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MECHANISMS IN PERIPHERAL DARK ADAPTATION.

by

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Introduction.

Probably under the visual functions the light and the dark adaptation are the most extensively studied, especially by the fact that various aspects of the physiological condition of the subject influence the behaviour of these functions less or more significantly.

In detail, for instance, vitamine A deficiency in their early stages becomes apparent in this behaviour, just as a diminishing of the oxy-hemoglobin amount of the blood by respiration of poisons like carbon monoxide or of air with decreased pressure or decreased partial pressure of oxygen.

By this reason this visual function is more extensively used for diagnositical purpose in clinical practice.

In spite of the considerable amount of work on adaptation phenomena only little definite is known concerning the mechanisms of light and dark adaptation. In studying the available litterature, it proved that most quantitative theoretical explanations particularly on the "kinetics" of the adaptation does not go much further than a more or less foundated speculation on a pure photochemical origin of adaptation whereas some authors stretched attention to phenomena in a qualitative way which can only be explained by nervous factors.

x) Kampweg 3, Soesterberg.

We do not intend to give a review on this subject but only present introductory remarks and considerations important to point out the quintessence of our investigations reported below.

Recently a few excellent reviews appeared from which we mention those of Sheard 1), Hartridge 2) and Jayle and Ourgand 3).

The pure photochemical theory introduced and extensively explored by Hecht 4) has the great attraction that it presents mathematical relations between the various variables in consideration. There is a general agreement between most investigators that the concentration of the active photochemical material in the receptors must be described by the mass action law introduced by Hecht for visual problems.

However when it is proved that also nervous factors come into play the foundation of the hypothesis of Hecht according to which only the photochemistry of the receptors determines the visual functions concerned must be corrected. For the possible activity of various components we had already indication from our recent investigations on the contrast threshold 5,6) just as from the study of Rose 7) of this visual function.

Evidently when the state of adaptation of the one eye affects this of the opposite one, the influence of a nervous factor is shown conclusively.

1) C. Sheard, J. Opt. Soc. Am. 34,464 (1944)
2) H. Hartridge, Recent Advances in the Physiology of Vision, Churchil I London (1950)
3) G.E. Jayle et A.G. Ourgaud, La vision nocturne et ses troubles, Masso Paris (1950)
4) S. Hecht, Physiol. Rev. 17, 239-290 (1937)
5) M.A. Bouman, J. Opt. Soc. Am. 40, 825 (1950)
6) M.A. Bouman, J. Opt. Soc. Am. 42, (1952).
7) A. Rose, J. Opt. Soc. Am. 38, 196 (1948)

Our findings 6) in this respect agree mainly with these of Mandelbaum 8). In our paper 6) we reported measurements of the absolute threshold of the darkadapted right eye when the left eye was stimulated by various adapting brightnesses just as during interruptions of this adapting field.

From these data it was concluded that the state of adaptation of the one eye is not affected by the light history or actual stimulation conditions of the opposite eye except for very high adapting brightnesses.

These very intensive stimulations can be considered as "inadequate" and possibly the rise in absolute threshold mentioned can also be achieved by very intensive noises or extreme stimulation of other sense organs.

Anyhow, the independence of the states of adaptation of both eyes under normal conditions is frequently used in every day practice for the preservation of the darkadapted state by closing one of the eyes so that this eye remains or becomes darkadapted while performing a visual task with the opposite eye.

Our conclusion 6) was based on measurements for which both by adapting field and test spot rods or cones were stimulated as well as for rods stimulated by adapting brightness, the threshold being determined for cones, and the reserve.

The independence of the states of adaptation of both eyes does not permit the conclusion that no nervous factors are active in adaptation phenomena for "adequate" brightnesses.

The rise in threshold of the one eye by stimulation of the opposite eye by very high "inadequate" brightnesses evidently is of nervous origin. It proved that the behaviour of this rise in terms of the dependence of it as a function of flashtime and visual angle of the test spot is described by a rise in the minimal number p of quanta that must be effectively absorbed in the receptors in order to perceive a flash.

8) J. Mandelbaum, Arch. Ophth. 26, 203 (1941)

By this reason we studied with the aid of measurements of the absolute thresholds as a function of the size of the test spot under various adaptational conditions whether the recent quanta theoretical speculations are of importance for the 6) description of adaptation phenomena.

Besides, it was checked whether the results of this study will lead to a still better convergence between experimental data on contrast thresholds and the quanta explanation of them 6).

In the next section we present the measurements, whereas in the following parts they are discussed with respect to their significance for a theoretical synthesis between various aspects of the visual functions.

The experiments.

In a previous paper 5) we described in detail the experimental arrangement with which the data are obtained.

Each 3 seconds the adapting field incident in the observer's right eye was interrupted 0,5 seconds. The adapting circular background subtended 15 degrees of the visual field and was projected with its centre 7° nasal from the fovea realized with the aid of a weak red fixation point observed with the right eye. An artificial pupil 0,5 mm in size was used.

During the interruptions Δt = 0,05 , 0,10 , 0,20 , and 0,40 seconds after the beginning of these the absolute thresholds were measured for sizes of the circular test spot from 4 minutes of arc to 7 degrees and for flashes lasting 0,02 seconds. The flashes were projected with its centre 7° nasal from the fovea in the right eye.

This was done for various brightness values of the background and for the four possible combinations of wavelengths of adapting field and test spot when light of 6500 A° and 5250 A° is used.

At the beginning of each session the eyes of the observer were darkadapted for half an hour. Each threshold was determined after a period of observation of the intermittent adapting field sufficiently long in order to reach a steady chance of observation of the test flash during the interruption.

Each chance was obtained with the aid of 20 - 30 presentations of the test flash under the particular situation of size d, value of f and intensity $\bar{n}$ of the flash.

The threshold $\bar{N}_{60\%}$ which we defined as the flash intensity for which the chance of being observed is 60% was found by interpolation between 3 to 4 measured chances surrounding the 60% value.

In the figures 1 - 4 we present the results. $\bar{N}_{60\%}$ is the total average number of quanta incident in the eye of the test flashes, $\bar{n}$ is the average number of quanta incident in the eye pro second and pro area subtending a visual angle of 10^{-3} radian from the adapting field, B is the brightness of this field in millilamberts corresponding to the illumination of the retina when the pupil has the constant size of 2 mm.

It seems that as far as the dependence of the absolute threshold on the size of the testobject is concerned the adaptational influence of the adapting field appears in three aspects:

1) The region of d values within which Ricco's law, $\bar{N}_{60\%}$ independent on d, is valid decreases with increasing $\bar{n}$ and decreasing f.

2) The slope of the curve representing $\bar{N}_{60\%}$ as a function of d for d large increases with increasing $\bar{n}$ and decreasing f from $\bar{N}_{60\%} \sim d$ to $\bar{N}_{60\%} \sim d^2$.

3) The complete curve generally shifts to higher values when $\bar{n}$ increases or f decreases.

For each of the particular cases from the figures 1 - 4 the three aspects have their special weights.

Indeed for green test flashes the decreases of Ricco's region is considerable, for red ones this aspect is hardly present. For green flashes the amplitudo of the general shift to higher values exceeds this for red flashes.

In the next section we discuss these phenomena with respect to a quantitative analysis of the various possible nervous and photochemical mechanisms.

Photochemical and nervous components in adaptation.

The initial act for the visual sensation is the absorption of radiation in the photochemical material of the receptors. Obviously the sensitivity of the eye for light of a particular wavelength will depend on the amount of this material that is available for the visual cycle so that a diminishing in this amount will result in a general shift of threshold values to a higher level From considerations given below it will be clear that a shift mentioned can also be due to a nervous factor. In the regeneration of the photochemical material decomposed by the absorbed light, vitamine A is indispensable 9). Evidently the influence of vitamine A deficiency on the behaviour of absolute thresholds is of photochemical origin.

It is generally accepted that the fundamental cause of the validness of Ricco's law in the region of small d values must be the integrate capacity in space of the nervous system connected with the end organs as far as this region exceeds the size of the individual receptor. By this reason one is inclined to assume that changes or differences in the size of Ricco's region are due to changes or differences in the properties of the nervous system.

Indeed, there is a general agreement between the various authors in concluding that the difference in size of Ricco's regions for peripheral rod and cone vision is due to the nervous systems connected with the rod and cones separately 11,12 Below it will be pointed out that a dedrease of Ricco's region can also be arisen by changes in the conditions for stimulation of the individual end organs.

9) l.c. page 395 leg. 3.

From previous work 10,11,12) it proved that under darkadapted conditions the slope of the curves representing $\bar{N}_{60\%}$ as a function of d for d large and as a function of t for t large is determined by the number of receptors which must be stimulated by the absorption of one quantum in order to perceive a flash.

An increase in this number will be apparent in an increase of the slopes mentioned and is another possible nervous component in adaptation. Indeed, when a receptor is stimulated by one effective absorption and more such stimulations are necessary for the light perception the number of these is determined by the properties of the nervous system.

However, the increase of the slopes mentioned can also be due to an increase of the number of effective absorptions in a separate receptor necessary for its stimulation. When this is the case it can be caused by the fact that for the formation in the receptor of a required constant amount of energy which is necessary for the stimulation of the nerve connection of it, the number of effective absorbed quanta must be increased or by the fact that the required amount of energy is not constant; the first being of photochemical nature, the second of nervous origin.

Anyhow, the number of possible mechanisms in adaptation is rather embarrassing. We will now investigate the merits of the recent quanta theoretical considerations with respect to the possibility to detect the activity of the various mechanisms.

We know that as far as the flashtime t and the visual angle d does not exceed Bunsen - Roscoe's region ($\bar{N}_{60\%}$ independent to t) respectively Ricco's region

$$p \cdot q = f_1 \cdot f_2 \cdot f_3 \cdot \bar{N} = \varphi \bar{N} \qquad \text{I}$$

in which $\bar{N}$ is the smallest number of quanta incident in the eye in order to perceive the flash,

10) H.A. van der Velden, Physica 11, 179 (1944) Ophthalmologica 111, 321
11) M.A. Bouman, H.A. van der Velden, J.Opt.Soc.Am. 38, 570 (1948)(1946)
12) M.A. Bouman, Doc. Ophthalmologica 4,23 (1950)

f_1 is the transmission of the ocular media and retina,

f_2 the fraction of the quanta incident in the receptors, that is absorbed by the available amount of active photochemical material in order to decompose it such that the resulting products contributes to the arising of a nerve impulse in the nerve connection of the receptor,

q is the number of quanta that must at least be absorbed in a receptor under the conditions just mentioned in order that a nerve impulse in the nerve connection of the receptor can arise,

f_3 the fraction of the nerve impulses of the receptors that succeeds in cooperation at the synapses in order to result in a light perception,

p is the smallest number of such nerve impulses which cooperation at the synapses can result in a light perception.

Variation in f_2 and f_3 only affects the general energy level of the absolute thresholds, variation in f_2 being of photochemical and in f_3 of nervous origin.

The area within which the q quanta must be absorbed cannot exceed the size of one receptor; for the interaction of the p impulses this area can content a large number of receptors. Evidently a decrease of Ricco's region can be arisen by a relative increase of q compared with p.

Theoretical observations lead to [10] [11] [12]

$$\bar{N}_{60\%} \backsim t^{pq - 1/pq} \cdot d^{2(pq - 1)/pq} \qquad II$$

From previous experiments we know [10,11,12,13,14] that for the darkadapted eye for rod vision for t very small and when the test object covers several hundreds of rods the absolute number of quanta incident in the eye at the absolute threshold is sufficiently low to make the conclusion possible that these quanta are absorbed in different receptors. By this reason for darkadapted rod vision $q = 1$ and as it proved $\bar{N}_{60\%} \backsim t^{\frac{1}{2}}$ for t large and $\bar{N}_{60\%} \backsim d$ for d large $p = 2$.

13) S. Hecht, J.Opt.Soc.Am. 32, 42 (1942)
14) Hl. de Vries, Physica 10, 553 (1943)

Similarly, for darkadapted peripheral and foveal cone vision 11,12) it was found $\bar{N}_{60\%} \backsim t^{\frac{1}{2}}$ for t large and $\bar{N}_{60\%} \backsim d$ for d large. However, the absolute number of incident quanta at the absolute threshold is under all conditions of size and duration of the test flash not small enough compared with the number of cones covered by the flash in order to conclude to q = 1. Anyhow, for darkadapted cone vision pq = 2. It is possible to rejedt the case p = 1 with the aid of measurements on the interaction of the various kinds of receptors at the absolute threshold within an area over which Ricco's law is valid. It was found 11,12) that the stimulation of separate cones in the periphery can cooperate with the stimulation of separate rods in order to reach the absolute threshold. In the fovea, the facts are similar for the various kinds of cones. Such cooperation between subliminal activation of different receptor systems is only possible when for these systems $p > 1$. By this reason it is quite conclusively that for the cones under darkadapted conditions $p \neq 1$ so that q = 1 and p = 2 as pq = 2.

Evidently for single peripheral or foveal cone vision the possibility can not be excluded that both nerve impulses p must originate from the selfsame receptor as in this case Ricco's region hardly exceeds the size of a single receptor.

