THE SENSATIONS EXCITED BY A SINGLE MOMENTARY STIMULATION OF THE EYE.

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Review of the present state of knowledge of the subject. Some of the causes of the prevailing lack of agreement and discrepancy of results of different workers. The effects of a single momentary stimulus observed under the simplest and most favourable conditions. The effects of stimulation by a travelling image. The explanation of the 'recurrent image' or 'Bidwell's ghost.' The delay of the reaction of the rod-apparatus. The 'ghost' following an image excited by pure red light. The reactions of the completely dark-adapted eye. Summary of results.

IT is now pretty well agreed that, on the one hand, light entering the eye initiates the visual processes by producing chemical changes in the rods and cones of the retina, and that, on the other hand, the physiological processes that immediately determine the visual sensations are confined wholly, or in chief part, to the cerebral cortex. If these views are well founded, it follows that between the physical stimulus acting upon the rods and cones and the sensations determined by those processes of the visual cortex there intervenes a long chain of physiological events.

Thomas Young, the originator, and Clerk Maxwell, v. Helmholtz, and Arthur König, the chief supporters of the theory of component visual processes[1], were physicists, and it was therefore but natural that they should have neglected almost completely this long chain of physiological processes. It was the great merit of Prof. Ewald Hering that in giving to the world his theory of the opponent[1] visual processes,

[1] I use the terms 'component' and 'opponent' to denote the two principal types of theory, those of T. Young and of Hering respectively.

he endeavoured to give some account of the nature of the physiological events that mediate between the physical stimulus and its psychical effects. But Hering has hitherto been content to give his scheme of these processes an extreme and unnatural simplicity, assuming that the physiological processes mediating between any particular kind of stimulus in the retina and the sensation excited by it are identical in character throughout the long chain of anatomical elements concerned in originating the excitation, in transmitting it to the cortex, and in determining there the quality of the sensation[1].

A complete theory of the visual processes must of course analyse the chain of physiological processes into its successive elements, and must describe the nature of each of these partial processes. In previous papers I have attempted to make some advance in this direction. Adopting Thomas Young's fundamental conception that the sensation white results from the fusion of the effects of three distinct kinds of nervous process, the elementary or simple colour-processes, I have distinguished and described what I believe to be the nature of the photochemical process in the retina, analysing it into two stages[2]: (1) a process of decomposition of stored mother-substances in the outer limbs of the rods and cones, by which are set free substances that are capable of acting on the nerve-endings as chemical stimulants; (2) the excitation of the nerve-endings by these substances, and the re-enforcement or acceleration of this action by light. In my paper "On the Seat of the Psycho-physical Processes[3]" I have attempted to throw light on the nature of those most highly specialised physiological processes of the visual cortex by which the sensations are immediately determined. I have been content to regard the chain of events mediating between the excitation of the nerve-endings in the retina and the psycho-physical processes of the cortex as essentially of one type, of the type, namely, of the simple conduction of the nervous impulse, but in the paper on "The Nature of Inhibitory Processes within the Nervous System[4]" I have suggested a scheme of the mechanism by which are produced those reciprocal modifications of the intensities of the excitation-processes in neighbouring retino-cerebral elements

[1] It is true that Hering is nowhere explicit upon this point, but this is the view to which he seems to incline; cp. *Zur Theorie der Nerventhätigkeit*, Leipzig, 1899.

[2] "Some new observations in support of Thomas Young's Theory of Light- and Colour-vision." *Mind*, 1901, N.S. Vol. x. p. 52, etc.

[3] *Brain*, 1901, Vol. xxiv. p. 577.

[4] *Brain*, 1903, vol. xxvi. p. 153.

which underlie the phenomena of simultaneous light- and colour-contrast. I have shewn, also, how this scheme of the visual processes, with its three partial processes or steps, the retinal, the afferent conduction processes, and the psycho-physical processes of the cortex, enables us to explain various other phenomena, especially those of simultaneous and successive spatial induction of light and colour, and those of enduring after-images, both positive and negative.

In this and other papers I propose to describe experiments that lend support to my scheme of the visual processes by shewing that other phenomena not yet dealt with fall naturally into place in it. In this paper I deal only with the effects of a single momentary stimulus to the retina. A brief survey of the present state of the subject seems necessary.

In 1872 C. A. Young[1] reported that when a discharge from a powerful electrical machine, giving a spark about seven inches long, momentarily illuminates a room, while the eyes are shaded from the direct light of the spark, objects in the room may be seen twice, three times, or even four times in rapid succession, although the spark is single[2]. He estimated the interval between successive appearances to be little less than one-fourth of a second, and he wrote, "The appearance is precisely as if the object had been suddenly illuminated by a light, at first bright, but rapidly fading to extinction, and as if, while the illumination lasted, the observer were winking as fast as possible....I have ventured to call the phenomenon recurrent vision."

Mr Shelford Bidwell has repeated and confirmed Young's observation, and he states that "Under favourable conditions I have observed as many as six or seven reappearances of an object which was illuminated by a single discharge[3]."

This phenomenon, which may be readily observed by anyone under suitable conditions, is of fundamental importance. The description of it we owe to the physicists, and it has been curiously ignored, and its significance has remained unappreciated, by the physiologists and experimental psychologists who have dealt with the effects of a brief stimulus applied to the retina. But the whole subject is, in fact, in

[1] *London and Edinburgh Philosophical Magazine*, 1872, vol. XLIII. p. 343.

[2] I understand that the spark is really multiple, but that the phases succeed one another so rapidly and the whole duration of the flash is so brief that for our purpose we may regard it as single.

[3] *Curiosities of Light and Sight*, London, 1899, and *Proc. Roy. Soc.* 1894, vol. LVI. p. 132.

a state of great confusion, and it is of some interest to point out the sources of this confusion before attempting to unravel it. The confusion is due, in the first place, to the imperfect understanding of the phenomenon first described by Purkinje many years ago and known in Germany as the after-image of Purkinje, rediscovered in this country by A. S. Davis[1], and commonly known as 'Bidwell's ghost.' This may be seen in typical form when a light of moderate brightness is moved across a dark field of view at a moderate speed while the eye remains at rest; the 'ghost' then appears as a second dimmer image following the principal or ordinary image of the light and separated from it by a dark interval. This also is a phenomenon easy to demonstrate, and familiar to all[2].

A ray of light falling for a brief moment upon a small area of the retina seems, then, to produce two very different effects according to the mode of its incidence; a stationary image momentarily exposed produces a rapid succession of pulses of sensation of diminishing intensity; a similar image travelling across the retina produces in every part of its path a double sensation, namely, a brighter image followed after a distinct dark interval by a much less bright image.

Of recent years several observers have studied these effects (Bosscha, Munk, Hamaker, v. Kries, Hess, Bidwell, Parinaud, Charpentier) but without explaining this apparent contradiction, without arriving at any agreement as to the exact description of the phenomena, and without evolving any tenable theory for the explanation of them. Without attempting to summarise the results of these recent researches or to criticise them in detail, I may be permitted to make two remarks which will apply to all or most of them:—Firstly, most of these workers have arranged their apparatus so as to expose to the eye an image narrowly limited as to its conditions of brightness, form, and rate and mode of movement, and (with the exception of v. Kries) they have not sufficiently studied the important differences resulting from different states of adaptation of the eye, and from the incidence of the stimulus on different parts of the retina. Now, as will be shewn below, the effects of the brief stimulus, whether travelling or stationary, vary markedly with every change in these conditions. It was thus inevitable that great diversity should obtain between the accounts of

[1] *London and Edin. Philos. Magazine*, 1872, Vol. XLIV. p. 526.

[2] It may sometimes be observed very prettily when travelling in one of our tube-railways, as the car passes one of the lamps which are hung here and there on the walls of the tunnel.

the different observers, each working with his own peculiar and limited set of conditions. The practical conclusion to be drawn is that in order to arrive at a complete description and a tenable theory of the phenomena, a single observer must use both methods, and in both cases must vary both the subjective and objective conditions of the experiments as widely as possible. Secondly, 'Bidwell's ghost' following a travelling image is a phenomenon much easier to observe, and far more striking than the multiple response of the eye to the stationary flash of light, and it is probably for this reason that those who have worked by the method of the stationary image generally seem to have attempted to bring their description of the effects into line with the 'ghost,' to describe, in fact, a 'recurrent image.' Now, as I shall shew below, Bidwell's ghost is but one specially striking and easily observed phase of a long series of appearances produced by variation of the conditions of observation. It is, therefore, very misleading to regard this one phase as the typical and fundamental phenomenon, and to seek to explain all other appearances as unimportant varieties of it, as has commonly been done. It is clear that when the momentary stimulus is applied by the method of the travelling image, the conditions are more complex than when the stimulus is applied by the momentary exposure of a stationary image. Instead, then, of observing and interpreting the appearances resulting from the latter, in the light of one particular phase of the appearances resulting from the former, kind of stimulus, we must reverse the procedure: we must observe accurately, and with an open mind, the effects of the momentary stimulus given under the simplest possible conditions, and must then interpret in the light of these observations the more varied and complex effects produced by the travelling image.

Momentary Stimulation by Stationary Image.

