COMMUNICATIONS

THE ACCOMMODATION REFLEX AND ITS STIMULUS*

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It is well known in the practice of subjective refraction measurement that when a low-power negative lens is placed before the emmetropic eye of a young subject, distant objects are still seen clearly, the eye having presumably accommodated by an amount equal to the effective power of the negative lens. When the lens is removed the distant object is again seen clearly, which shows that the accommodation has then been relaxed. The purpose of the investigation which is to be described, is the study of this reaction of the accommodative mechanism to changes in the vergence of the light caused by placing lenses before the eye, independently of other causes for the adjustment. It may, however, be profitable first to review briefly the whole function of the adjustment of the eyes for different distances in its relation to this special case.

In normal binocular vision the adjustment of the eyes for different distances is brought about by a complex voluntary innervation operating upon the recti muscles through the convergence centre and also upon the ciliary muscles *via* those parasympathetic fibres which pass through the ciliary ganglion. It is probable that the most powerful stimulus to this innervation is to be found in the disparity of the retinal images arising from the separation of the eyes, and although primarily this would apply only to the fusion centre and thus to convergence, its natural accompaniment of a corresponding change in the vergence of the light reaching the eyes, makes it necessary for the brain to order a change of accommodation as well as convergence.

In monocular vision other factors must operate to make the subject aware that the distance has been changed; in fact, all those characteristic appearances which give rise to the monocular perception of depth will constitute potential stimuli to the mechanism for adjusting the eyes for different distances.

Ittleson and Ames (1950) have shown that, under certain conditions, accommodation and convergence can be stimulated by altering only one of these factors, angular size of object, so producing an illusion of change of distance. They claim that in their experiments muscular effort of accommodation and convergence were related to a subjective change of apparent distance, with all other

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things remaining constant. We may summarize by saying that the normal adjustment for near vision, binocular or monocular, results from a voluntary effort initiated by the consciousness that the object of regard is nearer.

It is probable that convergence innervations are involved in all voluntary adjustments for vision at different distances; in fact, convergence may be the only truly voluntary component of the partnership, the synergic reactions of the ciliary muscle and sphincter of the iris being carried with it. It is, of course, well known that experimentally accommodation may be exerted to overcome centred negative lenses placed before the eyes, while binocular fusion is maintained for an object remaining at the same distance and viewed through the lenses. Although in these conditions the eyes are accommodating without actual convergence, the presence of the innervation to convergence is revealed by covering one eye, which will then be seen to turn inwards. It appears that in the special conditions of such an experiment, where different amounts of accommodation and convergence must operate together, the overriding control of the fusion faculty neutralizes the innervation to excessive convergence.

It has been shown by experiments with a haploscope system, that convergence may be made to exceed accommodation, but when the difference is measured objectively the excess is found to be smaller than that produced by the older subjective methods. Adamson and Fincham (1939) have shown that, within the amplitude of accommodation, it is not possible to alter convergence without causing some change in accommodation in the same direction. However, if the vergence of the light remains constant, the accommodation does not change as much as the convergence, apparently because the accommodative mechanism is governed to some extent by the vergence of the light at the eye. Thus, when the light is diverging from an object beyond the distance to which the eyes are made to converge, the accommodation will be less than the convergence but more than is required to focus the light from the object. It was found that in these special conditions there is quite a large subjective tolerance to the discrepancy between the refraction of the eye and the vergence of the incident light, within which the subject still has clear vision.

In the reaction of accommodation to lenses placed before the eye, there is no apparent change in the distance of the object to act as a stimulus; the only alteration is in the vergence of the light at the eye and the consequent loss of focus of the retinal image. This mere blurring of the image alone cannot be acting as the stimulus, because in these two conditions,

- (a) the unaccommodated eye viewing a distant object through a negative lens,
- (b) the accommodating eye being without the negative lens,

the degree of blurring will be approximately the same, but the required adjustments are in opposite directions. It is common practice during subjective refraction testing to keep the accommodation relaxed by producing a slight fogging of vision with positive lenses. It will be seen that unless the adjustment is made by a trial-and-error method, which would produce an unstable condition when the light entering the eye is too convergent (as for instance in myopia or when a weak positive lens is placed before an emmetropic eye), there must be some means of informing the brain of the state of the light at the retina, whether convergent or divergent.