For the observers investigated for darkadapted rod vision $f_2.f_3$ was between 0,50 and 0,06 12), f_1 is about 0,5.

As only a relative small fraction of the light incident in the receptors will be absorbed in an efficient way 13) it seems that $f_3 = 1$ for the darkadapted rods.

We computed from the slopes of the curves for d large in figures 1 - 4 with the aid of formula II the value pq. The resulting values pq were used for the determination of $f = f_1.f_2.f_3$ for d very small with formula I. The results are presented in the figures 5 - 8. The data for $^{2/}\bar{N}_{60\%}$ when d $\backsim$ 3 minutes are incorporated. Because of the repeated mathematical manipulations in order to obtain $f_1.f_2.f_3$ the accuracy of these values is relatively small. The dotted curves in the figures represent the general behaviour of f qualitatively.

The accuracy of the pq values is influenced by the deviation from the case pq = 2 of the slopes of the curves giving $\bar{N}_{60\%}$ as a function of d for large d which deviation is caused by the inconstant sensitivity of the receptor systems over the retina.

For rod vision (green test flashes) this deviation is very small 16,12) even when the test object is very large and includes the fovea. Indeed the relative constancy of the rod sensitivity over the retina 17) will hardly influence the slope mentioned. For large test objects the surface of the blind fovea is almost negligeable.

For cone vision the duration in the slope from $\bar{N}_{60\%}$ vs d is somewhat greater in agreement with the great variation 17) of cone sensitivity in the area of the retina concerned in our experiments.

By this reason we do not pretend that the conclusions present below can have more than a qualitative bearing.

From the figures 5a - b and 6a - b for green test flashes and green respectively red adapting fields it proves that pq as well as f_1 f_2 f_3 depends on the state of adaptation.

Particularly the dependence of pq on the intensity of the adapting brightness for both cases is similar and the velocity of the recovery of pq for a fixed adapting brightness in the region of times of darkadaptation studied by us is relatively fast. Also the shape of the curve giving f as a function of $\bar{n}$ for both cases is similar whereas for between 0,05 and 0,40 seconds the recovery of f is negligeable. We think it rather surprising that these complicated theoretical considerations applied to these two sets of measurements lead to data which can be evaluated as in satisfying agreement with each other. Indeed, in both sets mainly the same receptor systems will be activated by the test flashes so that the main features in the adaptational behaviour was expected to be similar.

16) M.A. Bouman and H.A. van der Velden, J. Opt. Soc. Am. 37,908 (1947)
17) C. Sheard, J. Opt. Soc. Am. 34, 464 (1944)

The variations in pq for red test flashes presented in figures 7a and 8a are smaller just as these of f from 7b and 8b. The velocity of recovery of pq for a fixed adapting brightness in the region of times of darkadaptation studied seems to be slower than for the green test flashes whereas in the f values this recovery is much faster compared with the results in figures 5b and 6b. Again there is agreement between both sets of results for red flashes so that we are inclined to assume that the quantatheoretical aspects discussed have indeed a real significance for the obtaining of information on the fundamentals of adaptational mechanisms.

It can be asked whether the change in pq with adaptation is due to variation in p, in q or in both.

From previous experiments we learned that p increases [6] when measured in the one eye the opposite eye being stimulated by a dazzling light source of increasing brightness. In these data a simultaneous occurrence of a decrease of the region within which Ricco's region is valid was not apparent.

By this reason it is very probable that the increase of pq in the experiments reported here is at least partly due to an increase of p. It can not decided whether q also depends on the state of adaptation. By this reason without further information no conclusions can be made concerning the effect by which Ricco's region decreases with increasing adapting brightness for green test flashes. It can be due to anconsiderable increase of q or by a decrease of the integrate capacity in space of the nervous system or by a mixture of these effects. It might be that the integrate capacity mentioned and the value p are mutually dependent.

The change in f can be due to variation in f_2 and f_3 or only f_2. It seems hardly reasonable to assume that the sense organ will completely ignore a fraction of the nerve impulses. We only mentioned this possibility in order to complete the discussion. By this reason we take $f_3 = 1$, so that the variation in f_2 determined by the effective absorption power of the lightquanta in the receptors only remains.

In our previous paper 6) we compared $^{2}/_{\bar{N}_{60\%}}$ as a function of $\bar{n}$ for d ∽ 3 minutes and t = 0,02 seconds and $\int$ = 0,3 seconds with the various possibilities of the values m and n in the steady state equation of the photochemical theories for the simple reversible system $S \rightleftharpoons P + A$

$$K_1/K_2 \quad I = x^n (a - x)^m \qquad \text{III}$$

a is the initial concentration of S.

I is the intensity of adapting field.

x is the concentration of the products P and A.

m and n are the order of the → and ← reactions.

K_1 and K_2 are the velocity constants of these.

In the quoted paper 6) the information on the nervous components in adaptation was not available. Now we can compare the shape of the f function deduced from the $^{2}/_{\bar{N}_{60\%}}$ curves with the aid of the obtained pq values with formula III.

The agreement of the shapes of the f functions from the figures 5b and 6b with the case m = 2 and n = 1 is striking (figure 9) and inspire confidence in the applicability of the detected nervous and photochemical aspects in adaptation to measurements of the various visual functions.

The variation in f for red test flashes is too small to confront them with the equation III.

From the presented discussion it proves that adaptation is a complex mechanism. Especially the recovery with time of the various aspects can differ widely and can be highly dependent on the preceding light history. The various ways in which the knick[1] 8) in the usual dark adaptation curves can appear might be influenced by the special weights of these aspects under the particular adaptational conditions.

For very small test objects for instance the nervous components will be much less important compared with measurements for large objects as the values p and q are represented in power functions of d according to formula II. For small objects the threshold is only proportional to p and q (see I).

18) l.c. page 105 leg. 3.

Another consequence for instance is that the question arises whether the presented treatment of the results allows an analysis of the influence of anoxia on the visual functions, especially whether this action is selective with respect to the nervous or photochemical aspect.

From the reported measurements it proved that the case $p = 2$, $q = 1$ is the lower limit of the possible values which is only reached at the dark-adapted state. It might be that even under these conditions sometimes $p = 2$, $q = 1$ not suffices and a frequency distribution including $p > 2$ and/or $q > 1$ exists. Elsewhere 12,16) we discussed this possibility and concluded that in such a distribution the case $p = 2$, $q = 1$ must be most frequent.

For large test objects or large flashtimes for the dependence of the absolute threshold as a function of d respectively t the lowest possible value of pq will become dominant.

In previous paper 5,6,12,16) we mentioned that in the measurements of absolute and contrast thresholds as a function of d or the flashtime t deviations from quanta-statistical explanations occur when both d and t are large. It proved that the value pq increases with increasing d and t. These deviations are described by an impeded chance for the perception of light or contrast by the action of the light of the test flash self. We are inclined to assume that this effect is related to the adaptational aspects discussed in this paper.

Because of the dependence of pq on the state of adaptation it is expected that the absolute threshold as a function of the flashtime will agree with formula II. It was impossible to measure this dependence with our experimental procedure as in the region of times of dark-adaptation τ 0,05 - 0,40 seconds the recovery in $\bar{N}_{60\%}$ was relatively fast.

We remark, that whereas the adapting field is presented intermittently to the observer the states of adaptation at the various times τ after presentation of this field are well defined when the precaution is made of a sufficiently large number of preceeding presentations before the measurement of $\bar{N}_{60\%}$ starts.

Recent measurements 5,6) of peripheral contrast thresholds were discussed with the aid of the quanta theoretical explanation of de Vries 14).

According to this theory contrast will be seen when at least in one of the recipient units during an averaging time T of the test flash covered by bakkground and test spot the average number of absorbed quanta by the test stimulus ΔN exceeds the average statistical fluctuation of the absorptions of the background pro recipient unit pro averaging time:

$$f\,\Delta N = K\,\sqrt{2 f\bar{n} + f\,\Delta N}\,, \qquad K = \text{constant} \quad (IV$$

In the quoted papers 5) and 6) this theory was also checked by comparison of f/K^2 as a function of $\bar{n}$ deduced with this formula from contrast measurements with measurements of $2/\bar{N}_{60\%}$ for d ∽ 3 minutes, t = 0,02 seconds and f = 0,3 seoncds.

The agreement in the behaviour of f/K^2 deduced with IV and $2/\bar{N}_{60\%}$ was already satisfactorily in spite of possible nervous components in adaptation for $2/\bar{N}_{60\%}$. Now we can incorporate these components quantitatively. In figures 10 and 11 for the cases of both adapting field and test stimulus red or green, the results of f/K^2 from paper 6) deduced with IV from contrast measurements and the data for f from the figures 5b and 7b are represented:

When the theoretical manipulations explored in this paper are applied to the values $2/\bar{N}_{60\%}$ in order to obtain the f value for which de Vries' concept must be valid the convergence between quanta interpretations of the visual functions concerned and experimental data is improved.

Summary.

Measurements of absolute thresholds as a function of the size d with test flashes lasting 0,02 seconds of the circular test stimulus, 7° nasal from the fovea of the right eye for various states of adaptation, demonstrate three adaptational actions of the adapting field.

1. the slope of the curve representing $\bar{N}_{60\%}$ as a function of d for d large increases with increasing $\bar{n}$ and decreasing time f for darkadaptation from $\bar{N}_{60\%} \backsim d$ to $\bar{N}_{60\%} \backsim d^2$. This increase can be described with the formula

$$\bar{N}_{60\%} \backsim d^{2(pq - \frac{1}{2})/pq} \qquad \text{II}$$

$\bar{N}_{60\%}$ is the absolute threshold

q is the number of quanta that must at leat be absorbed in a receptor such that the resulting effect arises a nerve-impulse in the nerve connection.

p is the smallest number of such nerve impulses which cooperation can result in a light perception.

For the four combinations of red and green light for adapting field and test field we deduced the value pq from the slopes of curves representing $\bar{N}_{60\%}$ as a function of d for various values of f and brightness of the adapting field $\bar{n}$.

The recovery with time of pq during the darkadaptation period studied (0,05 - 0,40 seconds) is for green test flashes fast compared with the behaviour of pq for red flashes.

2. The complete curve of $\bar{N}_{60\%}$ as affunction of d generally shifts to higher values when $\bar{n}$ increases or f decreases.

An explanation of this shift is given by

$$pq = f\,\bar{N}_{60\%} \qquad \text{I}$$

for d very small.

f is the fraction of the incident light that is absorbed by the available amount of the photochemical material such that it contributes to the light perception.

From the measurements f is determined as a function of f and $\bar{n}$ with the aid of I and II and the value pq.

The recovery with time of f in the intervals f studied is for green flashes relatively slow compared with the behaviour of f for red flashes.

The shape of the curves representing f as a function of $\bar{n}$ for green test flashes and red and green adapting field agrees with the case m = 2, n = 1 from the steady state equation in the photochemical theory:

$$XI = x^n (a - x)^m \qquad III$$

Indeed, it was expected that f is proportional to the concentration of the photochemical substances.

Deviations from quanta explanations for absolute and contrast thresholds for large d and large t are probable due to the adaptational action of the light of the test flash self on the value pq.

3. For green test flashes the region of d values within which Ricco's law is valid decreases with increasing $\bar{n}$ and decreasing $\int$.

For red flashes even for the darkadapted eye Ricco's region hardly exceeds the size of one receptor.

The decrease mentioned for green flashes can be due to the fact that the rise in the product pq is mainly arisen by an increase in q or by the diminished integrate capacity in space of the retina. 19)

There proved also to be a fair agreement between the shape of the curve representing f as a function of $\bar{n}$ deduced from measurements of the contrast thresholds ΔN for small d and t with the aid of IV representing de Vries' explanation of contrast threshold data and the same function deduced with the aid of I and II from the data in this paper.

$$f \Delta N = K \sqrt{2f\bar{n} + f \Delta N} \quad , \quad K = \text{constant} \qquad IV$$

The relative weights of the various components mentioned under 1 - 3 in this summary is demonstrated by the following examples abstracted from the figures.

The total variation in absolute threshold for the smallest time of darkadaptation $\int$ = 0,05 seconds, for d = 400', for the highest $\bar{n}$ value, for green test flashes and green adapting field is a factor 4×10^3.

This variation is achieved by a variation in f with a factor 16, pq is changed from 2,1 to 16 and Ricco's region is decreased from about 14 minutes to 2 - 4.

19) G.J. Fortuin, Philips Research Reports 6,352 (1951)

For red testflashes and red adapting field the greatest variation is a factor 30 from which a factor 3 is due to f variation whereas pq changed from about 2,3 to 7.

The measurements of the thresholds probably partly refer to the determination of the contrast threshold against the after-image achieved by the light which preceeds the subsequent darkadaptation.

Anyhow darkadaptation is generally defined by the sensitivity of the eye for various visual functions after a preceeding lightadaptation no matter what the mechanism for the diminished capacities may be.

Abstracts

Measurements of the absolute thresholds for red and green test flashes at various moments in interruptions of a red and green adapting field each 3 seconds of 0,5 seconds are presented under variation of the size d of the test spot between 4'-420' and the brightness $\bar{n}$ of the adapting field.
Peripheral vision 7° nasal from the fovea of the observers right eye is concerned.