These considerations have determined my experimental procedure, and with them in view I describe first the effects of the stationary momentary stimulus. In making these observations it is important to simplify the conditions to the greatest possible extent, and two precautions are of especial importance; (1) during and after the brief exposure of the object-image to the eye, all other sensory stimuli should be as far as possible excluded, *i.e.* the object should be the only source of light in an otherwise completely dark field of view, and auditory stimuli, such as the snap of a photographic shutter or the crack of an electric discharge, should be avoided; (2) the light should come and go over all parts of the surface illuminated as nearly simultaneously as possible. It is, I think, owing to the lack of these precautions that several workers by the method of stationary object-light have failed to observe the fundamental phenomenon roughly described by Young and Bidwell, the series of rapidly recurring images or pulses of sensation. One simple method by which these conditions may be approximately realised I have already described[1]. Three others I have found satisfactory: (1) the single electric discharge in a vacuum-tube enclosed in a box, of which one side is of ground-glass, a small area of which is exposed to the eye and lit up by the flash; (2) a slit in a large disc or pendulum-screen is swung through the focus of an arc-lamp so as to illuminate for a moment an area of a plate of milk-glass standing in the path of the ray; (3) the most satisfactory method is the following: Two plates of thin milk-glass are fitted into an aperture in the front wall of a dark-cabinet[2] parallel to one another, and one behind the other at a distance of 2 cm. Both are covered with opaque black paper; in the paper covering the outer plate is a vertical slit or aperture 4 cm. long and 1 cm. in width, and in the paper covering the inner plate is a circular aperture 1 cm. in diameter, immediately behind the centre of the oblong aperture in the other paper. A narrow ray of light (best is a ray of sunlight reflected from a heliostat) is thrown upon the exposed area of the outer plate. The ray is intercepted by a large opaque disc 60 cm. in diameter, rotating on a horizontal axis immediately in front of the outer plate and below the exposed area of it. In this disc is a radial aperture 20° in width, which, as the disc rotates at one revolution per second, allows the ray to fall upon the exposed area of the outer glass-plate for about 50σ ($\frac{1}{20}$ sec.)[3]. The too rapid recurrence of the illumination is prevented by a second disc, similar to the first, rotating between it and the source of light at a slower rate (on the principle of the apparatus described by v. Helmholtz, *Phys. Optik*, 2. Auf., S. 514). As the ray falls upon

[1] *Brain*, 1901, Vol. xxiv. p. 603.

[2] Described in *Mind*, 1901, N.S., Vol. x. p. 355.

[3] The duration of the stimulus must not be greater than that which just suffices to allow the stimulus to produce its full effect for sensation. If the stimulus is of longer duration the series of pulses of sensation does not occur. Stimuli of the intensities used in the above experiments require more than 50σ to produce their maximum effects. These facts I hope to deal with in a later paper.

the outer plate the circular area of the inner plate is illuminated in all its parts simultaneously, owing to the great diffusion suffered by the light in passing through the outer plate, and all parts are likewise simultaneously obscured as the ray is cut off by the onward motion of the disc. The intensity of the illumination of this circle may be controlled by altering the width of the exposed area of the outer plate, or by altering the intensity of the incident ray. Sitting within the cabinet I observed the momentarily illuminated circle with one eye only, at a distance of 50 cm., the head being supported on a chin-rest. When the circle 1 cm. in diameter is directly fixated by the eye at this distance, its image falls wholly on the rodless fovea of the retina. In the series of observations which follows, the source of light was an acetylene-lamp furnished with four burners closely set in a row, and separately controlled by four taps. Such a lamp gives a flame slightly yellowish, but much brighter and more nearly white than that of ordinary gas. It is stated by the vendors that each burner gives a light of 100 candle power, but this estimate is probably rather too high. The eye was throughout in a state of moderate dark-adaptation.

(1) I begin with one burner at rather less than one-half its full power. When the circle is illuminated by this light, transmitted through the two plates of milk-glass, it appears as very dull white. The discs being set in motion, and the eye being directed towards the circle, the image of it falls upon the fovea for about 50 σ and excites a single brief sensation of light, the image simply pops into consciousness and out again and I can only vaguely estimate its duration at about one tenth of a second. On then turning the eye towards any point a few centimetres to one side of the circle, so that the image of it falls on a part of the retina peripheral to the fovea, and repeating the observation, the first appearance of the circle is followed by a second dimmer appearance; the interval is so brief that it is impossible to say that the first image has completely disappeared before the second begins to rise, the impression is rather that of a double pulse of sensation without any appreciable interval. If now the light is still further diminished by about 50% the circle is so dim as to be hardly visible when its image is confined to the fovea, and its momentary illumination produces a single very feeble pulse of sensation, and when its image falls upon the peripheral retina it causes, in that case too, merely a single brief pulse of sensation; the reduction of the intensity of the stimulus has abolished the second pulse.

(2) With one burner at full power I repeat these observations: On direct fixation the image falling upon the fovea provokes a double pulse of sensation, just like that provoked by the duller image of the first case falling on the peripheral retina. On lateral fixation (*i.e.* such that the image falls outside the fovea) the circle of this brightness provokes four pulses of sensation succeeding one another more rapidly than the two pulses of the previous observation, and occupying together about one-third of a second. Immediately after the disappearance of the last of this series of four pulses there appears in the same area a very dull, ill-defined, grey, steady after-image of the circle, which dies away in from five to ten seconds.

(3) Repeating with two burners at full power, I see on direct fixation three pulses of sensation followed by a faint grey after-image that lasts two or three seconds only; and on lateral fixation I see five or six pulses of sensation of which series the earlier members succeed one another more rapidly than the later, and the pulses are of diminishing intensity throughout the series. It is with an image of about this degree of brightness that the character of the multiple response can be most accurately observed, and is most easily appreciated by an unpractised observer.

(4) Repeating with three burners, I see, on direct fixation, five rapid pulses followed by a grey after-image lasting some ten seconds, and on lateral fixation I see six or seven pulses followed by an ill-defined grey after-image which slowly and steadily dies away in about twenty seconds.

(5) Repeating with four burners, I see with both direct and lateral fixation a series of about seven pulses, of which the earlier members follow one another so rapidly that they cannot be counted; the whole series lasts about three-quarters of a second, and is followed by a grey after-image which is brighter and more persistent in the case of lateral than of direct fixation.

These observations are entirely concordant with those made by the other methods mentioned above. They shew that the brief stimulus of low intensity provokes, as the primary response of the eye, a single brief pulse of sensation, and that a stimulus of higher intensity provokes two, three, four or more pulses, according to its intensity, and that the extrafoveal region, being more sensitive than the fovea, responds to a stimulus of any given low intensity with a rather longer series of pulses than is provoked by the same stimulus when applied to the fovea.

The apparatus used in the above experiments does not allow of the use of a very bright light, but I have previously described the effects of momentary stimulation by bright light and may quote the description here for the sake of completeness. "When in this way a bright coloured image is allowed to fall on the retina for a moment, the character of the sensation is similar for all three colours used by me, namely red, green, and blue." "The effect falls distinctly into two stages; the first stage consists in a pulsating or quivering image of the same colour as the glass used, declining rapidly in brightness, each pulse being less bright than its predecessor, until, after a period that increases with the brightness of the light from a small fraction of a second to nearly one and a half seconds, this first stage ceases and is replaced by a steady, dull white after-image that dies away in the course of ten or more seconds. The pulses of colour are not separated by distinct intervals of darkness, rather each seems to begin before its predecessor has completely disappeared and the effect resembles the 'coarse flicker' of rotating sectors. The rate of the pulsation is slower in the image of a dull than of a brighter light, and it seems to decline with the brightness, so that, towards the end of this pulsating stage of the image of a light of moderate brightness the pulses can just be counted (which means that they are coming at about the rate of ten per second)[1]." It is only necessary to add to this description that bright white light produces similar effects, save that the pulsating image is apt to be tinged with one or other colour which is more saturated the brighter the light used, and that the series is noticeably shorter in the case of a red light than in the case of light of any other colour.

In describing these observations I have merely supplemented the original observation of C. A. Young, quoted on p. 80, by varying the intensity of the stimulus from the lowest to the highest degree, and noting the difference of reactions of the fovea and of the peripheral retina in the case of stimulus of low intensity. Young attempted to measure the interval between the first and second pulse of the primary response by touching a reaction-key with the finger as nearly as possible simultaneously with each one. It is I think hardly possible to arrive at an accurate estimate of the interval in this way, and the only point in which his description calls for amendment is as regards the interval between the pulses, which I think he estimated too highly

[1] *Brain*, 1901, Vol. xxiv. p. 603.

in describing it as nearly a quarter of a second. That several recent observers have failed to notice the discontinuous or pulsating character of the primary response is due, I think, to the use of unsuitable forms of apparatus. Thus H. Munk[1] used for the presentation of the object-image a photographic shutter. I have made many attempts to observe the effect of the brief stimulus, using a similar shutter, but I have always found the noise of the shutter and the fact that the dark screen sweeps across the bright field from one edge to the other to be very disturbing influences, and I think they may sufficiently account for the fact that Munk divides the primary response into two stages, a brighter and a less bright, separated by a very brief duller interval. Nevertheless the pulsating character of the primary response would seem not to have escaped him entirely, for he describes the second of these stages as shewing "eine gewisse Bewegung, von welcher man nicht genau sagen kann, ob sie von innen nach aussen oder von aussen nach innen geht"; and adds that it is "nicht ein stätes Bild, sondern selbst ein Process." Parinaud also seems to have observed something of the pulsating character of the primary response, for he describes it as "la sensation lumineuse tremblotante[2]."

Stimulation by travelling image.

