SPECIAL PROPERTIES OF MITOGENETIC RADIATION

The preceding chapter has revealed that the socalled mitogenetic radiation is a real radiation according to the strict physical definition of the word. It travels through space rectilinearly; it can be reflected (pp. 59 and 80); it can be absorbed (p. 59); it shows refraction and dispersion (p. 35).

The present chapter describes some peculiar properties of mitogenetic rays which are not common to all types of radiations.

A. INTERMITTENT IRRADIATION

Very early in the history of mitogenetic radiation, it was discovered that the effect could be intensified by irradiating intermittently instead of continuously. The customary method for this purpose is the insertion, between sender and detector, of a rotating disk which contains one or several openings or windows. The width of these, their number, and the rate of rotation of the disk allow one to vary the three items concerned in intermittent processes, i. e., the frequency of exposures, the duration of each, and the total time of actual irradiation.

The most striking result with intermittent irradiation is the much shorter total time of exposure necessary to bring about distinct mitogenetic effects. GURWITSCH (1932) determined the threshold value in mutual yeast irradiation by means of disks rotating at approximately 3000 revolutions per minute. The disks contained one or several windows of varying width. The width of the window is measured by the central angle (fig. 39). From this angle and from the number of revolutions, the duration of each interval and the frequency of interruption can be calculated. Table 31 gives the results obtained. It indicates that the minimal

the Threshold t	Mitogenetic effects	5; 1;1 50 10; 8 37	40; 51 22; 23; 27 50	-1; 2 42 1; 2 27; 28; 29; 26
posures upon on Method) mitogenetic effec	Total time of actual exposure in sec.	10 13 6.5 13	12.5 13 20	15 30 30
Detector (Bar s required for a	Total number of exposures	70 000 91 000 46 000	25 000 13 000 20 000	30 000 19 000 23 000 40 000
Value of the Detector Yeast as Sender and With continuous irradiation, 6-8 minutes exposure was	Frequency of exposures per sec.	800 800 400 ¹) 400 ¹)	400 100 100	ୟ ରୁ <u>ର</u> ୁ ନି
	Duration of individual exposure, in sec.	0.00014 0.00014 0.000281) 0.000281)	0.00100 0.00100	0.00050 0.00070 0.00070 0.00070
	The disk contained	windows of the angle 2.50	$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	$\begin{array}{cccccccccccccccccccccccccccccccccccc$

¹) The disks in these experiments were running only half speed.

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Influence of Frequency of Interruptions and of Duration of Individual Exposures upon the Threshold

Table 31

actual exposure must be more than 10 seconds, 12.5 to 13 seconds being sufficient. When the same experiment was tried with uninterrupted irradiation, it required 6 to 8 minutes to produce a distinct effect. The rhythmic interruption of radiation had decreased the threshold time to about 1/30th of the amount required with continuous exposure.

The frequency of interruption has some bearing upon the threshold value. When the frequency is between 800 and 100 per second, 13 seconds are sufficient for induction. However,



Figure 39. Rotating disk for intermittent radiation. at right: side view showing the position of the two agar blocks with the yeast sides facing each other, for intermittent muto-induction.

when it falls to 50 per second, 15 and 16 seconds of total exposure are usually insufficient, and 30 seconds are necessary to show a mitogenetic effect. This is to be expected, since it signifies an approach to continuous irradiation. ZOGLINA (quoted from GURWITSCH 1932, p. 256) repeated the same experiments with a half-disk rotating at 10 r. p.m. This meant uniform intervals of exposure and irradiation of 1/20th second each. The following percentages in increase of buds were obtained with a total exposure time of

50	seconds:	7	15	0	- 5	+ 4
30	,,	+28	+56	+64	+28	+36

The increase in efficiency of a photochemical reaction by intermittent irradiation has its analogy in the increase of photosynthesis of green plants by intermittent exposure. WARBURG (1919) measured the amount of CO_2 absorbed by an alga, CHLO-RELLA, during 15 minutes of actual exposure, either continuously or discontinuously. A rotating disk was used which was in principle like that of fig. 39, but the times for light and dark were made equal. The results are given in Table 32. An increase up to