From these measurements nervous and photochemical components in adaptation are detected with the aid of speculations on the validity of quantaexplanations for visual functions.

The dependence of the absorption power of the photochemical substances on the adapting brightness which we deduced from the reported data, agree with the steady - state equation in photochemical theories and also with the dependence mentioned abstracted from measurements of the contrast threshold with quanta theoretical considerations.

With increasing brightness of the adapting field for green test flashes Ricco's region in the curve representing the absolute threshold as a function of d diminishes whereas the minimal necessary number of quanta that is absorbed in the receptors such that they contribute to the light perception increases.

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figures 1a - 1d:

The absolute threshold $\overline{N}_{60\%}$ as a function of the visual angle d for flash time 0,02 seconds for various intensities $\overline{n}$ of the adapting field. $\overline{N}_{60\%}$ was measured for $\int$ = 0,05; 0,10; 0,20 and 0,40 seconds after the beginning of interruptions of the background lasting 0,5 seconds each 3 seconds.

$\overline{n}$ is the average number of quanta incident in the eye pro second and pro area subtending a visual angle of 10^{-3} radian.

Wavelenght 5250 A° both for adapting field and test stimulus.

figures 2a - 2d:

Similar to 1a - 1d:

Wavelength 5250 A° for test stimulus, 6500 A° for adapting field.

figures 3a - 3b:

Similar to 1a and 1d, $\int$ = 0,05 and 0,40 seconds.

Wavelength 6500 A° for test stimulus, 5250 A° for adapting field.

figure 4:

Similar to 1d, $\int$ = 0,40 seconds.

Wavelength 6500 A° for test stimulus, 5250 A° for adapting field.

figure 5a:

The value pq deduced with the aid of $\overline{N}_{60\%} \sim B\, d^{\,2(pq-1)/pq}$ from the slopes of the curves of figures 1a - 1d for d large.

B is the brightness in millilamberts of a surface corresponding to the illumination of the retina when the pupil has the constant size of 2 mm.

figure 5b:

The value f deduced with the aid of $f\,\overline{N}_{60\%} = pq$ for very small d from the data of figure 1a - 1d and figure 5a (dotted curve

The fulldrawn curves present $^{2}/\overline{N}_{60\%}$ from 1a - 1d for d=4 mintes

figure 6a and 6b:

Similar to 5a - 5b and deduced from the figures 2a - 2d.

figures 7a and 7b:

Similar to 5a - 5b and deduced from the figures 3a - 3b.

figures 8a and 8b:

Similar to 5a - 5b and deduced from figure 4.

figure 9:

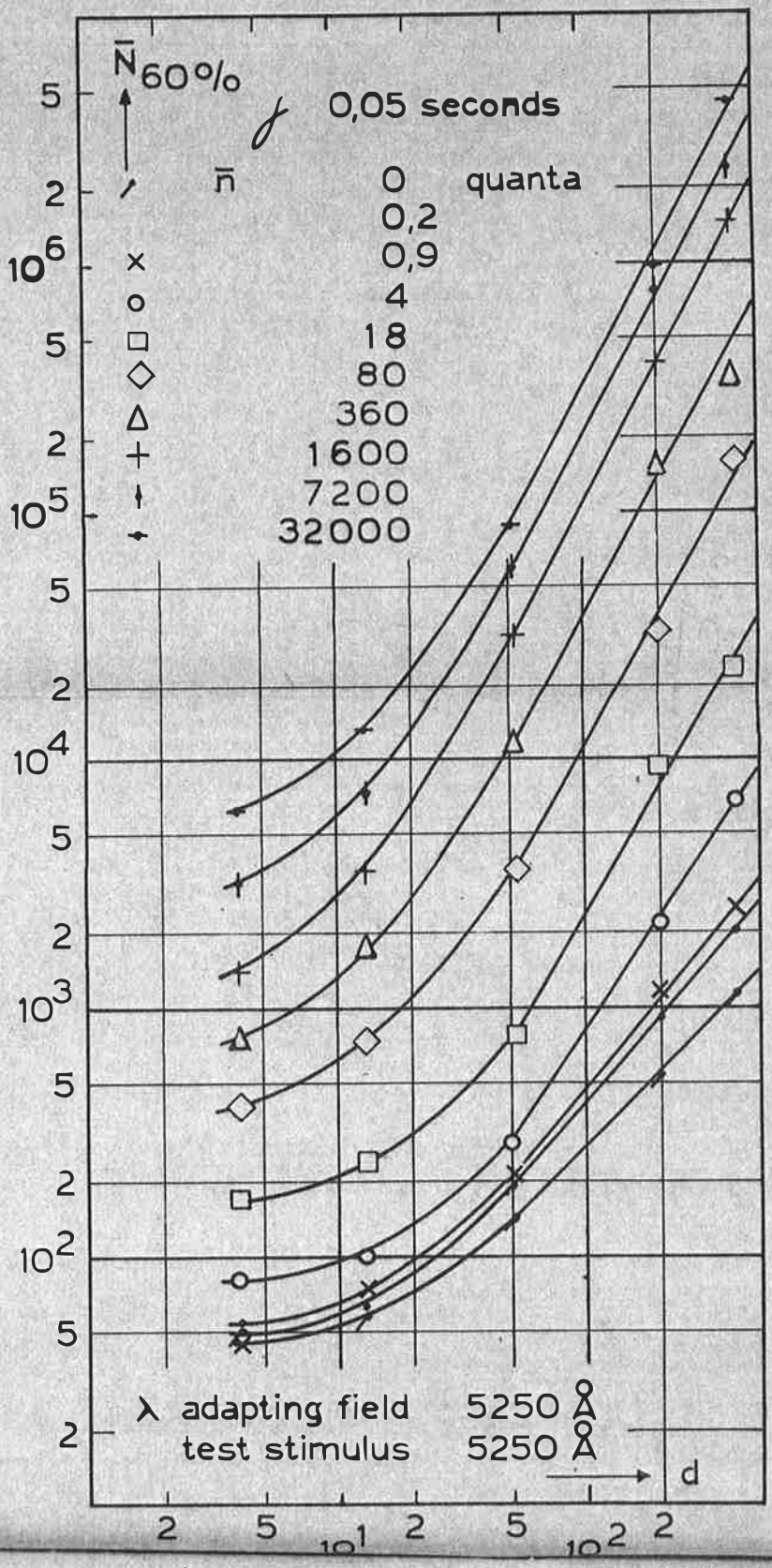
The concentration of the product S in the simple reversible photochemical system $S \rightleftarrows P + A$ as a function of the bleaching intensity $\bar{n}$; concentration log (a - x) and $\bar{n}$ in arbitrary units. The order of the reaction → 2, the order of the reverse one 1. (dotted curve).
The full drawn curves represent f in arbitrary units as a function of $\bar{n}$ from the figures 5b and 6b for green test stimulus.

figure 10:

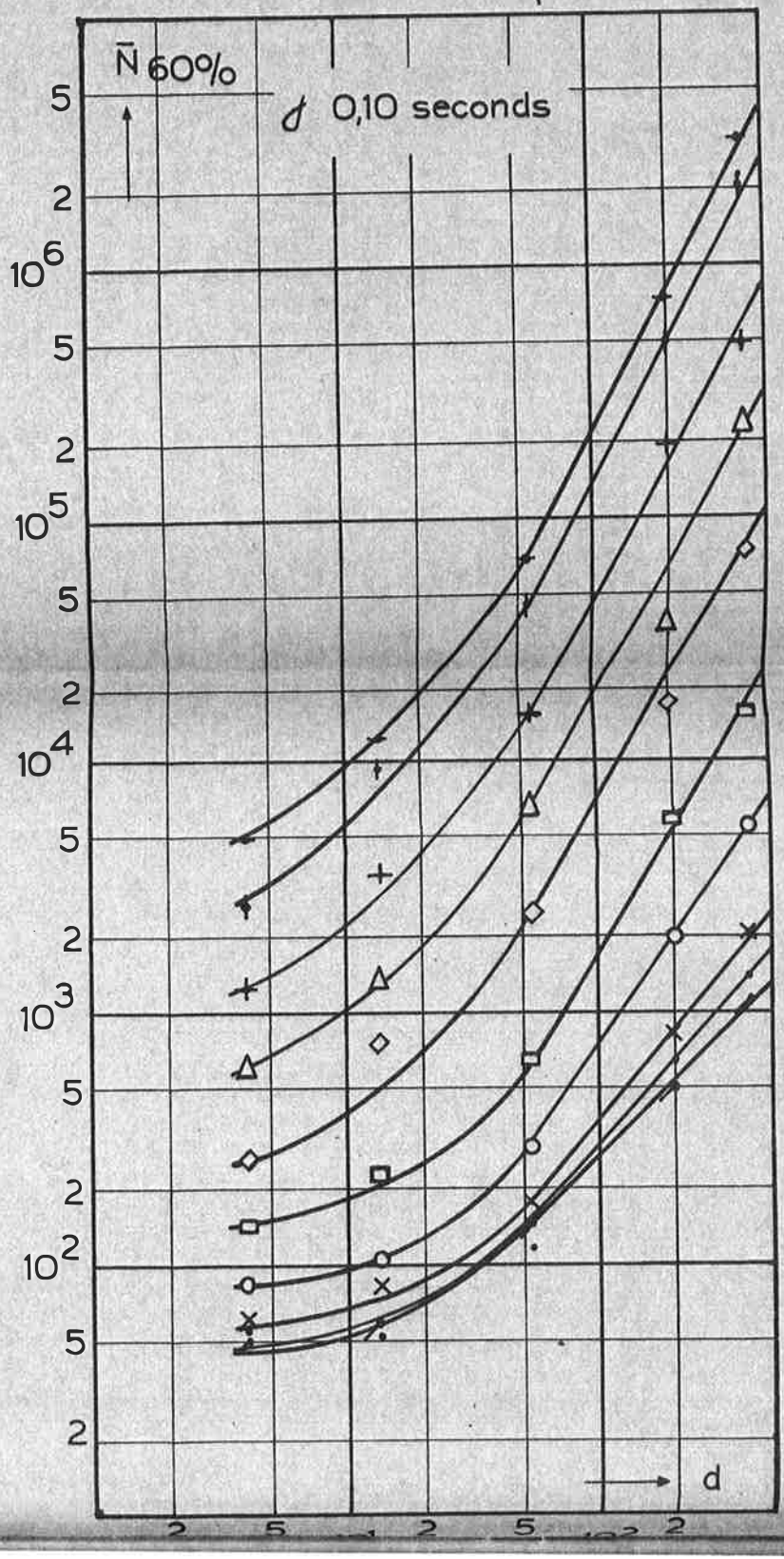
The values f/K^2 as a function of $\bar{n}$ deduced from contrast-threshold measurements 5,6) with the aid of de Vries' theory: $f \sqrt{\Delta N} = K \sqrt{2f\bar{n} + f \sqrt{\Delta N}}$, K = constant.
The value f from the figure 5b.

figure 11:

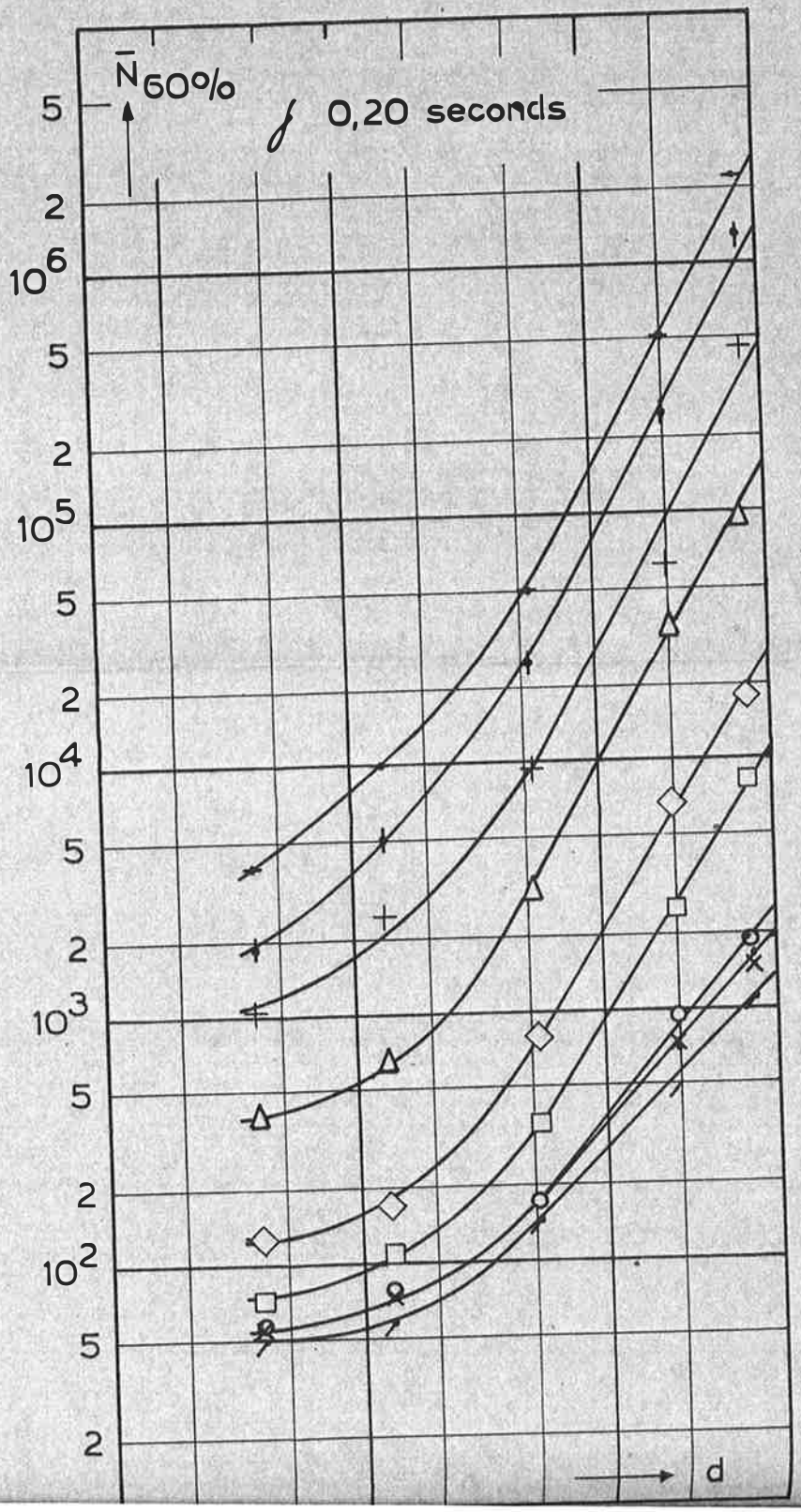
Similar to figure 10, f from figure 7b.