The fundamental fact of the multiple character of the response of the visual organ to a single momentary stimulus, and the increase of the number of the responses with increasing intensity of the stimulus, may be very well observed on fixating any point on, or in the neighbourhood of, a black disc bearing one narrow white sector and rotating at a moderate speed. The phenomenon has not, I believe, been described, and its significance is certainly not commonly appreciated. The larger the disc used for this observation the better in most respects, and in studying the phenomenon I have used discs as much as one and a half metres in diameter; but the following description applies to a disc of black card, 40 cm. in diameter, bearing a white sector 30° wide, of which the peripheral part, 10 cm. in radial length, only is exposed. This disc is rotated in bright diffused daylight

[1] "Die Erscheinungen bei kurzer Reizung des Sehorgans," *Zeits. für Psychol. u. Physiol. d. Sinnesorgane*, 1900, Bd. XXIII. S. 60.

[2] *La Vision*, Paris, 1898, p. 102.

before a black background. The eye fixates some point on, or in the neighbourhood of, the path of the white sector, but the fixation must be frequently changed from one point to another. When the disc rotates at one revolution per two seconds I see a narrow dark band lying upon the white sector, parallel to and a few millimetres behind its leading edge. (This is of course Charpentier's dark band.) When the rate of rotation is increased to 1 rev. per 1″, there appear other dark bands lying parallel to and close behind the first one, while the width of the white sector seems to be increased to about 50°. With further increase of rate the dark bands spread out over the white sector, so that at 2 revs. per 1″ the whole appears as a series of about six narrow white sectors of diminishing brightness separated by narrow dark bands, and filling about 90° of the periphery of the disc. At about 3 revs. per 1″ the whole series is so spread out that the leading band overtakes the last of the series, and the whole periphery of the disc is filled with a series of white radial bands separated by narrow dark intervals; the leading band is still distinguishable by its greater brightness. On still further increase of the rate of rotation the leading band ceases to be distinguishable, and the distinction between the dark and light bands becomes less and less clearly marked, so that it becomes increasingly difficult to estimate the width of the bands. The definition of the bands becomes less and less clear throughout the stage of coarse flicker, and in the stage of fine flicker no bands can be clearly distinguished, the eye receives merely a confused impression of a radially streaked grey ring. The multiple bands at the intermediate rates of rotation will be seen by any good observer when his attention is directed to the point. But the accurate observation of this series of appearances involves a considerable strain on the attention, and cannot in any case, I think, be satisfactorily carried out under these conditions.

For more accurate observation it is necessary to present the travelling image upon a perfectly dark ground, and I have, therefore, adopted the following arrangement:—One corner of the dark room was partitioned off by an opaque screen in which a circular aperture was cut 40 cm. in diameter, its centre being a little more than 1 metre from the floor (see Fig. 1). A plate of milk-glass was fitted so as to fill this aperture, and the acetylene-lamp with four burners was fixed 30 cm. behind this plate and at the level of its centre. The lamp being lit, there appears the circular area of milk-glass evenly illuminated by transmitted light. Immediately before this surface a black disc of stout millboard, 60 cm. in diameter, rotates on a smoothly running axle. This axle is opposite the centre of the bright circle and is supported on a single iron upright 30 cm. in length. It is driven by a cord which passes up beside the upright, over the axle and down again to a transmitter fixed below the disc. The transmitter consists of an axle bearing a number of pulleys ranging from 3 to 30 cm. in diameter. The transmitter is driven by

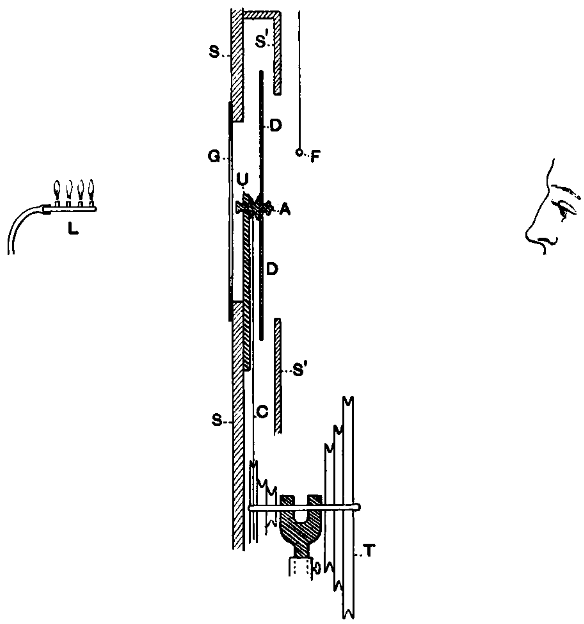

FIG. 1. Diagram to illustrate method of presenting a moving object image. *SS*, opaque screen; *G*, plate of milk-glass; *L*, acetylene lamp; *DD*, large disc of millboard on axle *A*; *U*, iron bar supporting the axle; *C*, cord passing over the pulley-surface of axle and returning to transmitter *T*; *S'S'*, anterior screen covering edges of disc *D*; *F*, bead suspended on thread and feebly illuminated by ray parallel to surface of disc *D*.

a cord from a large and very heavy boley wheel (not shewn in the figure), such as is used for driving a lathe, and this is kept in motion by a long treadle lying at right angles to the plane of the wheel. This arrangement enables me to drive the disc at any speed, from the slowest to the highest, while sitting at ease facing the disc and one or more metres distant from it. The great weight of the boley wheel secures uniformity of rate of motion of the disc, and the rate of revolution at slower speeds can be sufficiently accurately estimated with the aid of a metronome. If now any aperture is cut in the disc, and the disc rotated before the illuminated surface, the aperture appears as a bright image moving in a circular path upon a perfectly dark ground. I have found it convenient to cut a single large aperture in the disc (p in Fig. 2, A), and to put over this sectors of black card in which apertures of any desired form may be cut (Fig. 2, B). The central end of the card is perforated by the axle, its peripheral end is bound to the edge of the disc by a spring-clip. By pasting sheets of coloured gelatine over the aperture in the card the image may be given any desired colour, and if a sufficient number of layers of gelatine is used an approximately homochromatic image may be obtained.

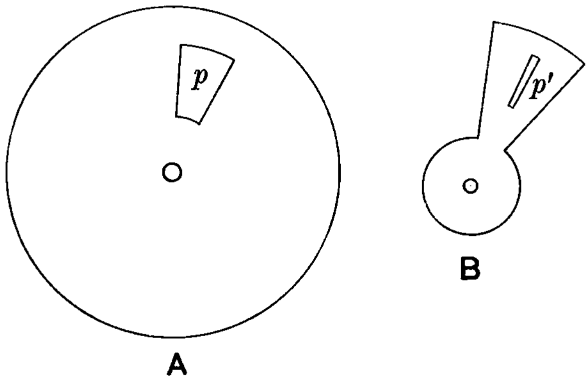

FIG. 2.

A fixation point is often desirable, and this was supplied by a porcelain bead, hung upon a fine black thread a few centimetres before the disc, and illuminated by a feeble ray of red light thrown across the front of the disc and parallel to its surface, so that the light is invisible save where it strikes the bead, which then appears to be self-luminous.

This apparatus allows the greatest possible range of variation of form, colour, and speed of the object-image and a considerable range of intensity, and when a greater intensity than could be given by the powerful acetylene lamp was needed, I used a modification of the arrangement which allowed the plate of glass to be illuminated by direct sunlight.

With this apparatus I have made a great number of observations, repeatedly studying the appearances under every combination of conditions. It may be stated at once that long-continued practice has greatly improved my power of directing my attention to peripheral parts of the field of vision while the eye remains at rest, and that no one who has had no such practice should expect to observe at once and with confidence all the appearances described below.

In making the following observations the eye was at a distance from the disc of about 1 metre and was kept steadily fixed upon the bead which was hung close to some part of the path of the image or about the centre of the disc.

A radial slit 2° in width and 7 cm. in length, its mid point 15 cm. from the centre of the disc, rotating at the rate of 1 rev. per 3″ before the glass lit by four burners, appears as a fanlike bundle of narrow bright rays of diminishing brightness from before backwards. Four such rays can usually be distinguished with certainty at this speed. They are not separated by distinct dark intervals but appear to overlap one another, and together they fill a sector about 12° in width. The bundle of rays is followed by a black space about 40° in width, and this by a dull white haze which fills the greater part of the path of the object-light. The appearance is represented with fair accuracy in Pl. I. Fig. 3. When the speed is a little increased the bright bands become more widely spread out and separated by narrow dark bands. This is the appearance (Pl. I. Fig. 4) described by Charpentier,—"on voit succéder des images doubles, triples, quadruples, separées par des intervalles sombres"[1]; and previously by Bidwell in 1894[2], and later in the following terms,—"The moving slit assumes the appearance of a fan-shaped luminous patch, the brightness of which diminishes with the distance from the leading edge. And if the eyes are steadily fixed upon the centre of the disc, it will be noticed that this bright image is streaked with a number of dark radial bands, suggestive of the ribs or sticks of a fan[3]."

When the speed of rotation is further increased to about 1 rev. per $1\frac{1}{2}$″, the bands become more widely separated, wider individually, and more numerous, and the diminution of brightness in the series from before backwards becomes very marked.

The appearance is roughly indicated in Pl. I. Fig. 5.

[1] *Arch. de Physiologie*, 1896, T. VIII. p. 677.
[2] *Proc. Roy. Soc.* Vol. LVI. p. 132.
[3] *Curiosities of Light and Sight*, p. 191. London, 1899.

With further increase of speed the bands become still more numerous, and at about 1 rev. per 1″, or at a rather higher speed, they fill nearly the whole circle. But with each increase of speed of rotation the time during which the light falls upon each retinal element is diminished, and this is equivalent to a diminution of intensity of the object-image; all the bands therefore lose correspondingly in brightness, and when they fill the whole circle the brightness of the whole is very much reduced so that the bands are obscure. In order to compensate for this effect of increased speed it is necessary to open the slit more widely. If then the slit is made 12° in width, and the disc rotated at 2 revs. per 1″, the whole circular path of the object-image appears filled with bright radial bands, separated from one another by darker bands, each bright band shading off on either side into a dark band (as in Pl. I. Fig. 6).