	k Light Increase by in- termittent light %		0
ntinuously, it)	Wea CO ₈ absorbed in mm ⁸		45; 45 42; 43
: 30 minutes disco als of equal lengh	Light Increase by in- termittent light %	14 36 14 36 36 14	96 77 9
(exposure was either 15 minutes continuously or with alternating light and dark interva	Strong CO ₂ absorbed in mm ³	55 55 5 5 3 33	46; 49 70 85 94
	Total Number of exposures	60 60 600 600 700 600 80 80 80 80 80 80 80 80 80 80 80 80 8	1 2 400 24000 24000
	Duration of each individual exposure	15 minutes 15 seconds 15 minutes 1.5 seconds 15 minutes 0.15 seconds 0.015 ,	15 minutes 0.375 seconds 0.0375 ,, 0.00375 ,,
	Number of revolutions of disk per minute	5000 0 50 5 5 0 5000 0 50 5 5 0	2000 0 2000 0 2000 0

Table 32

CO2-assimilation by an alga, with continuous or intermittent exposure to light

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CHAPTER V

practically the double amount was observed with strong light, but no difference with weak intensities¹).

WARBURG considers two possible explanations: either assimilation continues for some time after darkening (e.g. through some short storage of energy); or, assimilation is more rapid at the first moments of exposure because more substances have accumulated ready for photosynthesis while later, their concentration is only comparatively small. His intention to investigate in more detail the latter, more probable case seems never to have materialised.

It is not at all certain that this observation is really analogous to the increase of the mitogenetic effect. WARBURG could double the amount of photosynthesis by distributing the same total radiant energy over twice as long a period. GURWITSCH, however, found a 30-fold increase in the threshold value while the greatest difference between light and dark periods was only 1:9. Besides, there seems to be no difference between strong and weak intensities. On the other hand, we cannot be certain that these threshold times are reliable measures of intensity of radiation (see p. 114).

The greatly intensified susceptibility of the living detectors by rhythmic discontinuity of radiation shows that by this method, radiations can be detected which otherwise produce no effect whatever when applied continuously. This holds true not only with very weak senders, but also with very strong sources which produce either no effects or depressions (see p. 115). The greater susceptibility also permits transmission over longer distances. While mutual induction of yeast has its limits at 3—4 cm. with continuous exposure, very good results can be obtained over 15 cm. with intermittent irradiation (GURWITSCH 1932, p. 260). These facts differ greatly from WARBURG's observations with algae, where weak intensities of radiation could not be induced to produce stronger photosynthesis by intermittent exposure (Table 32).

A *rhythmical* interruption of the radiation seems to be essential for mitogenetic induction. Parallel experiments were made with

¹) After the manuscript was finished, a paper by EMERSON and ARNOLD (1932) came to our notice. They were able to increase photosynthesis 400% by intermittent irradiation whereas WARBURG (1919) could only double it.

two disks rotating at the same speed, both with a total window width of 75°. In one disk, the 75° were distributed uniformly; the other disk contained openings, varying in size from 2.5° to 30°, in irregular distribution. Only with the regular spacing were positive results obtained (GURWITSCH 1932, p. 261). This, could hardly be accounted for by any of the two explanations of WARBURG'S.

B. INFLUENCE OF DIFFUSED DAYLIGHT

Many of the common "senders" of mitogenetic radiation affect other organisms only when in daylight. Diffused light is entirely sufficient. This has been observed for onion roots cut off from the onion bulb, and for the pulp of the onion base, as well as for the pulp of a number of plant tissues. In 1930, POTOZKY gave several series of experiments showing that the same holds true also for yeast. The experiments were made by the Baron technique, measuring the percentage increase of buds on yeast grown on agar blocks. All experiments were made by mutoinduction of yeast, i. e. by exposing yeast to yeast.

Sender: Detector: exposed in	Dark Dark daylight	Yeast Yeast dark	Dayligł Dark daylight	nt Yeast Yeast dark	Dark Dayligl daylight	Yeast it Yeast dark	Daylight Daylight daylight	; Yeast ; Yeast dark
Percentage	0.7	16.0	21		0	-4.5	35	9
Increase	5.4	3.3	22	8.6	3.2	-1.8	30 :	8
in Buds	5.5	4.3	20		3.1	3.6	30 -	9
	-11.0	2.2	23	3.9	1.0	1.8	25	1.8
	2.1		30		11.0	İ	24	
	1.8		30		9.4		29	6.3
	3.3						20	9
	2.3	<u>.</u>					22	7
Average	+1.4	+6.5	24.0	5.9	+4.6	-2.9	27.0	+0.2

Table 33. Influence of Daylight upon the Yeast as Sender and as
 Detector of Mitogenetic Effects Obtained by Muto-Induction

Three factors were varied: the sender yeast, the detector yeast, and the light during exposure. Yeast grown in the dark had no effect upon yeast, whether grown in the light or the dark, and whether tested in light or dark. Yeast grown in daylight showed distinct radiation and mitogenetic effect upon the detector yeast, regardless of whether this had been grown in light or dark, but only when the exposure was made in daylight. This accounts probably for a number of negative results by some experimentors.