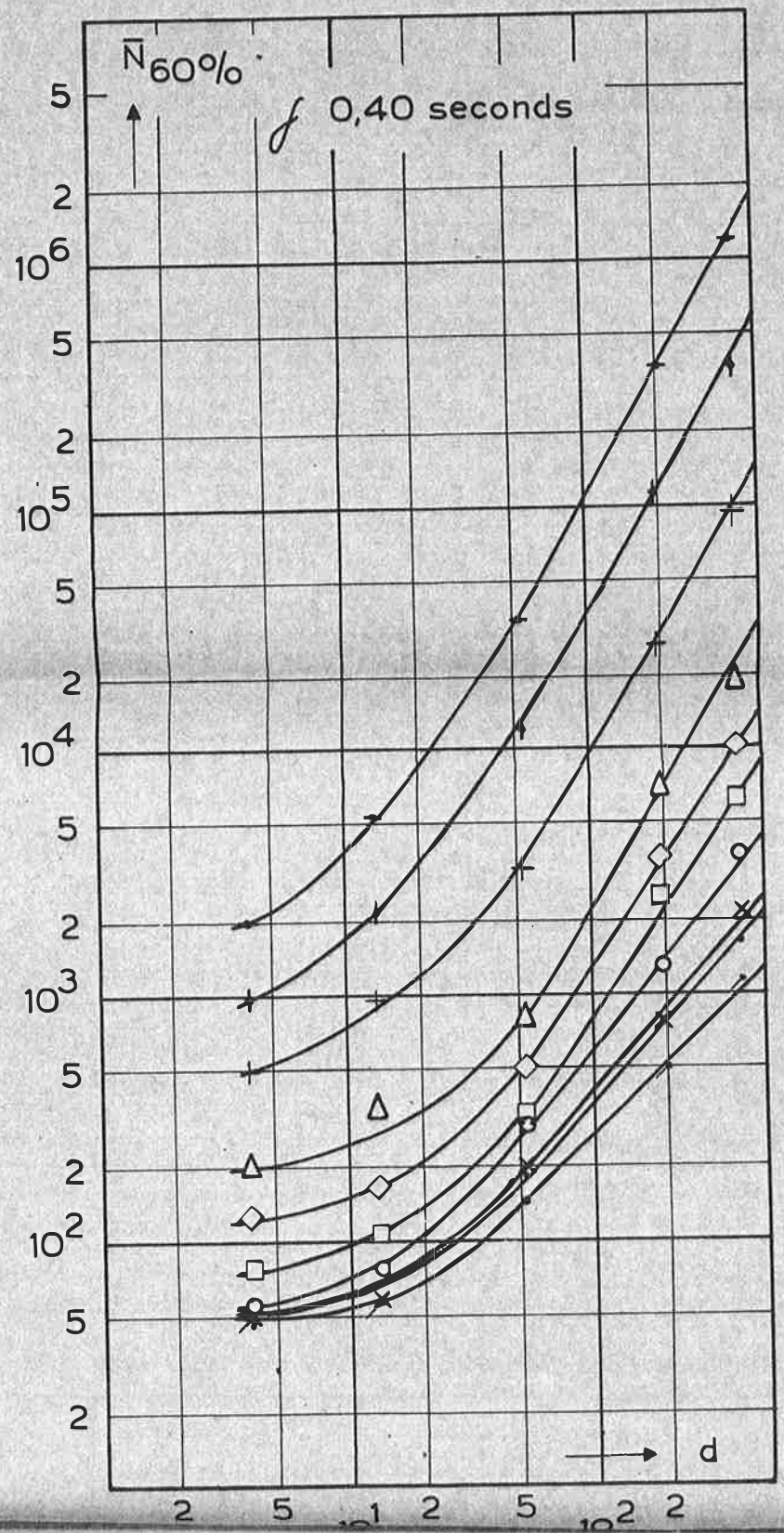

$\bar{N}_{60\%}$
0,05 seconds
$\bar{n}$
0 quanta
0,2
0,9
4
18
80
360
1600
7200
32000
10^6
10^5
10^4
10^3
10^2
λ adapting field 5250 Å
test stimulus 5250 Å
d
2
5
10^1
10^2