If now the brightness of the object-image is diminished in successive stages, and the rotation repeated at each stage, with corresponding rates of rotation and width of slit, the leading bands are less bright and the whole series is less numerous, so that with light from two burners only, the bands do not fill the circle until the speed is about 2½ revs. per 1″; with one burner, not until speed is increased to about 3 revs. per 1″, and with one burner at half-power, not until the speed is raised to nearly 4 revs. per 1″.

The observation of the travelling object-image by an eye at rest yields, then, results concordant in every way with the effects described above as following on brief momentary stimulation of a small area of the retina by a stationary object-light. By both methods we find that a single momentary stimulus evokes from each retino-cerebral element a multiple response, a series of pulses of sensation (save in the case of stimulus of very low intensity which evokes a single response only); we find that the more intense is the stimulus the brighter are the initial pulses of the series and the longer is the series, and that the brighter are the pulses the briefer are they and the more rapidly do they succeed one another. By both methods we find that this primary response is closely followed by a secondary response in the shape of a steady duller image which dies slowly away and is brighter and more persistent the more intense is the stimulus. The facts of the primary response are represented in the accompanying diagram, Fig. 7.

The curves represent the series of pulses of sensation evoked by a single brief stimulus of fair intensity; the series begins at *a* at some unknown and undiscoverable interval after the moment of incidence of the stimulus, and lasts throughout a period of about $\frac{2}{3}$ second represented by the length $a-i$. The height to which each curve rises represents the intensity of the pulse of sensation. The effects produced by a momentary stimulus of less intensity are represented by a part of the series of curves; thus the effects of a stimulus of intensity sufficient to give sensation of brightness indicated by the height of curve *e*, are represented by the curve *e* and by the series of curves from *e* to *i*, while a stimulus strong enough to give sensation of intensity indicated by height of *h* would be followed by two pulses of consciousness represented by the two curves *h* and *i*.

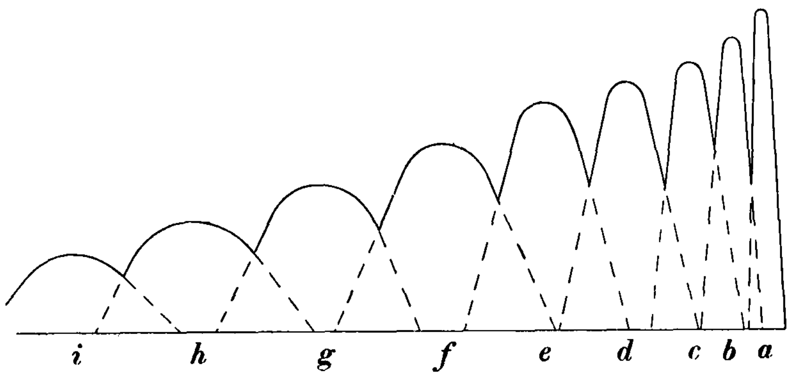

FIG. 7. Diagram illustrating the series of pulses of sensation, the primary response excited by a single momentary stimulus applied to any part of the retina.

The curves in the diagram are drawn overlapping one another. In this way I have sought to represent the fact that the successive pulses of sensation are usually separated from one another by intervals that are not completely dark. There seems in fact to be an overlapping, each pulse beginning before its predecessor has quite passed away.

The overlapping is greater the slower the speed. Thus in the case of a radial slit 2° wide rotating at 1 rev. per 3″ before the plate lit by four burners, the bright bands are not separated by darker intervals and are only distinguishable through being of different brightness. This appearance is represented in Pl. I. Fig. 3.

When the rate of rotation is increased to a little more than 1 rev. per 2″, the bright bands overlap to a less extent, and are separated by narrow darker intervals as in Fig. 4, the separation being most distinct at their outer ends where the rate of movement is greatest. With further increase of rate of rotation the dark intervals become still wider. If then the rate is gradually diminished, the bands close up again and overlap more and more like the bars of an ivory fan, until when the rate is only about 1 rev. per 5″ the image appears as a single homogeneous streak of bright light, not appreciably wider than the object-light. This strongly suggests that at this slow rate the image consists, in a sense, of the whole series of pulses of sensation succeeding one another so rapidly that the whole series runs its course before the image has moved to an appreciably different position, and so rapidly that they become continuous for consciousness.

These observations strongly support the view of the nature of the physiological processes underlying the visual sensations which I have put forward in a previous paper at some length[1], and which may be briefly summarised as follows:—The stimulus applied to the sensory end-organs, the rods and cones of the retina, determines in the afferent neurones of the retino-cerebral tract a liberation of energy. This energy which is possibly of a kind peculiar to the nervous system, we can at present only describe in terms of its behaviour in the nervous system, and for the sake of clearness and brevity I have proposed to speak of it as 'neurin.' Neurin seeks to escape from the stimulated afferent neurones, the place of high potential, to motor neurones and the muscles, places of low potential. In thus escaping it has to pass through the synapses of the visual cortex, the places of highest resistance on the sensory-motor paths. This resistance is overcome intermittently; the neurin escapes from afferent to efferent neurone across the cortical synapse in a rapid series of discharges, which are more voluminous and succeed one another more rapidly the higher the potential of the charge in the afferent neurones Each such discharge determines a single pulse of sensation of which the intensity is in some way a function of the quantity of energy transmitted across the synapse in that discharge. When the stimulus is continuously applied to the retinal ends of the sensory-motor chain of neurones the synaptic discharges are usually repeated at such a rate that the sensation appears continuous; but when the stimulus is a momentary one only, it liberates in the afferent neurones a charge of neurin which escapes by a series of discharges of diminishing volume and diminishing rapidity, so determining the series of pulses of sensation which we have studied above[2].

[1] *Brain*, 1901, Vol. xxiv. p. 577.

[2] This series of pulses of sensation provoked by a single brief excitation of the retina seems to me to present an interesting parallel to the series of contractions of skeletal

One important feature of the primary response of the eye to the momentary stimulus has yet to be described. We saw that as the rate of rotation of the narrow bright object-image is increased, the number of bright bands distinguishable, which is at first only three or four, becomes largely increased. One source of this increase, which has already been pointed out, is the spreading out of bands, which at the lower rate are so much overlapped that they form the single leading band of highest intensity. But there is a second source of this increase in the number of bands. As the rate of rotation increases there become visible several dim grey bands in the dark interval which separates the bundle of bright bands from the secondary response, the dull grey haze which fills the track of the object-light (see Figure 3). These are dimmer and broader than the leading bands and differ markedly in quality, the leading bands being yellowish-white, these others a neutral grey. This difference of quality is more marked if the object-light be made green (or blue). The bright leading bands are then green (or blue), while these later bands are again a neutral grey. The leading bright bands are in fact reactions of the colour-vision apparatus of which the cones are the retinal end-organs, while the later series of grey bands are reactions of the apparatus for vision in dim light of which the rods are the retinal end-organs. They may then be conveniently distinguished as cone-bands and rod-bands respectively. This view of their nature is borne out by the following facts. Firstly, a homochromatic red object-light produces a series of red bands only, corresponding in number and distribution to the leading coloured bands given by a green or blue object-light, and the rod-bands are brightest when the object-light is green; we know from the researches of v. Kries and others that the rods are not stimulated by pure red light, but are stimulated by all other kinds of light, and most effectually by green light. Secondly, if the fixation-point is put in such a position that the outer end of the green object-light passes behind it at one point of its path, the grey rod-bands appear to have their outer ends broken off at the moment they pass the fixation-point and restored in the succeeding moment, *i.e.* this later part of the series of responses is not given by the fovea where rods are absent. Thirdly, these rod-bands have that peculiar neutral ghostly quality, inclining perhaps slightly to blue, which I have learnt to recognise with some confidence as the

muscles that is evoked in a strychnized frog by a single excitation of the cutaneous surface. (Cp. *Proceedings of the Physiological Society*, July 19th, 1902. Note by J. Burdon-Sanderson and F. Buchanan, *Journal of Physiology*, Vol. XXVIII.)

quality characteristic of sensations due to the rod-apparatus. Fourthly, these rod-bands never appear when the eye is thoroughly light-adapted, and the sensitivity of the rods thereby reduced to a very low degree, or abolished.

I shall shew below that the beginning of the sensation evoked by stimulation of the cones follows the incidence of the stimulus at a shorter interval than that which intervenes between the stimulation of the rods and the resulting sensation, but that this relative delay of the rod-reaction amounts to $\frac{1}{18}$ second only. The interval which separates the rod-bands from the leading cone-band in the above-described series of pulses of sensation is much greater than $\frac{1}{18}$ second, and their appearance after the cone-bands is therefore not simply due to this more sluggish reaction of the rod-apparatus. It is, I think, rather to be explained by the greater sensibility of the rods in the dark-adapted eye. The stimulus which evokes a series of responses of a certain length from the cone-apparatus, produces a longer series of responses from the more sensitive rod-apparatus, and while the earlier of these rod-responses are overlaid and obscured by the more vivid cone-responses, the later members of the series appear as the dim grey rod-bands following the cone-bands, as described above. The non-appearance of the rod-bands during the slower rates of rotation of the bright object-light will be explained below in the section dealing with 'Bidwell's ghost.'

The Secondary Response.