This direct response of the accommodative mechanism to changes in the vergence of the incident light appears to be a reflex in monocular vision in young subjects. It appears to operate over a range of not more than 2 dioptres up to the age of about 26 years. For greater powers and at ages above 26 years the response is no longer involuntary.

The aim of this investigation is to find what characteristics of the retinal image constitute the stimulus which initiates this reflex response in the accommodative mechanism to changes in the vergence of the incident light.

EXPERIMENTAL METHOD

Only by an objective method of measuring the refraction of the eye can we be sure that accommodation is being changed. In this investigation the Coincidence Optometer (Fincham, 1937) was employed. By this instrument the retinal image of a vertical line target is watched throughout the test and changes in the refraction of the eye are

FIG. 1.—Photograph of the retinal image taken through the optometer.

indicated by a break in the coincidence of the upper and lower halves of the line[image]. A photograph of the appearance of the retinal image when the refraction differs from the setting of the instrument by 0.5 dioptre is shown in Fig. 1. A difference of 0.1 dioptre is visible, and the rate of change as the eye accommodates can be observed. The arrangement of the apparatus is shown in Fig. 2 (overleaf). The test object O, which was at a distance of 4 m., was presented to the eye by reflection at the transparent mirror M attached to the optometer. The axis of the optometer was about 4° away from the subject's visual axis. For the initial tests the object was a diffusely transilluminated clear plate bearing a number of black dots upon which the eye could focus. Illumination was from

either a 60-watt tungsten lamp or a sodium lamp. The whole luminous object subtended an angle of 1° at the eye; the angular size of the dots was about $3'$. The rest of the field was dark except for the target light in the optometer which had to be imaged on the subject's retina. The refraction was measured at about 4° from the visual axis.

The vergence of the light from the object was changed by means of the lens L interposed between the object and the mirror and close to the latter. This change could be brought about very rapidly, and the lens, being centred on the visual axis, produced no apparent lateral displacement of the object. In the routine test a -1.5 -dioptre lens was

FIG. 2.—Experimental arrangement of apparatus.

used to produce accommodation. Positive lenses were also used as a control. In some early exploratory experiments, the object described was replaced by an image projected upon a translucent screen in the position normally occupied by the object. This image could be put out of focus by an extent which imitated the blurred appearance which the normal object acquired when viewed through a +1-dioptre lens placed close to the eye. Keeping the surrounding field dark ensured that the subject saw the image in space and had no clues to its distance.

The 55 subjects examined were of both sexes and aged between 17 and 25. In no case was the refractive error greater than + or -1.0 dioptre.

EXPERIMENTS AND RESULTS

The first experiments were concerned with the general observation of the reaction and the verification of its reflex nature.

BLURRING THE OBJECT.—The effect of blurring the object, by projecting an out-of-focus image on to a screen, was tested on twenty young uninitiated subjects. Not one showed any change of accommodation when the image was altered from sharp focus to slight out-of-focus. Also, while the normal object was illuminated with white light, none showed any accommodation when a positive lens of 1.0 dioptre was placed before the eye, thus making the light at the eye more convergent. A few of the subjects who were low uncorrected hypermetropes were seen to relax accommodation and were not conscious of any change in vision.

On the other hand, all the subjects showed positive accommodation when a negative lens of 1.0 or 1.5 dioptre was brought into the path of the light from the object. The rate of the reaction varied somewhat. It is estimated that in no case was there a delay of as much as one second, and that in most cases the adjustment of the eye occurred with precision, and was completed in less than 0.5 sec. In a few cases, less than 10 per cent. of the whole, there were small fluctuations of power of about 0.25 dioptre while the eye was accommodating. The subjects were not conscious of these variations but said that their vision remained clear.

When the negative lens was removed, the state of the refraction of the eye returned to normal. The rate of this relaxation showed rather more variation from one subject to another than did the rate of positive accommodation. In most cases the change was rapid and precise, but in some there was a small hesitation. The delay was probably never more than one second.

These results show that the brain must be receiving messages which give the required information on the state of vergence of the light at the retina, whether it is convergent (calling for accommodation) or divergent (requiring relaxation of accommodation for the production of a focused image). It is necessary to refer to those few cases, less than 10 per cent. where the power was seen to fluctuate slightly, because such a process could by trial and error give the brain the necessary information, the mechanism feeling its way, as it were, to the correct adjustment. Such fluctuations are sometimes seen with the Coincidence Optometer when the eye is adjusted for distant vision and appear to occur in some low degrees of astigmatism. The results of the experiments show that in the normal reaction the brain is not depending upon such a trial-and-error process.