1a

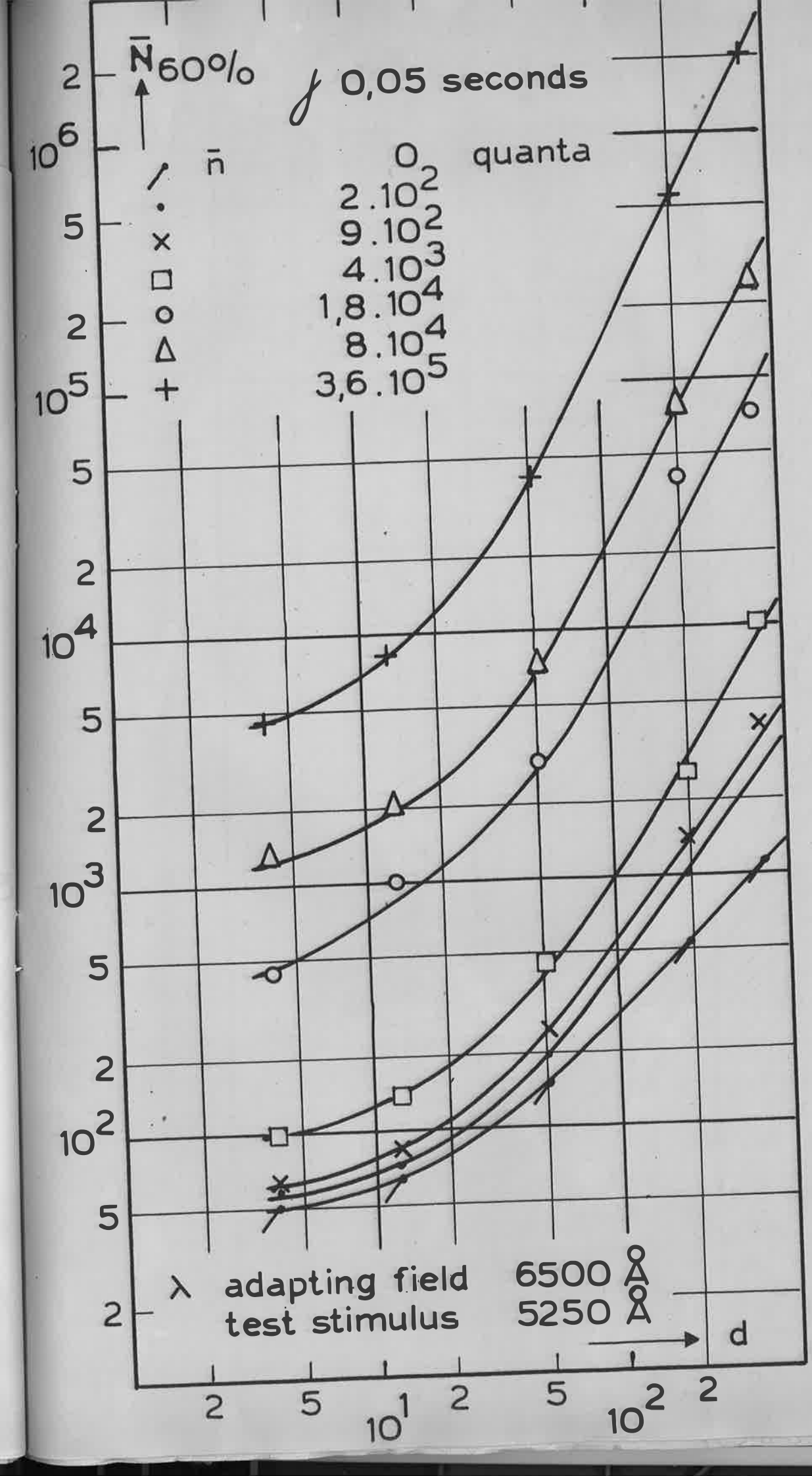


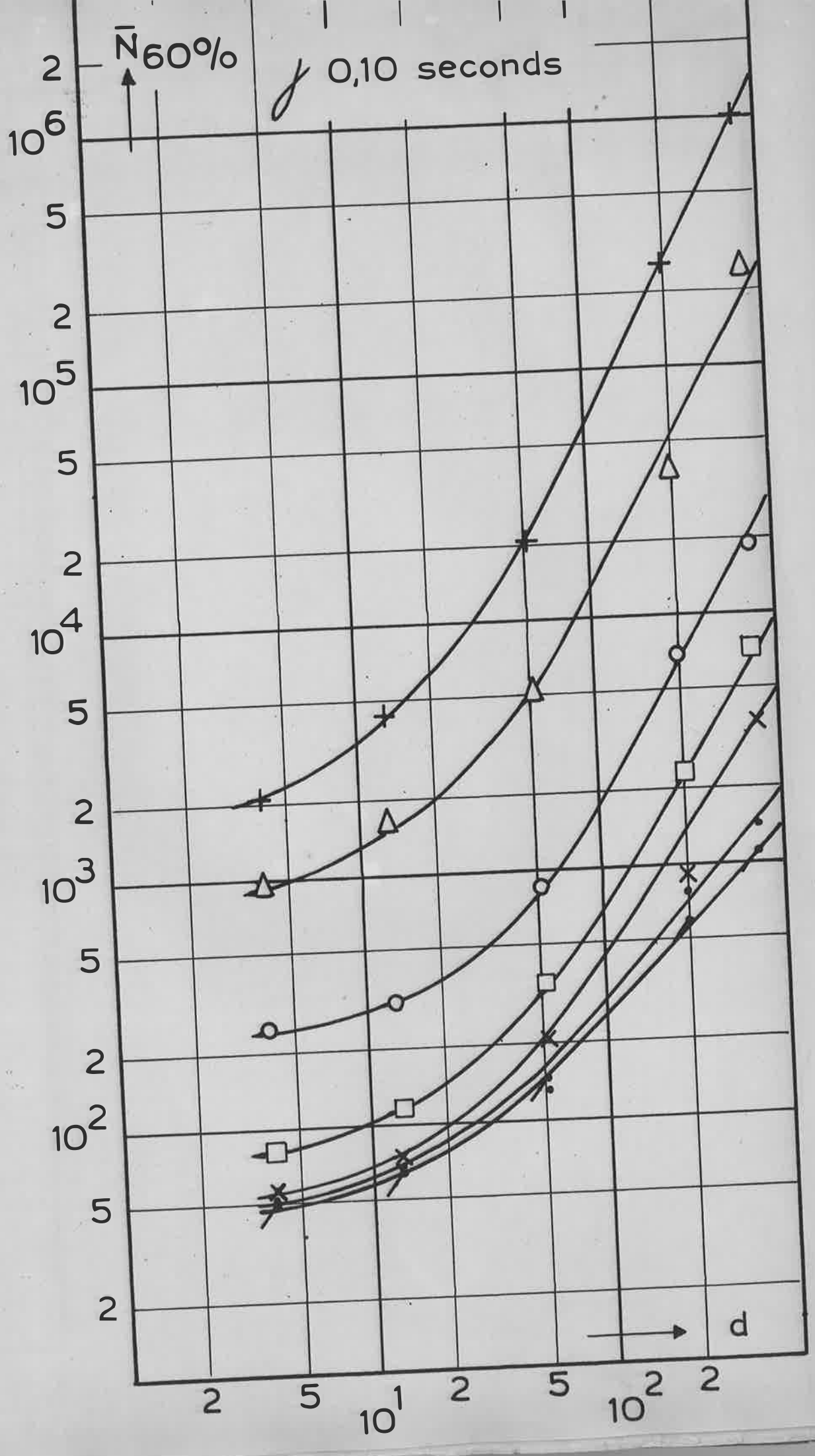
1b

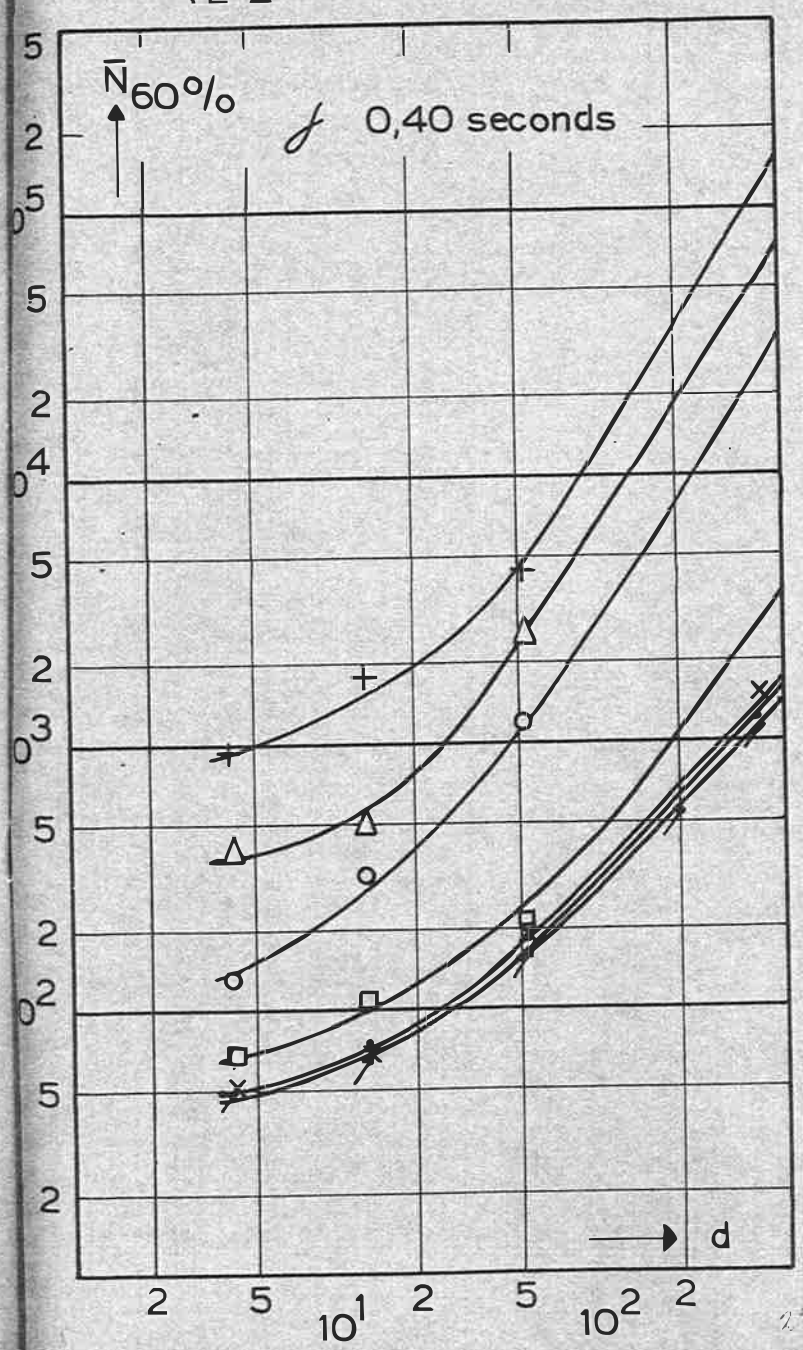

$\bar{N}_{60\%}$
$\int$ 0,20 seconds
5
2
10^6
5
2
10^5
5
2
10^4
5
2
10^3
5
2
10^2
5
2
d

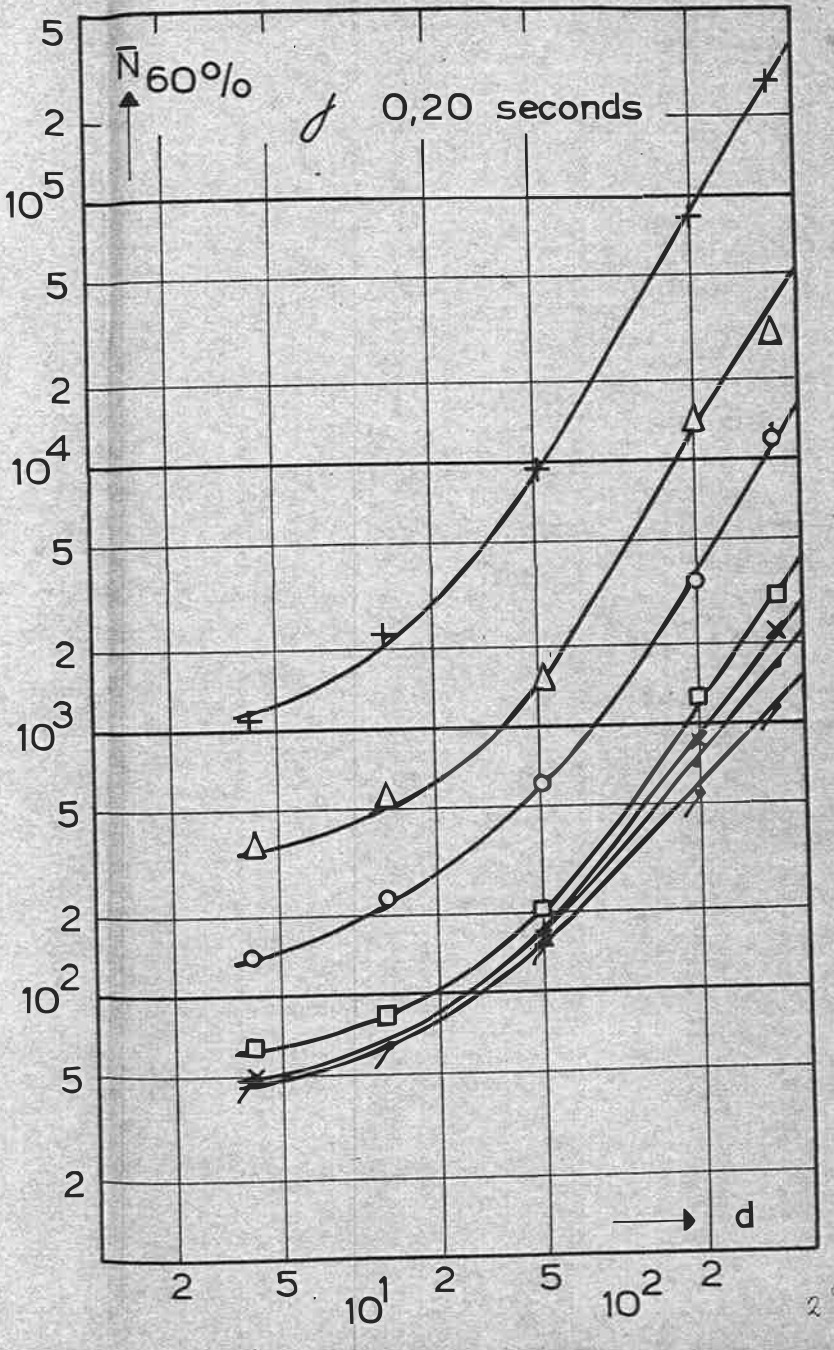

$\bar{N}_{60\%}$
f 0,40 seconds
5
2
10^6
5
2
10^5
5
2
10^4
5
2
10^3
5
2
10^2
5
2
d
2
5
2
5
2