Before going on to deal with this, I must say a few words about the secondary response which follows the pulsating primary image. This secondary image is much less bright and much more persistent than the primary image; it appears abruptly and dies slowly and steadily away. In the case of momentary stimulation by a bright stationary object-light, it seems to appear at a great distance at the moment in which the pulsating image comes to an end, and rushing up towards the eye to stop suddenly, filling the position of the primary image. This impression of rapid approach is, I think, due to its beginning in the centre of the area and spreading rapidly outwards, the whole process occupying only a small fraction of a second. This grey image then fades slowly and so gradually that the moment of its disappearance cannot be fixed. But it is brighter and of longer duration the brighter the object-image.

In the case of the travelling object-image the secondary image appears abruptly at a brief interval after the last of the bands of the primary image, and fills a part or the whole of the track of the image. In both cases, if the object-image is coloured and of high intensity the secondary image is tinged with the same colour; but if the object-image is coloured and of low intensity the secondary image is grey in case of blue and green light, but is absent in the case of pure red light.

This secondary image is simply the ordinary persistent after-image. In the case of an object-light of low intensity, it is due to the more sensitive rods alone, as shewn by its grey quality and its absence in the case of pure red light. In the case of a brighter object-image it is a combined rod- and cone-effect, the cone-effect preponderating the more the brighter is the object-image, as shewn by the greater saturation of the colour of the secondary image. In a previous paper[1] I have tried to shew that the ordinary after-image is in all cases primarily due to the continued action in the rods and cones of exciting substances set free in them from stored mother-substances (visual purple in the case of rods, similar, but hitherto unknown substances, in case of cones) by the action of light. This view is borne out by the following very constant feature of the secondary image or after-image which follows the primary pulsating image of the travelling object-light. When the object-image is a narrow band of only moderate intensity, the secondary image persists about one or two seconds only, so that at the rate of 1 rev. per 3″ it fills only about one-half of the circular path of the object-image. If then the eye remains fixed upon one point in the neighbourhood of this path (best the centre of the disc) the secondary image becomes brighter and longer drawn out with each revolution of the object-light until it fills the circle. Further revolutions cause it to become more and more bright so that it interferes seriously with the observation of the primary image, and if then the eye is closed it persists as a circle of light which is bright and persistent in proportion to the number of revolutions of the disc during which the fixation has been maintained. This effect is thoroughly concordant with my view of the nature of the after-image; for at each passage of the light over any part of its path upon the retina it seems to liberate a fresh quantity of the exciting substances, which therefore, accumulating with each revolution, determine an increasingly bright and persistent after-image.

[1] "Some new Observations, etc." *Mind*, 1901, N. S. Vol. x. p. 52 etc.

I regard, then, the primary pulsating response as due to the activity of the afferent neurones of the sensory-motor arc excited by the very brief but intense photo-chemical processes that occur in the rods and cones during the moment of the action of the light upon them, this activity being continued for a brief period beyond the moment of the incidence of the light; while I regard the secondary response or persistent after-image as due to the continued feeble stimulation of the endings of the optic nerve by the substances set free in the rods and cones by the action of the light, and not entirely used up during that action.

Among authors who have recognised the fact that the primary response of the eye outlasts the brief stimulus, Parinaud[1] alone, so far as I am aware, has sought to distinguish the seat of this continued activity from the seat of that which determines the enduring after-image. But curiously enough he regards the former as retinal and the latter as cerebral. He names the primary response "l'impression rétinienne persistante," and describes it as a "sensation lumineuse tremblotante," while the secondary response, the ordinary after-image, he names "l'image consecutive positive," assigning it a cerebral seat on grounds the fallaciousness of which has been frequently exposed, namely, the facts of the projection of the after-image of one eye on a surface presented to the other eye, and the movements of an after-image corresponding to those of the eye.

Of the authors who have observed the multiple character of the primary response, C. A. Young proposed a theory which may be best stated in his own words:—"The phenomenon at least suggests the idea of a reflection of the nervous impulse at the nerve extremities—as if the intense impression upon the retina, after being the first time propagated to the brain, were then reflected, returned to the retina, and, travelling again from the retina to the brain, renewed the sensation[2]."

Davis, who worked by both methods, that of the stationary and that of the travelling image, and who noted the absence of the ghost in the case of pure red light, gave the name 'recurrent image' to the phenomena observed by both methods, and attempted to explain them by the suggestion that when the retina is stimulated by light of one colour, the 'nerve-current' excited in the nerve-fibres subserving the sensations of that colour induces currents in the nerve-fibres subserving the

[1] *La Visión*, Paris, 1898.

[2] *Loc. cit.*

sensations of other colours, much as an electrical current in one wire induces a current in neighbouring wires[1].

Bidwell has suggested that the 'ghost' is due to a delayed reaction of the 'violet nerve-fibres,' but has not attempted to explain the multiple bands seen by him in the case of a bright moving slit, or the series of pulses of sensation excited by a brief stationary object-image.

Charpentier proposes to explain the multiple response in the case of the travelling image by a peculiar theory of retinal oscillations; he supposes that the outer ends of the rods and cones are thrown into transverse vibrations, and that waves of such movements pass across the retina, polarised, as he says, in two directions[2]. It is, I think, very difficult to suppose that the rods and cones, embedded as they are in the pigment epithelium, can be subject to any such vibrations, and I confess that I fail to understand how such oscillations, if they did occur, should produce the effect of a multiple response, a series of pulses of sensation. The hypothesis has the further drawback that, even if we should accept it as capable of explaining the effect in the case of the travelling image, it would seem to be inapplicable to the explanation of the similar effect following momentary stimulation by a stationary object-image.

'Bidwell's Ghost.'

The 'recurrent image' or 'Bidwell's ghost' in its typical or most usual and easily seen form may be observed by the following procedure. A narrow slit (from 2° to 5° in width) in the large disc rotates at 1 rev. per 3″ before the plate of milk-glass, moderately brightly lit (by rather less than the full power of one burner, in the place of the four burners used in the experiments described above, p. 91). The eye having been made thoroughly bright-adapted, is kept covered for about three minutes and then fixed upon any point in or near the path of the moving slit. There then appears (see Pl. I. Fig. 8) a bright leading image (which, as the practised eye can readily discern, is made up of several partially overlapping radial bands) followed after a dark interval of about 25° by a dim grey image, in the form of a narrow radial band. The two images differ not only in brightness but in

[1] *La Vision*, Paris, 1898. [2] *Archiv de Physiologie*, 1896, T. VIII. p. 677.

quality, the leading image (or bundle of images) is of the colour of the object-light, the 'ghost' is grey, or, at most, faintly tinged with colour.

This after-following image, which is the commonly described 'recurrent image,' the typical 'ghost' of Bidwell, is merely the last of the series of rod-bands described above, the last of that series of pulses of sensation which constitute the full primary response of the visual organ to the momentary stimulus, the intermediate bands of the series being inhibited by the bright leading bands. As I shall shew below, the 'ghost' is not in every case a pure rod-band, but it is always merely the last of the series of pulses of sensation excited by the moving object-light, the gap in the series being due to inhibition of intermediate pulses by the initial most vivid pulses. This proposition I must proceed to justify.

In the first place, this typical 'ghost' which follows an object-light of moderate intensity is shewn to be a reaction of the rod-apparatus by the facts, (1) that it jumps the fovea (this fact v. Kries[1] has carefully studied, and I can confirm his statement); (2) that it never appears in the case of a pure red object-light; (3) that it is relatively brightest with green object-light; (4) that it has commonly the peculiar neutral quality of rod-sensations (in some cases it appears tinged with colour, a fact to which I shall recur below).

That this 'ghost' is but one of the series of rod-bands described above may be shewn as follows:—A slit about 3° wide (white, green or blue) rotates at 1 rev. per 3″, and the illumination is so adjusted that the moderately dark-adapted eye sees the typical 'ghost.' The light is then gradually diminished, when a second 'ghost,' similar to the first, but dimmer, begins to be visible in the dark gap between the leading bright bands and the first 'ghost,' and as the light is further diminished this becomes equally bright with the original ghost, or if the rate of movement be a little greater, two such additional 'ghosts' appear, filling the gap between the bright cone-bands and the original 'ghost.' When the light is still further diminished these rod-bands begin to preponderate over the cone-bands, and a stage is reached at which the whole reaction consists of a series of five or six dim rod-bands. These are so dim and delicate that it is essential that the field on which the object-light moves should be absolutely dark.

Or again, if instead of diminishing the intensity of the object-light, and so diminishing the inhibitory power of the leading cone-bands, the

[1] *Zeits. für Psychol. u. Physiol. d. Sinnesorgane*, 1896, Bd. XII. S. 84.

rate of rotation of the disc is gradually increased, a similar effect is obtained, the inhibited intermediate rod-bands become visible, filling the gap between the cone-bands and the 'ghost.' The increased rate of rotation diminishes the inhibitory power of the leading bands in two ways; in the first place they are rendered less bright because the stimulus acts for a shorter time on each retinal element in its path, and secondly, the whole series of bands is more widely spread out on the retina, and we know that the inhibitory power of one image on another diminishes rapidly with increase of separation of the two on the retina.

We may reverse both these procedures, and we then find the reverse effects. Thus, if while the typical single 'ghost' is following the leading bands, the intensity of the illumination, *i.e.* of the object-light, is gradually raised, the 'ghost' becomes dimmer and then altogether invisible. The appearance represented in Fig. 8 gives way to that of Fig. 3; the 'ghost' is completely inhibited by the brighter cone-bands. (Bidwell and Charpentier in observing the multiple images of a moving object-light clearly used a light so bright that the leading cone-bands inhibited all the rod-bands, for the banded character of the image is most readily seen in the case of a narrow object-light of high intensity.)