Yeast grown in the dark regained the property of radiation after remaining in daylight for about two hours.

FRANK and RODIONOW have shown, by means of a GEIGER counter, that light affects greatly radiation from some chemical oxidations, as e. g. $K_2Cr_2O_7 + FeSO_4$ (p. 34).

C. SECONDARY RADIATION

The original experiments by GURWITSCH had shown that only the meristem, i. e. the growing tissue near the tips of onion roots radiated while the older parts of the root, where the cells had ceased to multiply, were inactive. Even the root tips radiated only when connected with the bulb, or at least with part of it. They lost their radiation completely when severed from the bulb.

In search for an explanation, GURWITSCH discovered that a root, after being cut from the bulb, will emit a radiation when it is exposed to ultraviolet light. This "secondary" radiation of the root ceases when the "primary" radiation does. It seemed quite impossible that the original rays as such could have been transmitted through the root by reflection without having been absorbed completely. A chemical effect could hardly be passed along so rapidly. There was only one alternative left: the radiation from the outside induced the exposed cells to produce some radiation of their own; these "secondary rays" again induced the neighboring cells to radiate, and so the effect was passed along the root without losing in intensity.

This explanation was proved by many variations of the original experiment. For some time, it was believed to be a phenomenon characteristic of the living cells only, until in 1932, A. and L. GURWITSCH found it to occur also in nucleic acid solutions, and WOLFF and RAS (1933, 1934) proved it to be primarily a photochemical phenomenon.

Many illuminating details have been worked out by POTOZKY and ZOGLINA (1928), ALEXANDER, ANNA and LYDIA GURWITSCH and others. Secondary radiation was observed in muscle, in liver, in nerves, in suspensions of yeast, of bacteria, of protozoa. In

all these cases, secondary radiation seemed to be glycolytic. The fact that livers from starving animals which are free from glycogen, did not radiate, supports this view. However, this cannot be generalized because the secondary radiation from nucleic acid is *not* glycolytic.

By this mechanism, primary radiations can be spread and transmitted to distant parts of the plant or animal body. It will be shown later that the tips of onion roots are only secondary senders; the primary rays are produced in the onion bulb, by oxidation.

This spreading of the mitogenetic effect can be plainly shown with densely grown agar surface cultures of yeast. GURWITSCH irradiated such a culture through a slit 0.1 mm. wide. When the percentage of buds was counted, there was a distinct increase not only in the irradiated region, but as far as 10 mm. distant. The increase in buds was 65% at the irradiated zone, and at a distance of

1 mm. 2 mm. 3 mm. 4 mm. 5 mm. 6 mm. 7 mm. 8 mm. 9 mm. 10 mm., it was 100% 87% 86% 79% 55% 80% 80% 43% 33% 25% respectively Experiments with larger irradiated surfaces gave the same amount of spreading, 9-12 mm. from the border of the irradiated area.

The ability of roots to produce and conduct secondary radiation is limited to a short time after the severing of the root from the bulb; POTOZKY and ZOGLINA (1928) found a positive effect after 30 minutes, but not after 40-45 minutes.

The same authors could also show that the production of secondary radiation exhausted the plant rapidly. Freshly-cut roots which gave strong secondary effects during the first 5 minutes of irradiation showed no reaction after 10 more minutes of exposure to monochromatic light of 2020 Å.

Another experiment with starving yeast cells may help to throw some light on this phenomenon. Yeast cells radiate immediately after being washed, but not 30 minutes later. Even then, the organisms will still produce secondary radiation under the influence of an arc light spectrum. This exhausts the yeast so much, that one hour later, it has produced 41% less buds than the unirradiated control. Exhaustion has also been demonstrated with chemical solutions (see p. 44).