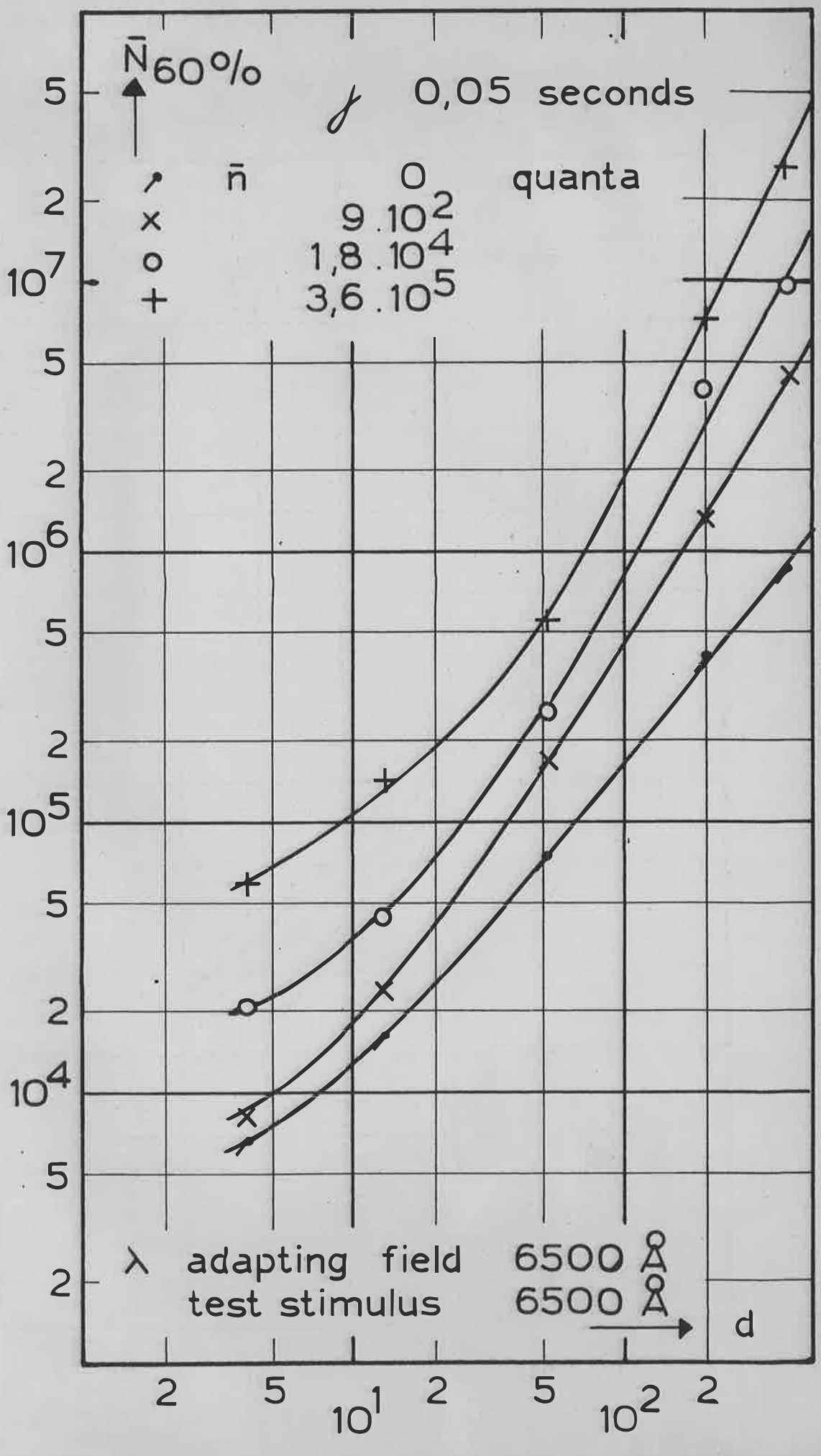
1d

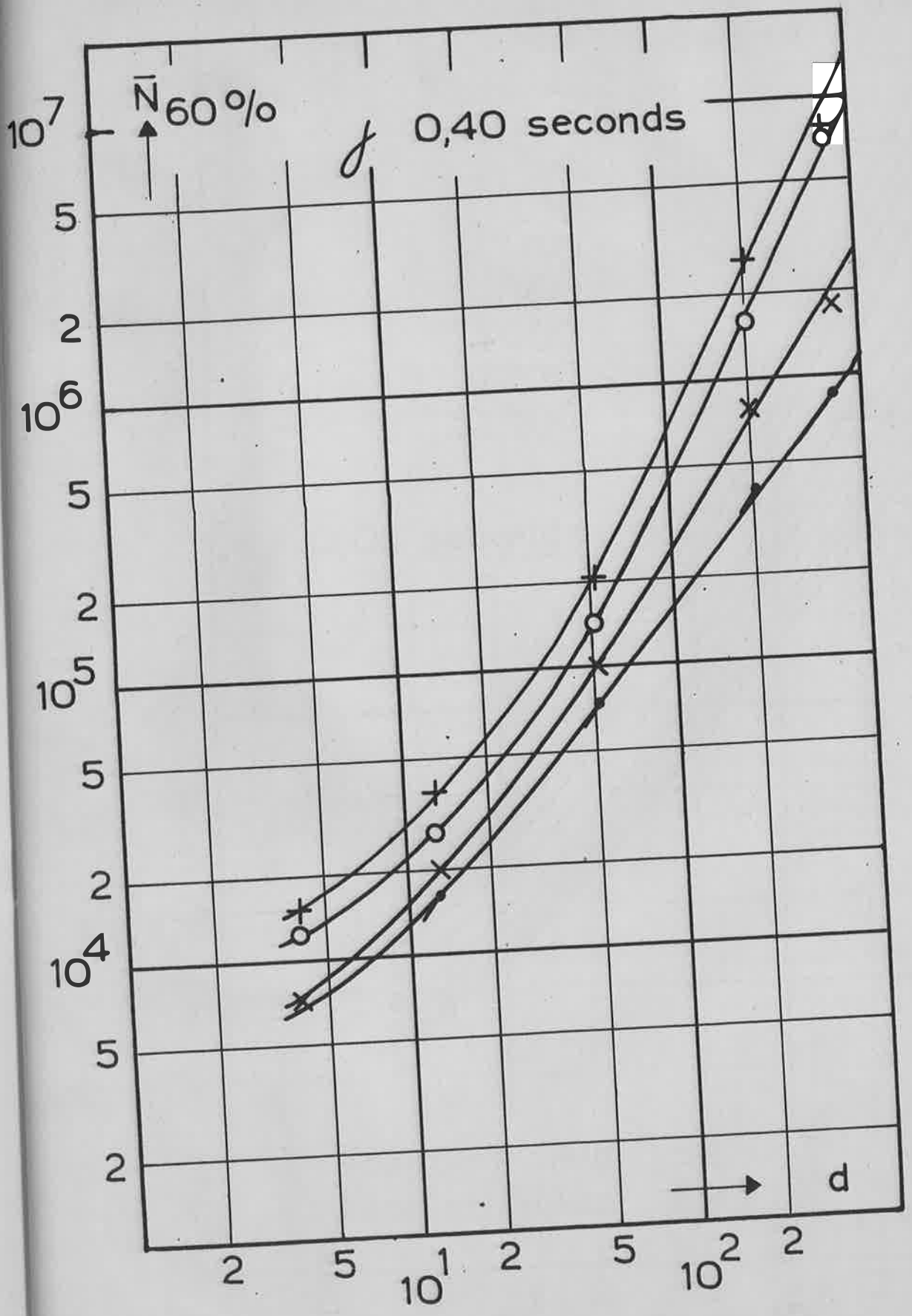

$\bar{N}_{60\%}$
0,05 seconds
$\bar{n}$
O_2 quanta
2.10^2
9.10^2
4.10^3
$1,8.10^4$
8.10^4
$3,6.10^5$
10^6
10^5
10^4
10^3
10^2
10^1
λ adapting field 6500 Å
test stimulus 5250 Å
d

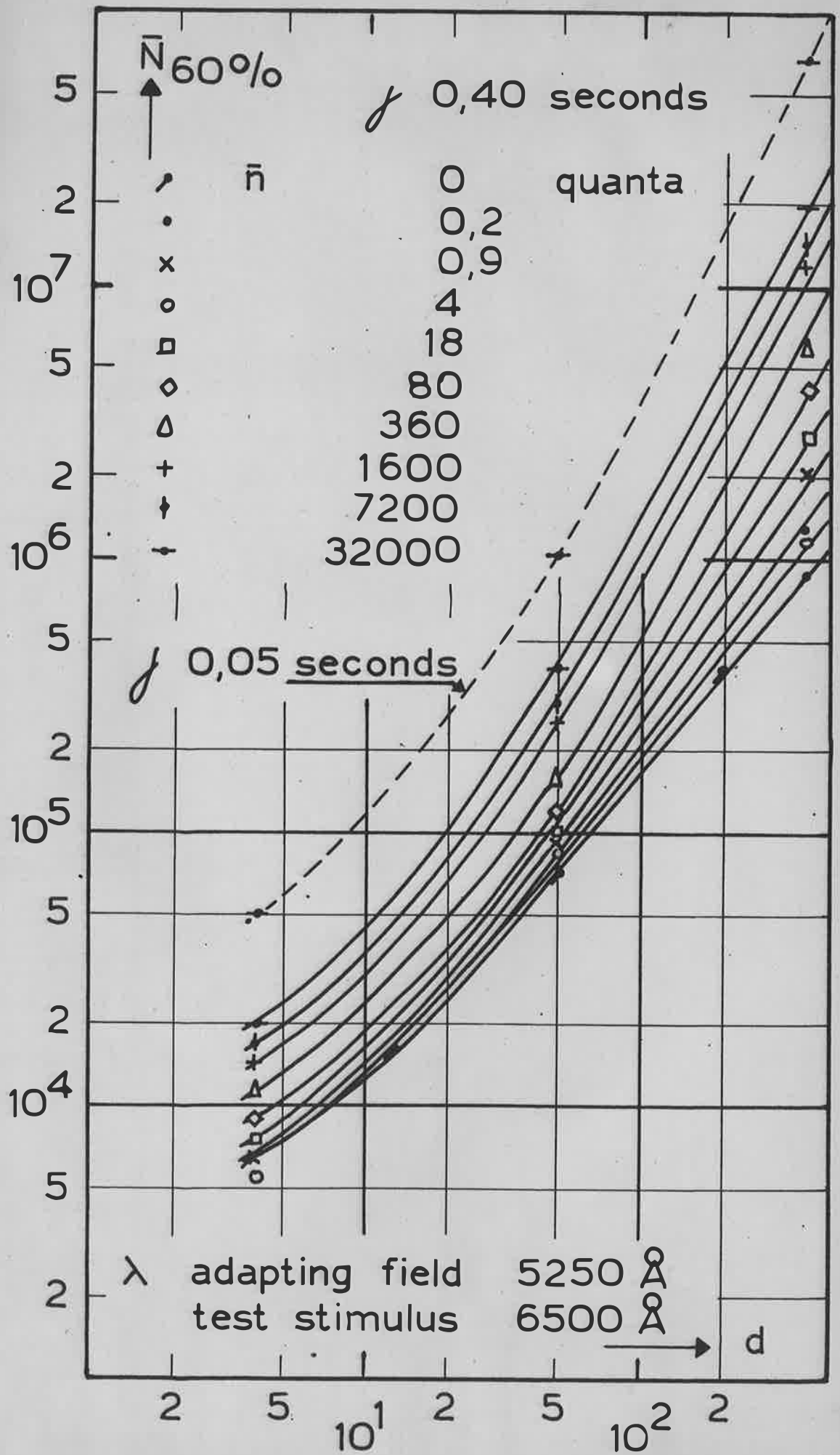

$\bar{N}_{60\%}$
0,10 seconds
2
10^6
5
2
10^5
5
2
10^4
5
2
10^3
5
2
10^2
5
2
2
5
10^1
2
5
10^2
2
d


$\bar{N}_{60\%}$
τ 0,40 seconds
d

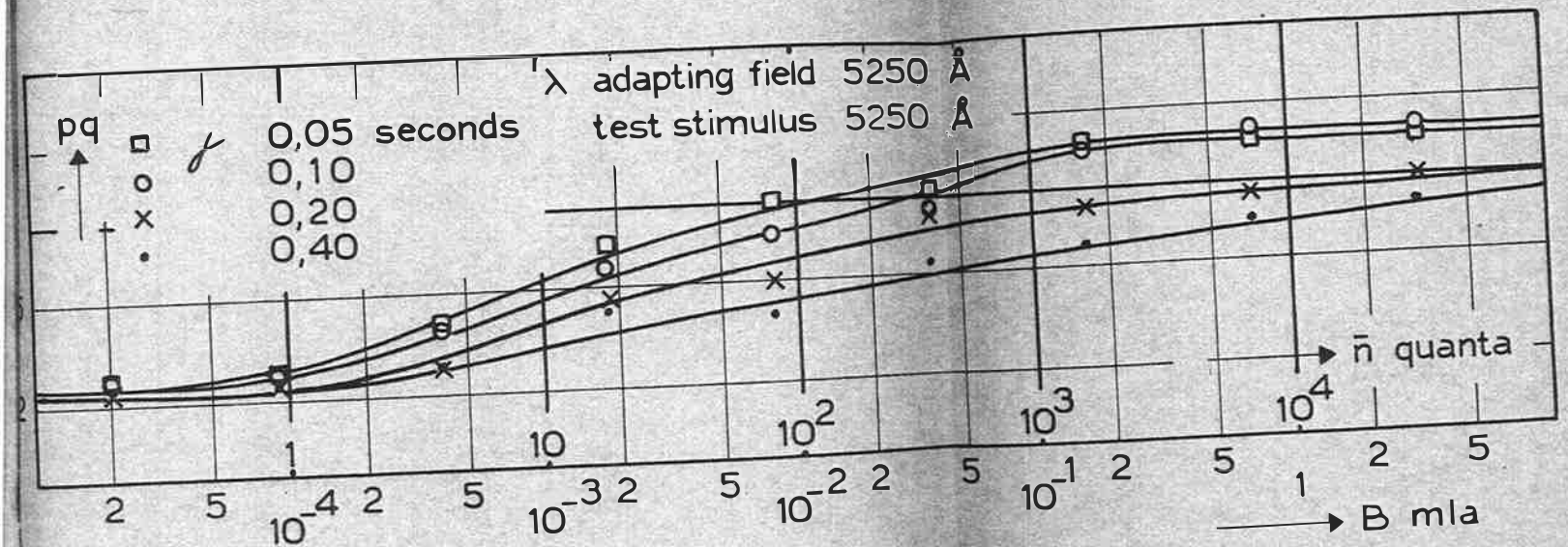

$\bar{N}_{60\%}$
τ 0,20 seconds
d


$\bar{N}_{60\%}$
τ 0,05 seconds
$\bar{n}$ 0 quanta
9.10^2
$1{,}8.10^4$
$3{,}6.10^5$
10^7
10^6
10^5
10^4
10^1
10^2
λ adapting field 6500 Å
test stimulus 6500 Å
d

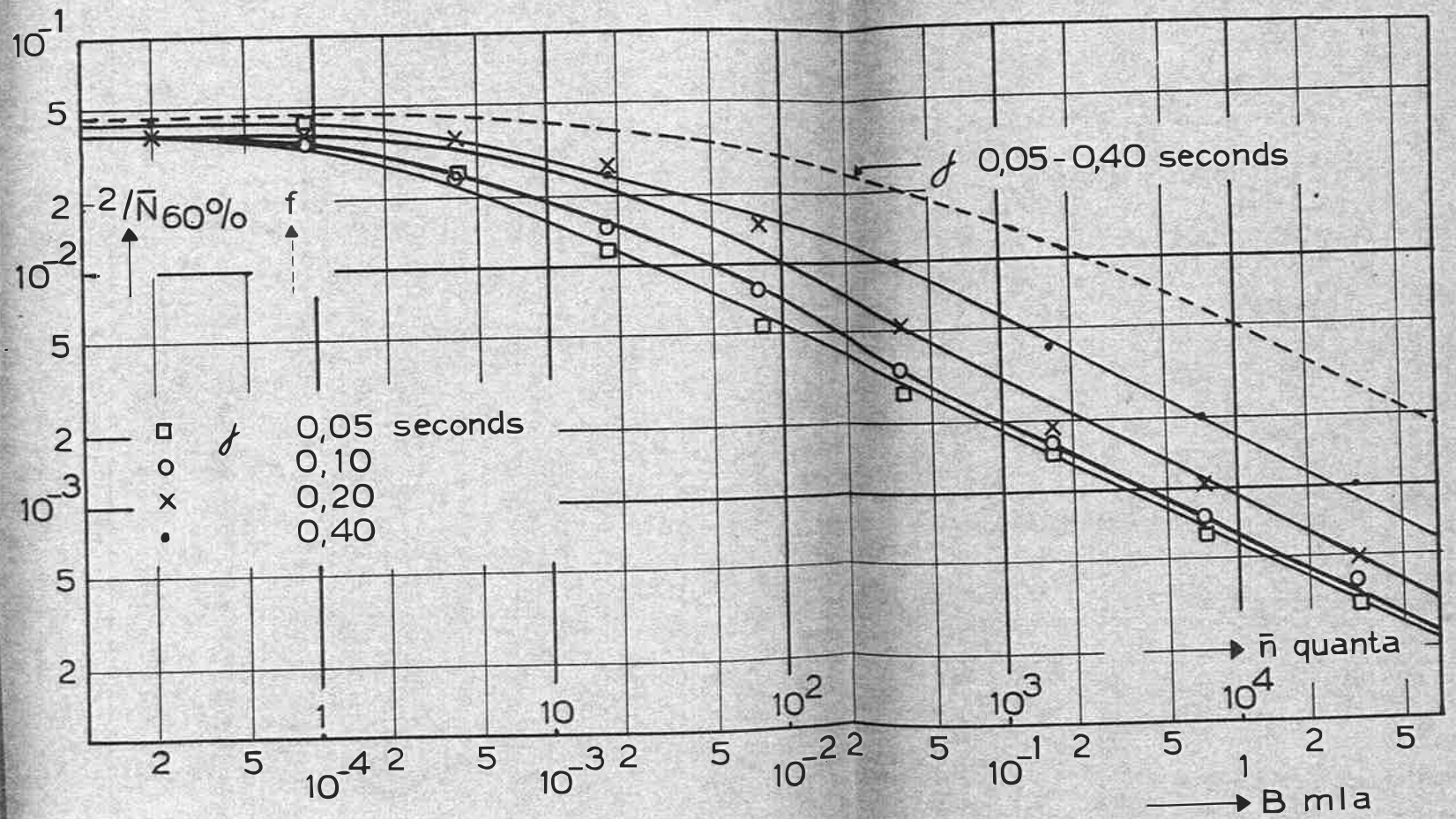

$\bar{N}$ 60 %
0,40 seconds
10^7
5
2
10^6
5
2
10^5
5
2
10^4
5
2
2
5
10^1
2
5
10^2
2
d