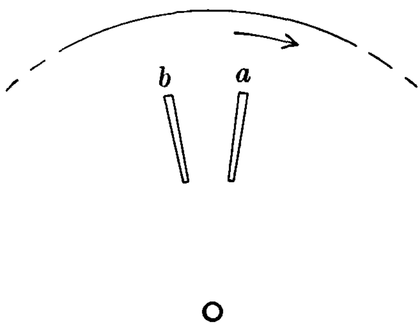

FIG. 9.

Again, if the object-light be made of such intensity that, while moving at a rate of 1 rev. per 2″, it gives the appearance of the typical 'ghost' following the leading cone-bands at an interval of about 35°, and the rate of movement is then gradually diminished, the interval between the cone-bands and the 'ghost' is correspondingly diminished, and as the 'ghost' approaches the bright cone-bands it becomes dimmer, until, when the interval is reduced to about 20° it becomes altogether invisible, *i.e.* it is completely inhibited.

That the initial images or reactions provoked by the travelling object-light really exert a strong inhibitory influence upon the retino-cerebral elements over which the image has passed in the preceding moments, and that the gap in the series of images is due to this influence, is proved by the following experiments:—Two radial slits 3°

wide and 7 cm. long are made in the disc at an angular interval of 20° as in Fig. 9, so that on rotation the slit *b* follows in the path of slit *a*. Then, on rotation at 1 rev. per 3″ before the brightly lit surface, *b* appears much less bright than *a*; and if then a sheet of white paper is pasted over *b*, so as to reduce the brightness of that slit by rather more than 50°/₀, and the rotation repeated, *b* is quite invisible so long as the eye remains at rest. That this effect is due not to inhibition alone, but also to fatigue, is shewn by reversing the direction of rotation, when *b* is visible[1].

I found that as a lecture-demonstration this experiment is made more striking if *b* is made red (or of other colour) while *a* is white. Then while the disc rotates in direction of the arrow in the figure and the eye remains at rest, no trace of the red image can be seen, though it becomes visible immediately if the eye is allowed to follow the moving image. This variety of the experiment has an interesting bearing upon theories of the visual processes because it proves that a white image produces fatigue for a coloured image, and also exerts an inhibitory effect upon a coloured image, facts which, as I have previously pointed out, seem to be inexplicable by Hering's theory of opponent colour-processes.

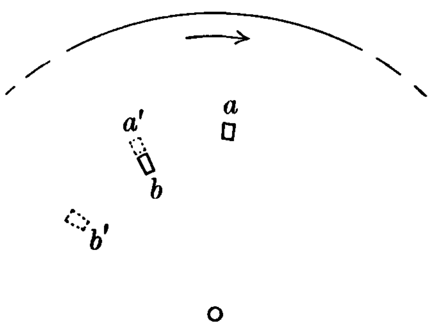

FIG. 10.

That the 'ghost' is easily inhibited by other brighter images is also proved by other experiments, of which the following may serve as an example:—Two radial small slits, *a* and *b*, 3° wide and 1 cm. long, are made in the disc at an angular interval of 30°, and in such a way that the path of the one lies immediately outside the path of the other (as in Fig. 10). Then one of them, *b*, is covered over and the illumination and the rate of rotation are so adjusted that the other one,

[1] This inhibitory phenomenon falls readily into the scheme of the inhibitory processes which I have proposed (*Brain*, 1903, vol. XXVI. p. 153). According to that scheme the most intensely-excited chain of retino-cerebral elements forms the path of least resistance of the whole retino-cerebral tract and therefore drains to itself some or all of the energy liberated in other parts of the tract, this drainage being more effective in proportion to the proximity of the two chains of elements concerned.

a, gives the typical 'ghost' (the rotation being in the direction of the arrow), following the leading image at an interval of 30°. On uncovering *b* and repeating rotation at the same rate and in the same direction as before, *b* is followed by a 'ghost' at an interval of 30°, while no 'ghost' is visible following *a*; and on rotating the disc in the opposite direction, but at the same rate as before, *a* is followed by a 'ghost' and *b* has none; in each case the 'ghost' of the leading image is inhibited by the other bright image upon the immediately adjoining part of the retina.

The typical 'Bidwell's ghost' is, then, a reaction of the rod-apparatus, as v. Kries has suggested[1]. But in making that suggestion v. Kries believed that we have a single cone-reaction, followed by a single rod-reaction which is normally about $\frac{1}{5}$ sec. slower than the cone-reaction. Now I shall shew below that the normal rod-reaction begins only about $\frac{1}{18}$ sec. later than the cone-reaction, and I have to shew also that a pure red light may be followed by a 'ghost' (a fact denied by v. Kries and Bidwell) and that the 'ghost' is therefore not in all cases a rod-reaction.

The Delay of the Reaction of the Rods.

We have no means of determining the length of the interval which intervenes between the moment at which light falls upon the retina and the moment of the beginning of the resulting sensation[2], but we can compare the duration of this period in the case of sensations of different quality and intensity. The visual reaction-time exceeds the auditory reaction-time by about 40σ, and in all probability this repre-

[1] "Ueber die Funktion der Netzhautstäbchen," *Zeits. für Psychol. u. Physiol. d. Sinnesorgane*, 1895, Bd. IX. S. 81.

[2] Charpentier ("Durée de l'excitation latente de l'appareil visuel," *Compte Rendu d. Soc. d. Biologie*, 1888) claims to have measured this interval. He shews that, if three similar flashes of light be thrown in rapid succession upon an area of the retina, the interval between the first and second must be greater than that between the second and third by about 20σ in order that both intervals shall be appreciable. From this he infers that the interval between the first stimulus and the first sensation is 20σ greater than that between the second stimulus and the second sensation. Even if we accept this questionable inference we shall not be justified in accepting the figure 20σ as a measure of the interval in question; it is at best merely the measure of the difference of the intervals in the two cases. The interval between stimulus and sensation may be indefinitely large, as much as one second, one minute or even a year, and, if it is the same for all kinds of sensation, I do not think that we shall ever be able to discover the fact; though in all probability it is less than the time of a simple sensory reaction.

sents the time occupied by the chemical changes in the retina. Now since the chemical changes produced in the rods are different from those in the cones, and since the rods represent the more primitive, and the cones the more recently and more highly developed, parts of the visual organ, we may fairly expect to find that the photo-chemical changes of the cones occur more rapidly than those of the rods, just as the modern photographic plate excels the more primitive plates of thirty years ago in the rapidity of its reaction to light. And this we find to be the case; we find that sensations due to the cones are more rapidly developed than those due to the rods. If a slit 20° wide and transmitting light of any colour, other than pure red, and of low intensity, is rotated at 1 rev. per 3″, and the dark-adapted eye is fixed upon any point near the path of this object-light, the image appears as a band of colour rather more than 20° in width, and the colour of the leading part of this band is much more saturated than the remainder of it, which, if the intensity of the object-light is low and the eye thoroughly dark-adapted, may appear almost colourless. V. Kries has described this appearance, and has rightly ascribed it to the more sluggish reaction of the rods, and he has roughly estimated the delay of the rod-reaction as compared with the cone-reaction, at about $\frac{1}{50}$ sec. or 20 σ[1].

It is easy to measure the amount of this delay with fair accuracy, by taking advantage of the well-known fact that the eye can appreciate with great delicacy any departure from the same straight line of two straight lines lying end to end. It is necessary, in the first place, to answer the questions, Do two cone-sensations of different quality develope at different rates? and secondly, Do cone-sensations of similar quality but different intensity develope at different rates[2]?

A radial slit 2° wide and 10 cm. long, its inner end being at 10 cm. from the centre of the disc, is covered in its outer half with several layers of red gelatine so chosen as to transmit very nearly pure red light; the central half of the slit is covered with layers of blue gelatine until the two halves appear to be about equally bright, though differing in colour. The disc is rotated before the brightly lit surface

[1] "Ueber die Wirkung kurzdauernder Lichtreize auf das Sehorgan," *Zeits. für Psychol. u. Physiol. d. Sinnesorgane*, 1896, Vol. XII. S. 97.

[2] The papers by Exner "Die zur Gesichtswahrnehmung nöthige Zeit" (*Ber. der k. Akad. Wien*, 1868) and by Kunkel (*Arch. f. d. ges. Physiol.* 1874) which are sometimes referred to as giving answers to these two questions, really deal with closely allied but different problems which I hope to treat in a separate paper.

at a rate of 1 rev. in $1\frac{1}{2}''$, while the eye is fixed upon any point near the path of the slit. The two halves of the slit then shew no departure from the same straight line. If one of these two sensations, the red or the blue, developed more rapidly than the other, the leading edge of the image of that colour would appear to precede that of the image of the other colour, even if the difference amounted to no more than 4σ (for I find that the eye can detect with certainty a difference of less than 1°). Comparing in this way the rates of development of red, green, blue, and white sensations I find no appreciable difference so long as the two parts of the slit are made of approximately equal brightness[1].

If now the two halves of the slit are made of similar quality, but of very different intensity, by covering the one half with layers of tracing-paper sufficient to cut off about 80 % of the transmitted light, and if the reaction of the rods is excluded by using pure red light or by making the observation with a very thoroughly light-adapted eye, then, on rotation at 1 rev. per $1\frac{1}{2}''$, the image of the brighter half of the slit begins more abruptly and its leading edge precedes that of the duller half by about 2°, and to a proportionally greater extent if the rate of revolution is increased. The rate of development of the dull and the bright sensations is then not quite the same, and, in the case of this very considerable difference of brightness, the difference of rate of development is about 8σ in favour of the brighter sensation[2].