REACTION TO CHANGES OF COLOUR.—In an attempt to find a means other than lenses of changing the vergence of the light at the retina, and one that would not alter the apparent size of the object, use was made of the chromatic aberration of the eye. The object was still illuminated with white light, and two coloured filters which could be rapidly interchanged were placed in the lens-carrier instead of the lens *L*; a blue of maximum transmission 0.45μ , and a red of maximum transmission 0.63μ . (Wratten C4 and F). The difference in refraction of the eye for these two colours is in the region of 1.3 dioptries; thus an eye made emmetropic to the blue by means of a negative lens would have to accommodate 1.3 dioptries to see the object clearly through the red filter.

When this test was applied to a few subjects no reaction occurred. When the light changed from blue to red the subject was conscious that the image was blurred, and although a trained subject was able to focus it, a distinct voluntary effort was needed. With untrained subjects the image remained blurred. Tests on more subjects made at a later date have shown that some eyes do show a positive accommodation reaction for changes in colour, but the chance result that all the first group of subjects failed to react to this test led to the discontinuance of this experiment in the belief that there was a satisfactory psychological explanation of the result.

Because of the chromatic aberration of the eye, differences of definition must normally accompany retinal images of objects of different colour. In normal vision the scene which is viewed may

contain objects of many colours, and to focus each in turn would call for a continual adjustment of accommodation as the attention scanned the scene. But as the recognition of difference of light vergence and the consequent adjustment of accommodation are associated, in normal vision, with difference of distance, it seems unlikely that this recognition occurs when the difference of light vergence is due to the eye's differential focusing of coloured objects, which are known (by binocular and monocular parallax, perspective, etc.) to be at an equal distance from the eyes. The well-known stereoscopic effect with colours is binocular, and although it depends upon the chromatic aberration of the eyes, it is due to the relative displacement of the retinal images when, as is usual, the pupils are decentered with regard to the visual axes.

It is perhaps remarkable that red and blue objects placed at the same distance from the eye do not appear by monocular vision to be at different distances since the light from them is focused in different planes in the region of the retina. It appears that there must be some compensating sense by which colour differences are correlated with vergence differences and thus the brain accepts the fact that the eye is relatively hypermetropic to red and myopic to blue.

EFFECT OF ELIMINATING THE INFLUENCE OF CHROMATIC ABERRATION OF THE EYE.—It was suggested to the writer by Prof. Hartridge that the solution of the problem of how the brain learns the nature of the necessary adjustment of accommodation, might be found from a consideration of the chromatic aberration of the eye. Certainly, if we consider the retinal image of a simple object (such as a point of white light) apart from other aberrations and diffraction, the chromatism of the eye will produce in the image a certain characteristic disposition of the colours for the state of refraction which we call emmetropia. In hypermetropia this colour figure will be altered, the light disk will be surrounded by a red fringe, while in myopia blue will appear on the outside of the disk. It is possible that by this means the brain would know the nature of the light vergence at the retina. This hypothesis could be tested by repeating our first experiments with the object illuminated with monochromatic light instead of white light.

Subjects who had been tested with white light were again tested while viewing the same object illuminated with sodium light. The object was seen in a dark field. As before, the effects of negative and positive lenses were observed, and showed a marked difference from the uniformity of response obtained with white light. The accommodation reaction of the 55 subjects tested to changes in the vergence of sodium light, may be summarized as follows:

Group A	...	...	No reaction (19)
Group B	...	...	Partial reaction (14)
Group C	...	...	Reaction as with white light (22)

With regard to Group A, there is little comment to make. In most cases the image seen in the optometer remained quite steady, showing that no change occurred in the accommodation. In others there was a small fluctuation in power, not exceeding half a dioptré, when a negative lens of 1.5 dioptré was placed before the eye. The eye did not accommodate for the divergent light and the subject was conscious of a blurred image.

In Group C the reaction in both directions was complete, and in almost all cases the accommodation to the negative lens and the relaxation when it was removed were as precise and rapid as in the experiment with white light. In one or two cases the relaxation was slightly hesitant and slower. None of these subjects accommodated when positive lenses were placed before the eye while an object illuminated with sodium light was being viewed.