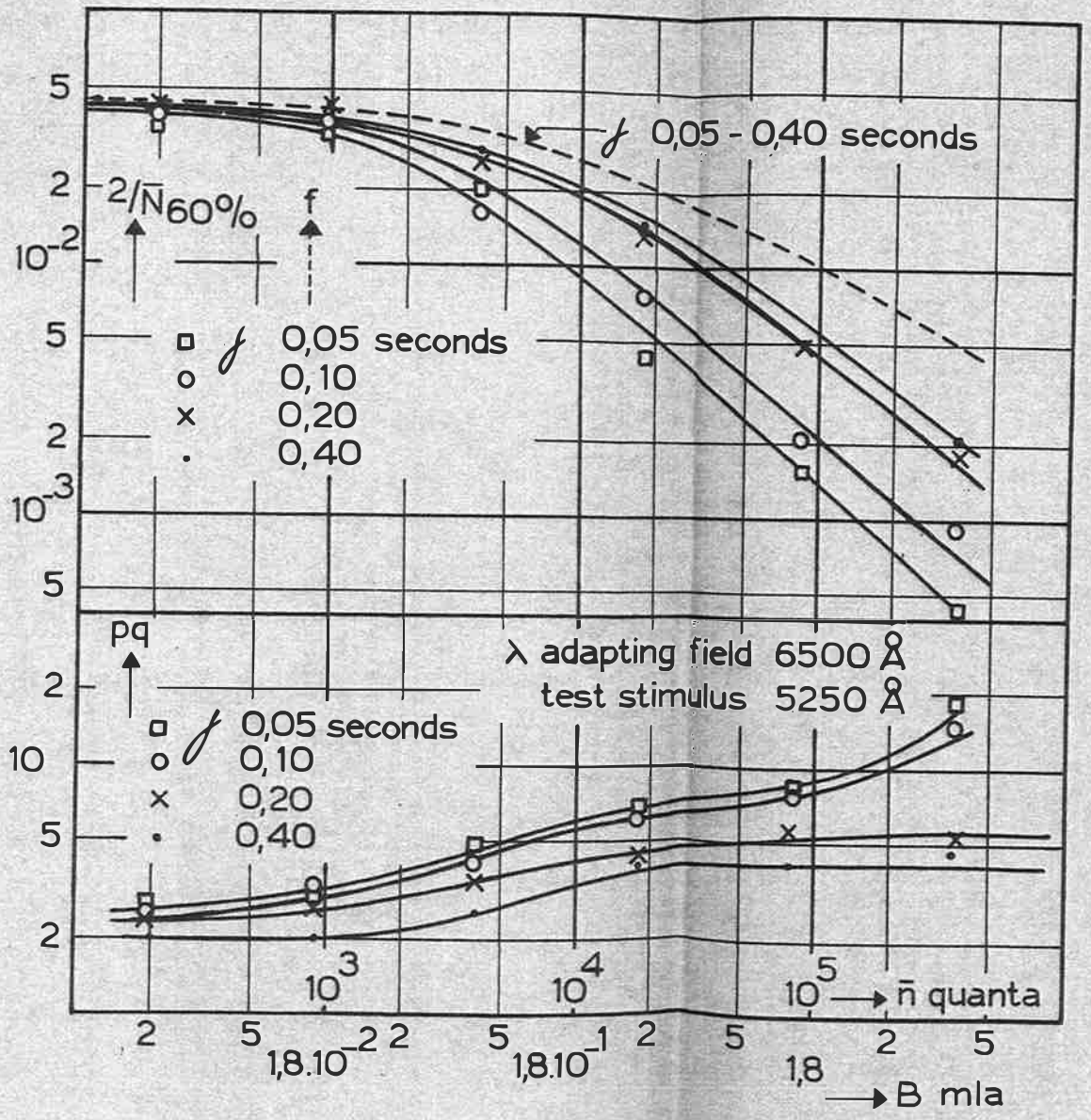


N̄ 60%
γ 0,40 seconds
n̄ 0 quanta
0,2
0,9
4
18
80
360
1600
7200
32000
γ 0,05 seconds
λ adapting field 5250 Å
test stimulus 6500 Å
d
5
2
10^7
5
2
10^6
5
2
10^5
5
2
10^4
5
2
2
5
10^1
2
5
10^2
2



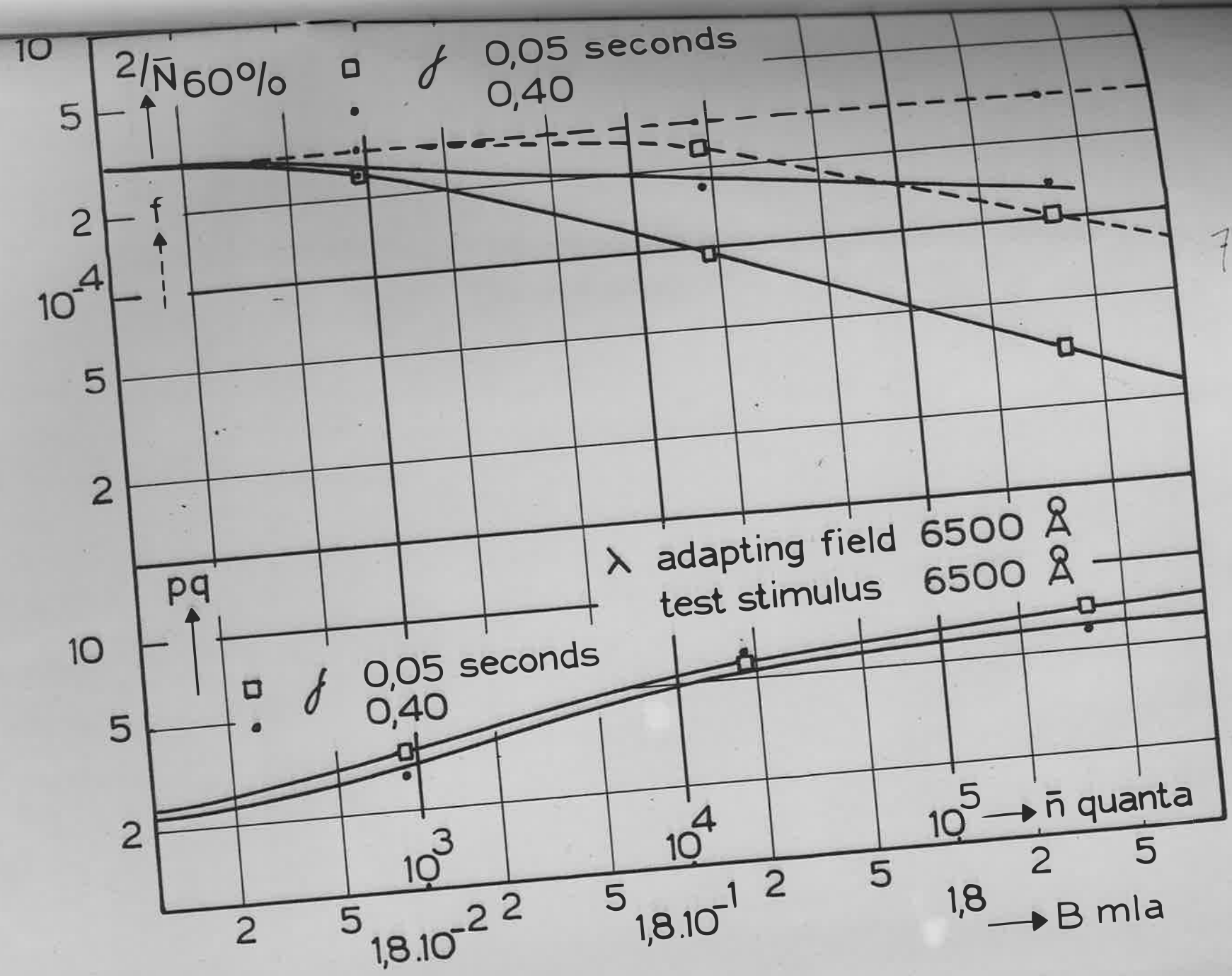
λ adapting field 5250 Å
test stimulus 5250 Å
pq
γ
0,05 seconds
0,10
0,20
0,40
n̄ quanta
B mla


10^{-1}
5
2
10^{-2}
5
2
10^{-3}
5
2
$2/\bar{N}_{60\%}$
f
□ 0,05 seconds
○ 0,10
× 0,20
• 0,40
0,05 - 0,40 seconds
$\bar{n}$ quanta
B mla
1
10
10^2
10^3
10^4
10^{-4}
10^{-3}
10^{-2}
10^{-1}
2
5


5
2
10^{-2}
5
2
10^{-3}
5
$2/\bar{N}_{60\%}$
f
0,05 - 0,40 seconds
0,05 seconds
0,10
0,20
0,40
pq
λ adapting field 6500 Å
test stimulus 5250 Å
0,05 seconds
0,10
0,20
0,40
10
5
2
10^3
10^4
10^5
$\bar{n}$ quanta
2
5
$1{,}8.10^{-2}$
2
5
$1{,}8.10^{-1}$
2
5
1,8
2
5
B mla

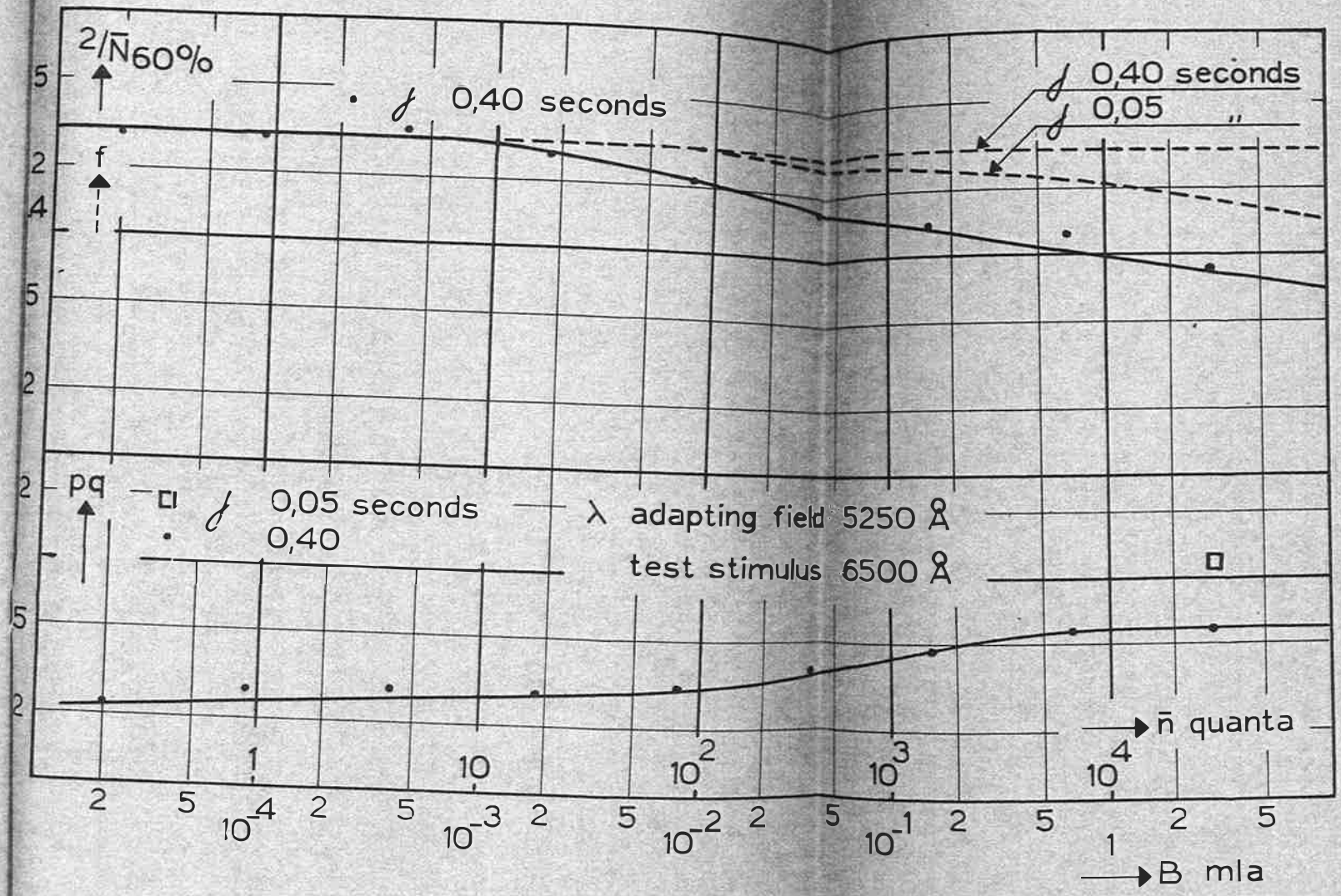
6b

6a


10
5
2
10-4
5
2
2/N̄60%
f
0,05 seconds
0,40
λ adapting field 6500 Å
test stimulus 6500 Å
pq
10
5
2
0,05 seconds
0,40
2
5
1,8.10-2
2
5
10³
2
5
1,8.10-1
10⁴
2
5
10⁵
n̄ quanta
1,8
B mla