A slit of this kind, of which both halves transmit green light, the one half being made considerably brighter than the other, serves to shew the lagging of the rod-sensation, in the following way:—The slit is rotated at 1 rev. per $1\frac{1}{2}''$ before the plate of milk-glass, lit with full power of four burners, and observed with thoroughly dark-adapted eye fixed upon any point. The slight lagging of the duller half

[1] Charpentier (*Arch. de Physiologie*, 1893, "Différence de Temps perdu suivant les couleurs") finds, by experiments similar to those described above, that the development of the sensation of red is more rapid than that of green by some 3σ to 6σ and than that of blue by twice this amount. I can only suppose that individuals differ in this respect, for since reading this paper of Charpentier's I have repeated the comparison of blue and red very carefully and can detect no difference. If in my case so large a difference as 6σ existed I should certainly detect it.

[2] This fact suggests the possibility that the sluggish development of blue sensation observed by Charpentier may have been due to his using a blue object-image considerably less bright than the red image. Since he used lamplight transmitted by coloured glasses, this would necessarily be the case unless special precautions were taken.

amounting to about 2° is then perceptible, and as the illumination is gradually diminished this amount of lagging of the duller half persists so long as the duller half remains distinctly green in colour. But when the illumination is so far reduced that the duller half appears colourless to the dark-adapted eye (and is invisible to the light-adapted eye), the lagging of this duller half suddenly increases to about 12°.

It is important to note that a similar sudden increase in the lagging of the duller half occurs when the two halves of the slit are white, or of any colour but pure red.

This lagging of the rod-reaction may be displayed by many modifications of this experiment, but the extent of the lagging may be best measured as follows:—Two slits, each 5 cm. long and 2° wide, are made, lying on radii of the disc at an interval of 10°, and in such a way that the path of the one is immediately outside that of the other, as in Fig. 11.

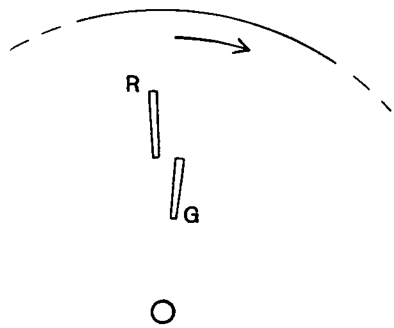

Fig. 11.

The one slit *R* is covered with several layers of red gelatine, so chosen as to transmit almost pure red light; the other slit *G* is covered with layers of green gelatine, until to the light-adapted eye it appears by transmitted light rather less bright than the red slit. The illumination of the glass plate is then lowered until the green slit appears colourless to the thoroughly dark-adapted eye. On rotation of the disc in the direction of the arrow in the figure (*i.e.* so that *G* leads), the image of slit *G* falls back relatively to the image of slit *R*, so long as the eye remains at rest, and if the rate of rotation be as much as 1 rev. per $1\frac{1}{2}''$, *G* appears actually to follow after *R* at a considerable interval. The rate of movement at which the leading edges of the two slits appear to fall along the same radius may then be found by varying the rate of rotation. This rate is, for my eye, as nearly as possible 1 rev. per 2″; that is to say, the rod-image *G* lags, relatively to the cone-image *R*, 10° when the rate of movement is 1 rev. per 2″[1]. The

[1] In this experiment the lagging of the colourless sensation excited by the green object-image is not in any degree due to a difference of intensity of the two sensations, for to the thoroughly dark-adapted eye the colourless rod-sensation is distinctly brighter than the red sensation.

amount of this delay seems to be about the same for different individuals, for some dozen persons, to whom I have demonstrated this experiment, see the two images fall into line at the same rate of revolution of the disc. We may conclude, then, that the rate of development of the cone-sensations exceeds that of the rod-sensations by about 55 σ or $\frac{1}{18}$ second.

In the above descriptions I have assumed that the colourless image of the green object-image of low intensity seen by the dark-adapted eye is a sensation excited by the rod-apparatus or apparatus for vision in a dim-light, accepting as established that view of the function of the rods which we owe to Max Schultze and to Parinaud, and which has been presented in the most satisfactory form by v. Kries. That view is, I think, abundantly justified, and the experiments last described seem to me to constitute one of the strongest pieces of evidence in support of it. It is considered by some a grave objection to this view that it involves the acceptance of white or neutral-toned visual sensations of two different physiological origins, the primitive neutral sensations yielded by the rods and the 'trichromatic white' resulting from psychical fusion of the elementary colour-sensations. The fact demonstrated above, that of the physiological processes underlying the two grades of colourless sensation, those underlying the dim vision of the dark-adapted eye require for their completion as much as 55 σ longer than the processes underlying the white sensations of the bright-adapted eye, while the latter run their course in exactly the same time as the processes underlying the colour-sensations, this fact goes far, I think, to compel us to accept v. Kries' view of the function of the rods.

The 'ghost' of a pure red light.

V. Kries and Bidwell have stated that no 'ghost' can be obtained with a pure red light, but this, like most of the other misunderstandings of this subject, arises from an insufficiently wide variation of the conditions of observation, as is shewn by the following experiment. A radial slit, 3° wide and 10 cm. long, is covered with layers of red gelatine until, on inspection through the spectroscope, it is found to transmit only red light. This, when made of about the same brightness as the white, green or blue object-light that gives a typical single ghost, gives of course no rod-bands, and therefore no 'ghost.' It appears as a bundle of closely set red cone-bands only. But if the intensity of this red object-light is much increased there appears, at a certain degree of brightness and at a moderate speed of rotation, a narrow bundle of bright red bands followed after a dark interval of about 25° or more (according to the speed) by a single narrow red band of low intensity but of good saturation, forming a 'ghost' very similar in general appearance and behaviour (except as regards colour) to the typical 'Bidwell's ghost.' The only difficulty in demonstrating this red ghost is that of securing a sufficiently intense source of light, for the plate of milk-glass used in the preceding experiments, together with the five or six layers of red gelatine, cuts off so much of the light that my acetylene lamp proved insufficiently powerful. This difficulty I have overcome by using direct sunlight, and I have also been able to demonstrate the red 'ghost' as a lecture-experiment by using a plate of ground-glass as the background for the rotating disc, and focussing on to it from behind the direct ray of an arc lamp, while the observers sit directly in front of the disc.

There can be no doubt that this red 'ghost' is merely the last of the long series of pulses of sensation evoked by the intense red object-light, the intermediate bands of the series being inhibited by the very bright leading bands; for by careful adjustment of the brightness of the object-light, and by varying the rate of its movement, the whole long series of red cone-bands may be made visible.

Other kinds of coloured 'ghost.'

With lights of other colours the 'ghost' is not always colourless, *i.e.* it is not always a pure rod-reaction. Some observers have described it as being of the same colour as the object-light, others as being of the complementary colour. In the case of a blue object-light of moderate intensity I have frequently seen the 'ghost' distinctly tinged with blue, and rarely I have seen it yellowish in tone. In the case of a green object-light I have frequently seen the 'ghost' tinged with the complementary purple, rarely I have seen it greenish in tone. These colours have been in all cases of very low saturation, and their appearance depends upon so complex a conjunction of conditions that it is difficult to define those conditions with any accuracy. But in general terms it may be said that these tinges of colour are apt to appear in the 'ghost' when the eye is but very little dark-adapted, and the colour of the object-light is of low saturation, and that the complementary colour is especially apt to appear when the object-light is made so bright that any further increase of brightness produces total inhibition of the 'ghost.' These faintly coloured 'ghosts' seem to be compounds of rod-reaction and cone-reaction in which the former predominates, that is to say, these late rod- and cone-reactions are synchronised so as to fall in the same moment and appear as superposed or mixed bands, hence the colour; and the complementary tinge which sometimes appears is due to the stronger inhibitory effect of the leading coloured bands upon the constituent of the compound which is of its own quality, *i.e.* the complementary colour is a contrast effect.

That there obtains a synchronisation of the reactions of the retino-cerebral elements subserving the different elementary colour-processes, is shewn by the fact that in the case of a white object-light (or one of compound colours such as purple), the series of bright cone-bands are white (or purple). If there were no such accurate synchronisation of these reactions we should find these compound processes analysed to some extent under these conditions[1]. And that this synchronisation is not absolutely perfect is shewn, I think, by the phenomenon well known under the name of Fechner's colours. These are brilliant scintillating colours seen on fixating any point of a disc made up of black and white sectors, and rotating at about 5 rev. per 1″, under bright sunlight. It is usually said that violet predominates, and that is true under certain conditions; but with very bright sunlight and with variation of the proportions of the sectors and of the rate of rotation all colours may be seen, constituting a very splendid and fascinating spectacle. If the synchronisation of the reactions of the retino-cerebral elements subserving different colour-processes is not quite perfect, some such appearance of colours must necessarily result under these conditions.

It is perhaps worth noting in this connexion that these colours appear more readily and are more brilliant in binocular than in monocular vision. Individuals seem to differ considerably as regards the conditions under which they see these colours, and as regards the

[1] Charpentier (*Compte Rendu d. Soc. d. Biologie,* 1892) reports that by causing a narrow white image to pass across the field of view while the eye remains at rest and by the observance of special precautions he has been able to analyse the physiological and psychical complex resulting from stimulation of the retina by white light into its constituent colour-processes. I have not hitherto been able to observe this effect.

purity and brilliancy of the colours seen. These individual differences may be due, I would suggest, to differences in the degree of accuracy of the synchronisation of the elementary colour-processes. It may be added that these brilliant colours, resulting from stimulation by pure white light, constitute one of the many phenomena which the theory of opponent colour-processes seems to be incapable of accounting for.