The results in Group B were the most interesting. With small individual variations they showed the following responses to changes in the vergence of the light from an object illuminated with sodium.

The interposition of a negative lens caused the eye to accommodate as with white light.

When the lens was removed, the accommodation was not relaxed although the subject was conscious of a blurred image.

This condition lasted for fully one minute, after which, in most cases, the power began to fluctuate, probably on account of conscious effort, and slowly returned to normal. In other cases it was not until the eye was turned away to view the target light of the optometer that the accommodation was relaxed.

The most distinctive characteristic of this group was that they would all accommodate to positive lenses when viewing the sodium-illuminated object. This was a definite and steady change; in fact it lasted long enough for the subject to experience the increased blurring which the effect produced and which developed after the lens had been placed in position.

As a further test of the influence of the chromatic aberration in respect of the stimulus to accommodation, the subjects were tested again when viewing an object illuminated with white light. In the path of the light was placed a lens constructed to correct the chromatic aberration of the average eye while not affecting the vergence of yellow light. This lens was placed in the cell C (Fig. 2); particulars of it have been given by Thompson and Wright (1947). The results of these tests in all three groups were precisely the same as with monochromatic light.

These experiments show that, while the influence of chromatic aberration and the consequent alteration of the colour figure of the retinal image for changes of vergence of the light is the governing factor in stimulating the accommodation reflex in a large group of subjects, some other factor must exist to explain the behaviour in those cases (at least 40 per cent.) who have the normal reflex when the information derived from chromatic aberration is denied them. Further experiments were therefore directed mainly to the investiga-

tion of subjects in Group C who so far had been found to react equally to monochromatic and white light.

EFFECT OF SPHERICAL ABERRATION OF THE EYE.—The particular characteristics of the retinal image which arise from the spherical aberration of the eye will change as the vergence of the light at the retina changes. It was necessary, therefore, to test whether this change gave rise to the stimulus to the accommodative mechanism. This was done by allowing the light from the test object to enter the eye through a narrow peripheral zone of the pupil only. The following method was used to achieve this condition. In the cell of the apparatus was mounted a small telescope system of unit magnification which had its exit pupil formed at about 35 mm. from the eyepiece and thus in the plane of the subject's pupil. In the plane of the objective was placed one of a series of central stops of diameters varying between 2.5 mm. and 4 mm. This stop, being imaged in the subject's pupil, prevented light from the object from passing through a central region of that diameter. The centring of this imaged stop was important, but presented no difficulty with the apparatus which was used. The Coincidence Optometer is provided with a means of centring the axis of the instrument accurately upon the subject's pupil, and of checking it at any time during the test; hence, by fixing the small telescope and the transparent mirror M with regard to the axis of the optometer, it was possible to ensure that the image of the stop was kept in the centre of the pupil.

Several subjects who had been found to possess the reflex with monochromatic light were tested with this apparatus while the object was illuminated with sodium. It was found that the limitation of the pupil to a relatively narrow peripheral zone did not prevent the reflex.

SIZE OF OBJECT.—Some experiments were made to determine the minimum angular size of object for which the eye would accommodate when the light was made divergent. A single spot of light of 1' angular diameter was the smallest that was used. With this it was found that no stronger lens than -0.75 dioptre could be employed without causing a degree of blurring which was too great in proportion to the object size. Using this small object illuminated with white light, some subjects were found still to show the reaction, but most required an object of 2' diameter to evoke the reflex. When the object was illuminated with sodium light it was necessary to increase its size to 4' or 5' to produce any reflex to the negative lens, and it was usually slower than normal for objects below 8'.

FIXATION, SCANNING, AND THE EFFECT OF DIRECTING FIXATION AWAY FROM THE OBJECT.—When the retinal image was being viewed

with the optometer in the course of making the observations described above, it was noticed that fixation was not constant. Details of the fundus, such as small retinal blood vessels in the region of the image, were seen to be making small oscillating movements with regard to the image. By comparison with the width of the image of the line of the optometer target, the amplitude of the movements could be estimated as rather less than $10'$ of angle. In most cases it was found that the subject could not prevent the movement, particularly when a lens was placed before the eye. For these experiments on fixation, lenses not exceeding 0.75 dioptré were used. Four subjects were found who could maintain good fixation and the following experiment was carried out on them. They viewed an object consisting of a luminous field of about 1° diameter, having upon it some black dots of $3'$ diameter arranged in pairs of various separation.