7b

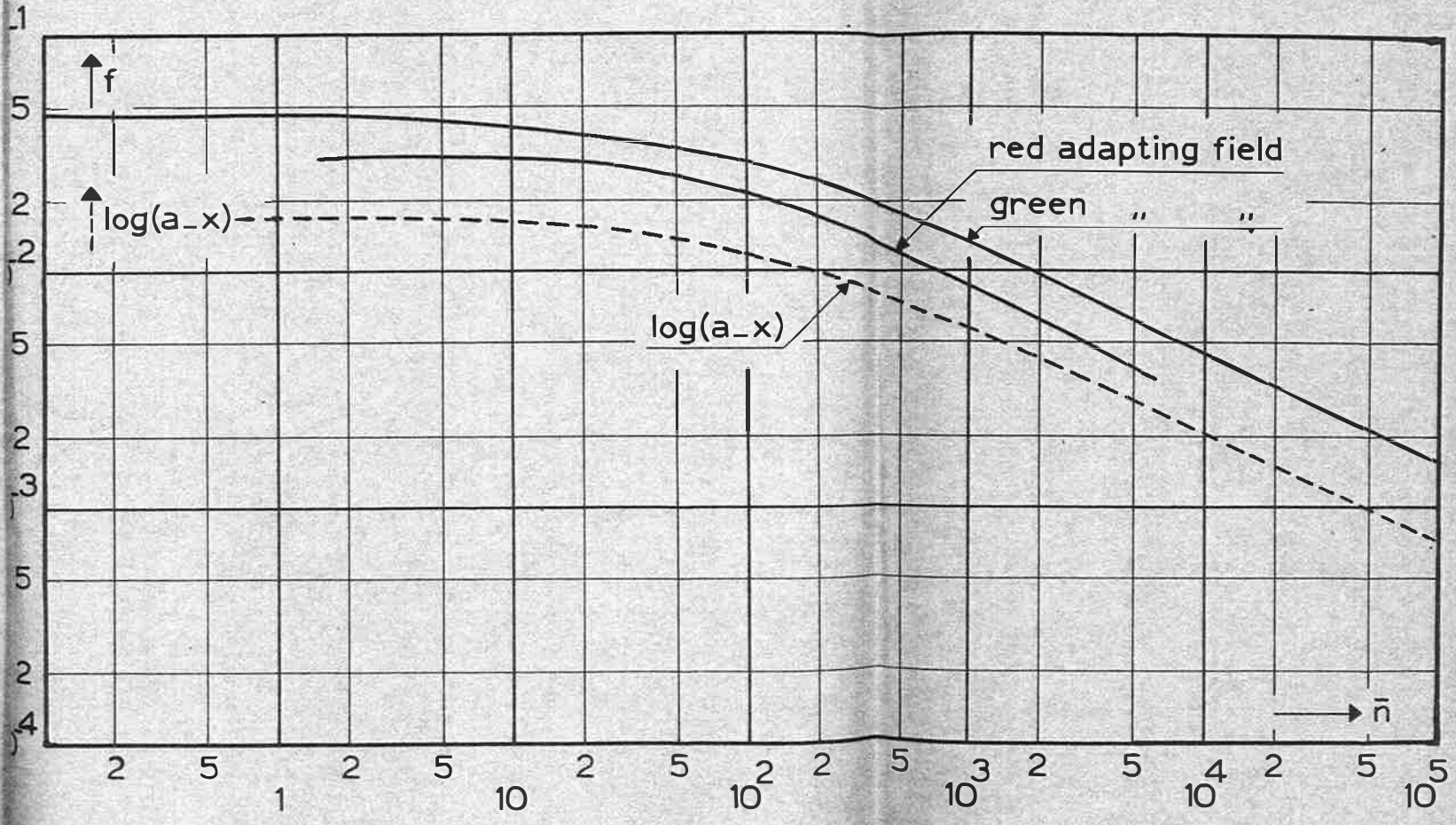
7a

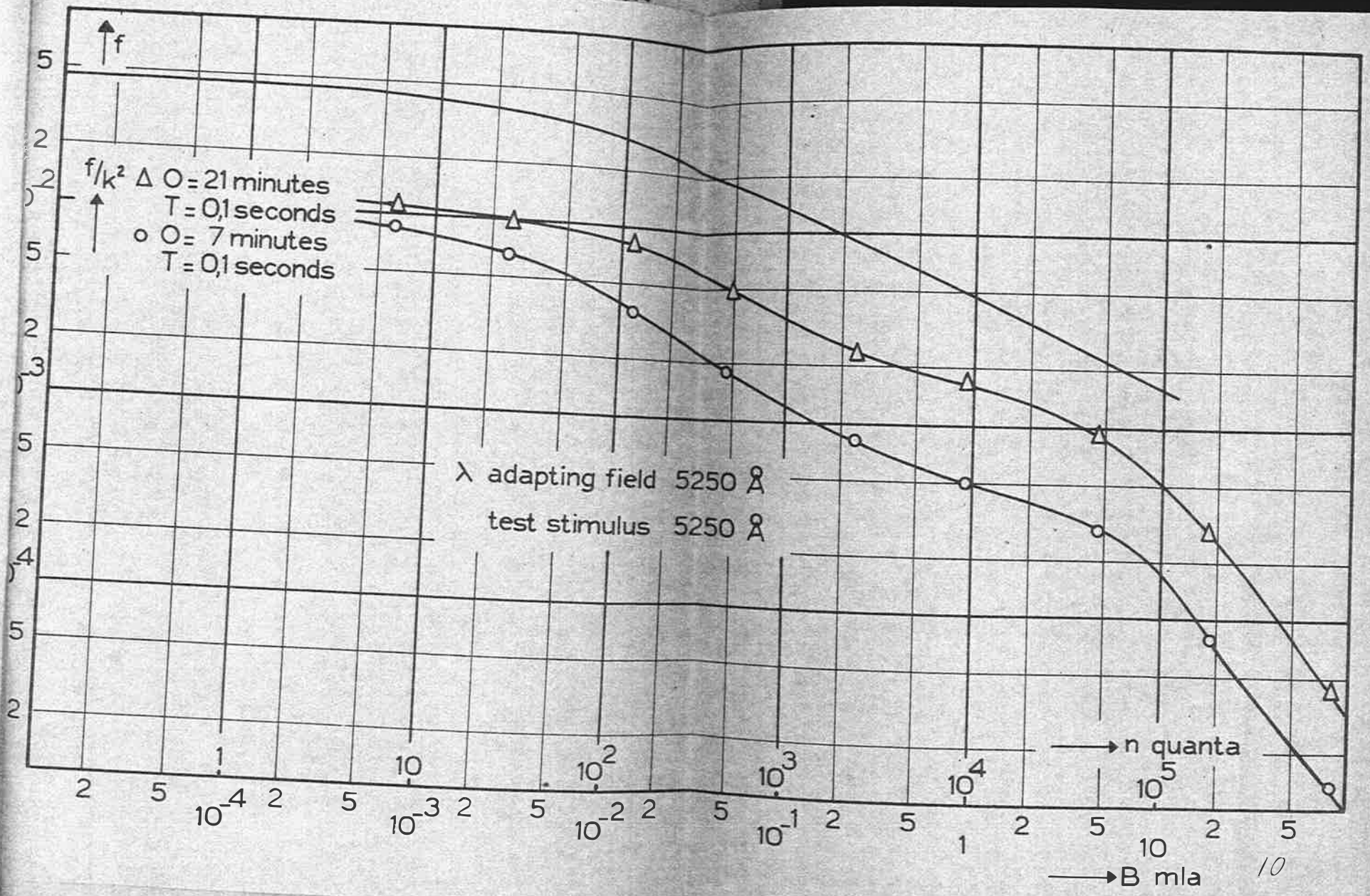


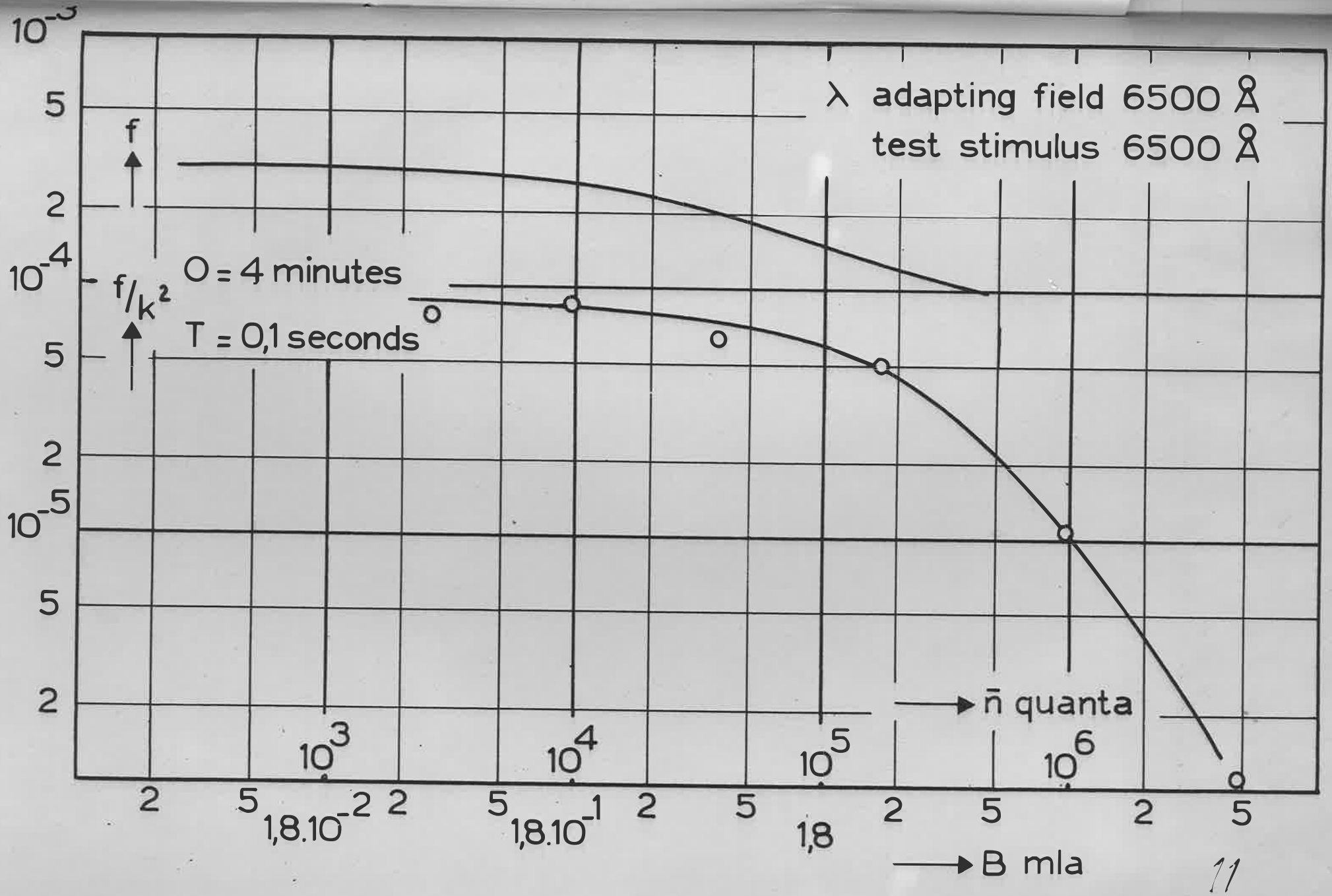
2/N̄60%
f
0,40 seconds
0,40 seconds
0,05 "
pq
0,05 seconds
0,40
λ adapting field 5250 Å
test stimulus 6500 Å
n̄ quanta
B mla

8b

8a


f
log(a_x)
red adapting field
green " "
log(a_x)
n̄
1
10
10²
10³
10⁴
10⁵


f
f/k² Δ O = 21 minutes
T = 0,1 seconds
o O = 7 minutes
T = 0,1 seconds
λ adapting field 5250 Å
test stimulus 5250 Å
n quanta
B mla
5
2
5
2
5
2
5
2
5
2
10⁻⁴
10⁻³
10⁻²
10⁻¹
1
10
10²
10³
10⁴
10⁵


λ adapting field 6500 Å
test stimulus 6500 Å
f
f/k²
O = 4 minutes
T = 0,1 seconds
10⁻³
5
2
10⁻⁴
5
2
10⁻⁵
5
2
10³
10⁴
10⁵
10⁶
2
5
1,8.10⁻²
2
5
1,8.10⁻¹
2
5
1,8
2
5
2
5
n̄ quanta
B mla