermore, he argued that by pressure on the eye, light sensations are evoked and finally, that in many animals and some men light was observed in the eyes. Seiler himself claimed to have seen the glare in eyes of cats in totally dark cellars, all the brighter, the more excited the animals were by an affect, hunting the prey etc . . .'*

Müller, of course, contradicted this opinion and wrote that Seiler could easily have refuted his hypothesis by going into a dark room, deforming his eye till the deformation phosphenes appeared and then trying to read by the light of these phosphenes. Finally Müller '*regretted that such an illustrious and commendable scholar had in this case supported medical superstition*' [64, p. 140–42].

With the exception of Tyler's study [1] on binocular deformation phosphenes, no new essential discoveries on phosphenes were made after Půrkyne, but the mechanisms leading to this curious percept were discussed anew by each generation of physiologists [65, p. 236–241]. During the first decades of the 20th century some sensory physiologists believed deformation phosphenes to be caused by the *increased intraocular pressure* accompanying eyeball deformation and leading to retinal ischemia [66]. Others, such as Stigler [67], maintained the hypothesis that it is primarily the *retinal stretch* which leads to the phenomenon. This idea was also supported by the appearance of accommodation phosphenes [68, 69, 70]: When one looks at an imaginary distant object in total darkness and then directs the eyes as quickly as possible to the tip of the nose, the strong accommodation changes the force transmitted from the ciliary muscle and the elastic lens via the *Zonula Zinnii* fibers to the retina. This stretch leads to a ring-shaped phosphene of mild intensity seen in the outer periphery of the field of vision. Since the intraocular pressure is not essentially changed by such accommodative processes, the retinal stretch hypothesis seemed to be more plausible than that of retinal ischemia or hypoxia. The stretch hypothesis is also supported by the appearance of saccadic phosphenes, repeatedly mentioned above. Saccadic phosphenes are circular or semicircular light sensations located around the projection of the optic nerve in the visual field (observation in total darkness). When the eyes are moved by horizontal saccades to

the right, this light ring is seen excentrically on the left side, and when the eyes perform a saccade to the left, the light ring appears on the right side. From this it is concluded that inward movement of the eye stretches the retina near the optic papilla and thus evokes the ring-shaped or half-ring-shaped phosphene. Patients suffering from *optic neuritis* frequently report seeing rather bright saccadic phosphenes. This is presumably caused by the increased sensibility of the swollen optic nerve to retinal stretch and the edema of the papilla.

7. Neurophysiology of deformation phosphenes, a postscript

During the last 15 years we became interested in the neurophysiological basis of deformation phosphenes and consequently performed experiments in anaesthetized cats [51, 71, 72, 73]. By means of tungsten microelectrodes the activity of single *on-center* or *off-center ganglion cells* was recorded from optic tract fibers. These essential results can be summarized in one sentence: *The great majority of on-center ganglion cells*, normally activated when the retina is *illuminated* by light and inhibited when the light is turned off, increased their neuronal activity after a latency of 0.2 to 3 seconds during constant eyeball deformation in total darkness, while the *off-center ganglion cells*, which normally are transiently inhibited by illumination of the retina, were inhibited with a delay of 0.2 to 4 seconds by eyeball deformation. This response scheme and the explanation of deformation activation are shown in Fig. 8.

We interpreted our neurophysiological results by the hypothesis that eyeball deformation leads to retinal stretch, which in turn increases the surface of *horizontal cells*. This surface increase leads to depolarization of the membrane potential of horizontal cells, which then is transmitted to the bipolar cells connected with the horizontal cells. Hereby (as is normally the case when the horizontal cell membrane potential is depolarized), the *on-bipolars*, i.e., the cone on-bipolars in the light-adapted retina and the rod-bipolars in the dark-adapted retina, are depolarized and the *off-bipolars* are hyperpolarized by the depolarization of the synaptic contacts between horizontal cells and bipolar cells. This mechanism induces the activation of on-center ganglion cells and the inhibition of off-center ganglion cells, which corresponds nicely to what the observer perceives in his visual field, provided that one accepts the idea that the information 'brighter' is conveyed by on-center ganglion cell activity and 'darker' by off-center [for details see 55, 73].

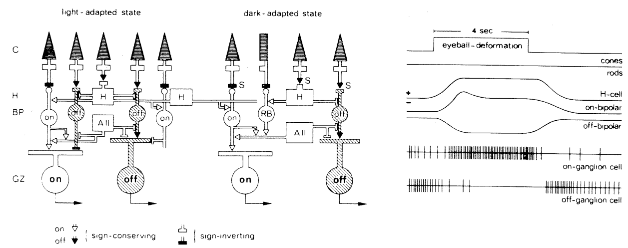

Fig. 8. Scheme of the effect of eyeball deformation on the activity of retinal neurons. The deformation stretches and increases the retinal surface, whereby the horizontal elements in particular (horizontal cells and amacrines) are affected. This leads to an increase in cell surface of these structures and to a *depolarization* of the horizontal cells (H), which in turn causes a depolarization of on-bipolars (BP_{on}) and a hyperpolarization of off-bipolars (BP_{off}). These changes are transmitted to the corresponding ganglion cells (G), which are activated (on-center ganglion cells) or inhibited (off-center ganglion cells). A similar depolarization of the amacrine cells (AII) could also lead to a modification of the ganglion cell responses. Due to their antagonistic innervation of on- and off-ganglion cells, the amacrine type II is a candidate for the mediation of direct stretch responses. The responses of retinal ganglion cells during and after eyeball deformation, however, are dominated by the horizontal cell depolarization. In the dark-adapted retina, the horizontal cell depolarization is mediated through the rod bipolar cells (RB), which activate AII-amacrines, activating in turn on-ganglion cells and inhibiting off-ganglion cells. Excitatory ('sign-conserving') synapses are drawn as arrows, inhibitory ('sign-reversing') synapses as bars. When the *rod-amacrine* cell is directly depolarized by deformation, this depolarization would also lead to an activation of on-ganglion cells and an inhibition of off-ganglion cells, since the synaptic endings of the rod-amacrine cell are functionally not uniform and have a 'polar' organisation.

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