It was found that no accommodation occurred for a negative lens while the subjects maintained fixation of one dot, which they were able to do for at least 30 sec. As soon as the subject under direction turned the eye to look at the next dot, accommodation was seen to take place. The experiment was also tried in the reverse direction, *i.e.*, the eye was made to accommodate with a negative lens and then fixation was held on one spot of the object. When the lens was removed, accommodation remained unchanged so long as fixation was held. Accommodation was relaxed as soon as the subject directed his vision to another spot. These effects were found to be independent of whether white or sodium light were used, except that white light had to be employed with those subjects who had previously been found to show no reaction to monochromatic light.

In an attempt to determine the minimum angle of scan required, the reaction was found to occur when the subject looked from one to the other of a pair of dots separated by an angle of $6'$. This is not an easy task for the subject to perform, particularly as the image becomes somewhat blurred by the lens. Hence it cannot be said with certainty that the angle of rotation of the eye was not greater than $6'$, and on the other hand the subjects felt they could not guarantee fixation of one or other of a pair of spots of less than $6'$ separation; thus no accurate value for the angle of scan can be given. However, the effect was found to be the same in all four subjects, and they were each tested on several occasions. It was noticed that the reaction in each direction was very rapid as soon as the subject was instructed to scan.

Using an object consisting of a white spot subtending an angle of $10'$, it was found that there was no reaction to a negative lens if the subjects kept their direction of vision away from the object by more than its width. It was not permissible to use fixation or

directing marks for this purpose as they would have acted as stimuli, but many subjects found it possible to look at imaginary points around the object at a radial displacement from it equal to its width. The reaction was found to occur only when vision was directed to within 10' of the object.

DISCUSSION

These experiments have shown that when the vergence of the light at the retina is altered in a young subject, a message is sent to the brain giving information of the change, and thus initiating, where possible, the necessary adjustment of the state of accommodation. This adjustment is a reflex and is independent of the conscious knowledge of the relative distance of the object. We may assume that no mechanism exists in the retina for the direct recording of actual differences of light vergence, and the only results of these differences which occur in perception are in the definition of the image. That differences of definition do not provide the stimulus to this reflex is shown by the results of those experiments in which the object consisted of an image which could be put out of focus, and also by the absence of reaction in the eye when a weak positive lens is placed in the path of the light from the object.

The behaviour of the subjects in Group B, who show a partial reaction when the object is illuminated with monochromatic light, is particularly instructive in this respect. These subjects were found to react to a negative lens with the object illuminated with monochromatic light, but when the lens was removed they did not relax accommodation. If we assume that in these cases the brain is taking undue notice of the blurring of the image, we see that from the zero position an effort of accommodation, which is the only adjustment that can be made to improve vision, succeeds. When the lens is removed the retina is left with a blurred image again, but as the eye is now accommodating, the brain has a choice of either increasing or relaxing the accommodation. Without the information given by the chromaticity of the image, however, there is no clue to the direction the adjustment should take, and the brain is unable to give the necessary innervation. That these subjects depended to some extent upon the definition of the image when monochromatic light was used, is shown by their reaction to a positive lens. The fact that they accommodated showed that, in the absence of the differences in the image due to chromatic aberration, they were unable to distinguish between the effects of positive and negative lenses, and reacted in the same way to both.

With an object illuminated with white light, there were no such mistakes or hesitations in the reaction, and the change in accommodation was always in the correct direction.

In our enquiry into the nature of the stimulus at the retina for this reflex, we may assume that the retina can send to the brain only two types of fundamental information; a difference of light and a difference of colour. Thus it must be by one or both of these that the brain is informed of the change in the state of vergence of the light at the retina. Upon this basis the results of the experiments on the influence of chromatic aberration appear to offer a partial explanation. The fact that, in the absence of the effects of chromatic aberration, no reaction took place in about 34.5 per cent. of the cases tested and a quite false reaction in 25.5 per cent. means that in 60 per cent. the change in the retinal image due to the differential focusing for colours acts as a stimulus to the accommodation reflex, for without it the reflex is absent. It may appear remarkable that chromatic aberration, which might be considered a fault in the optical system of the eye, not only has no noticeably harmful effect upon the image which is perceived, but is instrumental in providing the information which enables the brain to carry out an important adjustment.