The influence of the state of adaptation of the eye.

V. Kries[1] has stated that when the eye is completely dark-adapted no 'ghost' can be seen, and that the rod-reaction then follows immediately upon the cone-reaction as a long drawn-out white streamer, so that the circular object-light, which he used, assumes the appearance of a comet. I was at first much puzzled by this description, and could not see how to bring it into line with my general scheme. To arrive at an understanding of the effects of adaptation I have made several series of observations, beginning each with a light-adapted eye, and making observations at short intervals throughout a two hours' sitting in the dark room. A slit 3° wide and transmitting green light of moderate intensity gives a well-marked slightly purplish 'ghost' when the light-adapted eye has been in the dark room two minutes. After five more minutes in the dark room the intensity of the object-light must be a little reduced in order that the 'ghost' may be seen, and it is then grey in colour. Five minutes later the intensity of the object-light must be again lowered a little in order that the 'ghost' may appear, and there then appear between the 'ghost' and the green cone-bands one, two, or more rod-bands (according to the rate of rotation) similar to the 'ghost' but dimmer. From this stage onward it is difficult to obtain a single 'ghost' separated from the leading image by a dark interval, because the whole series of rod-bands tends to be present at all rates of rotation; nevertheless it may be obtained by careful adjustment of the intensity of the object-light and of its speed of movement, even when the eye has become completely dark-adapted. In order to make certain of complete dark-adaptation I have several times put a closely-fitting shade upon one eye before opening it, on awaking after eight hours of sleep in a well-darkened room, and have proceeded at once to the dark room. And I have then been able to obtain by

[1] *Zeits. für Psychol. u. Physiol. d. Sinnesorgane*, 1896, Bd. XII. S. 91.

careful adjustment both the complete series of rod-bands, or an interrupted series with terminal 'ghost.' It is necessary to add that these rod-bands, seen by the dark-adapted eye, are, like the rod-bands seen by the partially dark-adapted eye following the cone-bands in case of object-light too dim to give the typical single 'ghost,' extremely delicate phenomena and both practice and patience are needed for the satisfactory observation of them. It is essential too that the object-light should travel upon a perfectly dark ground, a condition which can hardly be fulfilled if, as in the method commonly employed by Bidwell and v. Kries, the object-light is an optical image reflected from a white surface over which it travels.

But that v. Kries failed to observe any discontinuity in the comet-like white tail which he describes as following the leading image when the eye is completely dark-adapted, was chiefly due, I think, to the fact that he used a circular object-light. It would be impossible to choose a form of object-light less suited to reveal the finer phenomena, because as the circular image travels across the retina the elements over which its centre passes are stimulated for a much longer time than those over which its upper and lower parts pass. Since the intensity and the duration of stimulus are complementary factors (in case of such brief durations as we are here dealing with) the retino-cerebral elements are excited to very different degrees by the central and peripheral parts of the circular image, the reactions of neighbouring elements are therefore not synchronous and the discontinuous or banded character of the total reaction is obscured.

For the accurate observation of the more delicate phenomena it is essential, in fact, that the moving object-light shall be narrow and sharply defined, and that, if it describes a circular path, its borders shall be radii of the circle described. The lack of this precaution has been, I think, one of the chief sources of confusion. Thus Hess has used as object-light a small electric glow-lamp, Bidwell has used a vacuum tube illuminated by electric discharges.

Bidwell has used, too, a circular object-light, and pictures both the leading image and its 'ghost' as well-defined circles. If this were an accurate description of the appearances it would at once throw my scheme of explanation of the phenomena out of court. But as a matter of fact this description is misleading. The leading image appears not as a circle but like the moon when a little less than half-moon (as v. Kries has noted) or like several such half-moons partially overlapping; and the 'ghost' in such a case has a very ill-defined shape.

Summary.

The following are the principal propositions towards the establishment of which I have endeavoured to contribute experimental evidence in this paper:—

1. The primary response of the visual organ to a single momentary stimulus is in all cases (save in the case of a very feeble stimulus) a series of pulses of sensation of diminishing intensity rapidly succeeding one another. The series is longer and the initial pulses are briefer, more intense, and succeed one another the more rapidly, the more intense is the stimulus.

(2) The initial pulses of such a series are predominantly due to processes initiated in the cones of the retina, while the terminal pulses are due to processes initiated in the rods, save in the case of stimulation by pure red light and in the case of the completely bright-adapted eye, in which cases there is no reaction of the rod-apparatus and the series is correspondingly shorter.

(3) The series of pulses of sensation is probably due to a series of discharges of the sensory neurones across synapses of the cortex into the efferent neurones of the sensory-motor path.

(4) The primary response, the series of pulses of sensation is followed after a very brief interval by the secondary response, a steady persistent after-image which is brighter and of longer duration the more intense is the stimulus. This is the ordinary after-image and is due to the continued action in the rods and cones of exciting substances liberated in them by the action of the light upon stored mother-substances (visual-purple in the case of the rods).

(5) The so-called 'recurrent image' or 'Bidwell's ghost' following a moving image and separated from it by a dark interval is merely the last of the series of pulses of sensation, the intermediate members of the series being inhibited by the bright initial reactions which constitute the leading image or images.

(6) The reality of this inhibitory effect may be proved by many different experiments, some of which were described.

(7) The 'ghost' seen in the case of a travelling object-light of moderate intensity is wholly or predominantly due to a reaction of the rod-apparatus, the apparatus for vision in a dim light.

(8) A pure red object-image of high intensity may yield a red 'ghost' very similar in general behaviour to the ordinary 'Bidwell's ghost' save that it does not jump the fovea.

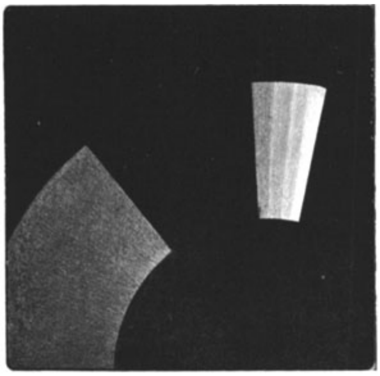

FIG. 3. In this figure and in Figures 4, 5, 6 and 8 the direction of rotation is from left to right or clockwise.

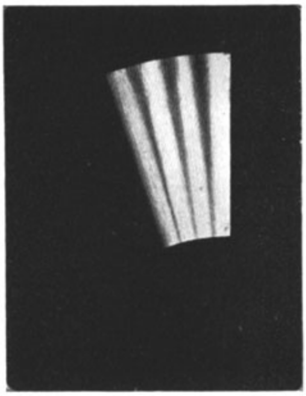

FIG. 4.

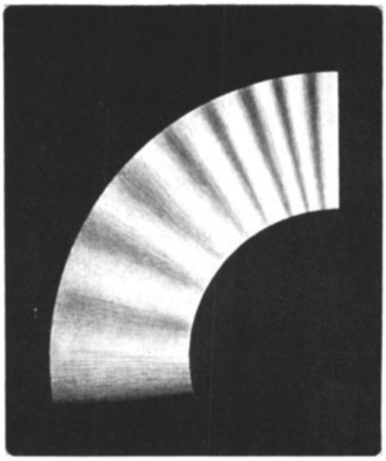

FIG. 5.

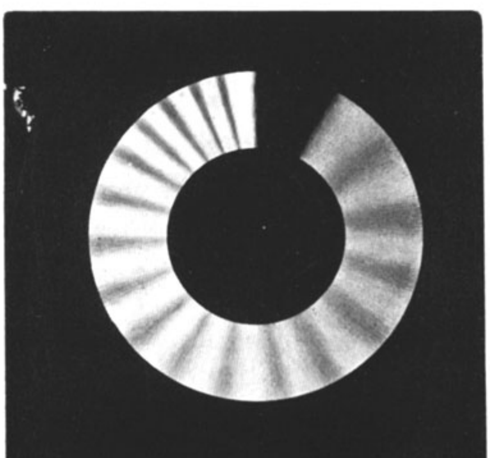

FIG. 6.

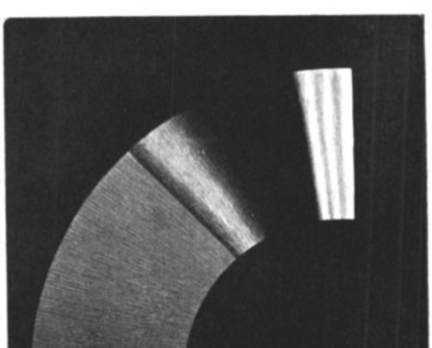

FIG. 8.

(9) The completely dark-adapted eye may see either a similar 'ghost' or the complete series of rod-responses, when the form of the object-image is suitably chosen and the illumination and speed of movement and other conditions are carefully adjusted.

(10) The sensations of different quality, due to excitation of the cones, are developed at the same rate when they are of about the same intensity; but the more intense sensations are developed slightly more rapidly than the less intense.

(11) The colourless sensations which arise from excitation of the rods are developed more slowly than those due to excitation of the cones, the interval between the moment of stimulation and the moment of the appearance of the sensation in consciousness being greater in the case of the former by about $\frac{1}{18}$ second.

(12) This considerable difference in the rate of the physiological processes underlying the colourless sensations due to the cones and those due to the rods respectively, affords a strong support to the view (advanced by v. Kries) that the colourless sensations having these two origins are determined by physiological processes entirely separate and different in character.