This, however, is not the only factor in the process, because 40 per cent. of the cases studied were found to have the normal reflex when chromatic aberration could play no part. It is unfortunate that up to the present the experiments on fixation and scanning could be made on no more than four subjects, but it is understandable that it will not be possible to find many subjects who can maintain a high order of fixation in the conditions of this test. However, the results in these four cases have shown that, irrespective of the effects of chromatic aberration, no accommodation reflex to changes in the vergence of the light takes place while fixation is held. To produce the reflex it is necessary for the eye to scan so that the image travels across a certain area of retina. It has not been possible to measure the angle of rotation of the eye in this scanning process, but such observations as have been made indicate that a rotation of 6' may be sufficient.

The necessity for scanning seems to indicate that the Stiles-Crawford effect is the means whereby the visual mechanism interprets difference of vergence into terms of difference of light stimulus. Fig. 3 shows the hypermetropic and myopic conditions; in each case the eye has turned to the right from the point of fixation, so that the out-of-focus image is falling to the right of the centre of the fovea M. This simple treatment shows that the limiting rays of the blur circles acquire differing degrees of obliquity at the retina for small movements of the eye. In the hypermetropic condition, the rays nearer to the centre of the fovea become more normal to the retina; in the myopic state the rays farther from the centre of the fovea become more normal. Thus on the basis of the Stiles-Crawford effect a

FIG. 3.—Application of the Stiles-Crawford effect when the retina is receiving an out-of-focus image while the eye makes a scanning movement.

difference of brightness stimulus between the two sides of the area could be produced, and by this means the brain could detect whether the light at the retina was converging or diverging. This difference of brightness for the small angle of rotation and for dioptric differences as low as 0.5 dioptré will be very small; but we need not relate it to the light difference sense, since here no sensation is involved but only the operation of a reflex of the lower centres. The effect of directing the vision slightly away from the object (10' from fixation) was to prevent the reaction, although scanning was still permitted. Thus it appears that only a limited area of retina is used for this reflex and it is known that the Stiles-Crawford effect applies only at the fovea.

There appear, therefore, to be two factors concerned in stimulating the accommodation reflex; chromatic aberration of the eye, and a minute rotation of the visual axis or scanning. Of these the scanning process is probably more essential, since many subjects were found to have a normal reflex without the effects of chromatic aberration, and all were seen to be making the scanning movements except those few who could arrest it by voluntary effort, which prevented the reflex. Therefore, whereas probably all subjects are using both factors, some do not react without the application of both, whereas others can dispense with the chromatic effects.

It is interesting to speculate on the purpose of this reflex with its operation independent of the nearness of the object which is, of

course, the normal reason for accommodation. It appears to constitute an automatic focusing device, governed by the actual vergence of the light irrespective of the real, or apparent, distance of the object. The clearest case of its operation in natural conditions is in the uncorrected low hypermetropic eye, where the inherent error is automatically corrected by the accommodation. In such a case, the normal equality relationship between accommodation and convergence cannot hold. Some machinery must exist for allowing the eyes to accommodate by the amount of the error before convergence is called into play. Although accommodation and convergence operate together in normal vision, some considerable latitude exists between them—the relative amplitude. This entails that although apparent distance is the overall controlling stimulus for the dual function, when the linkage between accommodation and convergence is loosened they must each be dependent to some extent upon their own stimuli. Just as convergence is governed by the disparity of the retinal images and the necessity for fusion, so accommodation has an independent fine adjustment in the reflex discussed in this paper, which is stimulated by changes in the vergence of the light at the retina.

It is realized that this investigation is far from complete. In particular, the function of scanning with regard to the reflex calls for more experiments on a greater number of subjects and for a full theoretical consideration of the process by which it operates in the interpretation of differences of light vergence into differential impulses in the retinal nerves.

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REFERENCES

- ITTELSON, W. H., and AMES, A. (1950). *J. Psychol.*, **30**, 43.
ADAMSON, J., and FINCHAM, E. F. (1939). *Trans. ophthal. Soc. U.K.*, **59**, 163.
FINCHAM, E. F. (1937). *Proc. phys. Soc. Lond.*, **49**, 456.
THOMSON, L. C., and WRIGHT, W. D. (1947). *J. Physiol., Lond.*, **105**, 316.