A very recent illustration for such exhaustion has been given by LATMANISOWA (1932) on the secondary radiation from nerves

after mitogenetic irradiation. The sciatic nerve of a frog was irradiated by a yeast culture. Another yeast block, serving as detector, was placed near the irradiated part of the nerve so that it was exposed only to secondary radiation from the nerve, but not to primary radiation from the yeast. This block was changed every 5 minutes. Fig. 40A shows that the induction effect of secondary rays is very strong at first, but decreases after 5 minutes.

Figure 40. Secondary radiation from a nerve exposed to continuous yeast irradiation. A: the first 40 minutes, showing exhaustion of the nerve; B: a nerve, exhausted after 35 minutes, is given 10 minutes rest after which irradiation is continued.



and after approximately 30 minutes, it has disappeared, and does not appear any more upon continued irradiation.

If, however, the nerve is given a "rest" for 10 minutes, by removal of the source of irradiation, it will recover sufficiently to react again upon renewed irradiation (fig. 40 B). But the nerve is still "tired" and will become much more readily exhausted than the first. This phenomenon, too, is not characteristic of nerves only. It can be duplicated with cell-free solutions (p. 43).

The observation that secondary radiation could be passed on over considerable distances, suggested measuring the rate of travel. After some preliminary experiments by ALEXANDER GURWITSCH, ANNA GURWITSCH (1931) made some accurate measurements with onion roots, by means of a rotating disk (fig. 41). This had two windows, one nearer the center through which the primary rays (from a yeast culture) fell upon the older part of the root, and another towards the periphery of the disk through which the radiation from the meristem of the root fell. upon the detector. These two slits were so arranged on the rotating disk that after the primary rays had fallen upon the root, the disk had to be turned through 50° before the secondary rays from the meristem could fall upon the detector. This central angle was varied from 20° to 85°. With a definite speed of rotation of 3000 r.p.m., only the angles between 25° and 50° gave positive

results. This signifies that a certain time (0.0022 seconds) must pass before primary radiation falling upon one part of the root, is conducted to another part and is emitted there. These values refer to a condition over 2.5 cm. Then, the distance was increased to 5 cm. The central angle for positive effects was hereby increased to between 40° and 70°, which means an average increase of 15°. This corresponds, at 3000 r.p.m., to 0.00083 seconds, and this is



Figure 41.

Rotating disk for measuring the rate of travel of secondary radiation in onion roots. At right, side view showing position of primary sender S, onion root, and detector D.

the time required for the secondary radiation to pass the additional 2.5 cm. The rate of conduction is therefore about 30 meters per second.

Allowing the same time for transmission through the other 2.5 cm. of root, the total time required for transmission through 5 cm. of root is 0.00166 seconds. The total time corresponding to the average angle of 55° is 0.00306 seconds. The difference, 0.00140 seconds, was required for processes other than conduction, such as local reactions at the points of absorption and emission.

Recently, LATMANISOWA (1932) has measured the rate of conduction of secondary radiation in the sciatic nerve of the frog. The method was exactly the same, except that the 2200 Å area of the copper arc was used as primary source. This was sufficiently intense to permit the reduction of the window for primary radiation to 3° and that for secondary radiation to 1° . The accuracy of the method was thus greatly increased, and the rate of conduction in the nerve was found to be 30 ± 3 meters per second. This is in good agreement with physiological measurements on the rate of conduction of nerve impulses.

In the experiments with secondary radiation of onion roots, radiation was observed from the same side of the root which had been exposed to primary radiation. Further experiments showed

that the radiation effect was transferred longitudinally with great ease, but that no conduction occurred transversely across the root to the opposite side. In the nerve, however, strong radiation has been obtained from the unexposed side (LATMANISOWA 1932).

An important phenomenon for the explanation of mitogenetic effects is the observation (GURWITSCH 1932, p. 300) that radiating cells or tissues lose this power rather readily when they are themselves exposed to mitogenetic rays. Even young, actively radiating cultures lose their power when exposed to their own wave lengths. Four yeast agar blocks were placed so as to irradiate one another. The first mutual induction was plainly noticeable. After 15 minutes, they were separated and tested as senders; one was tested at once, the others after 15 and 30 minutes. None produced an increase in budding, as the following data show:

Mutual induction during 15 minutes	37%	increase	over	control
After 15 minutes muto-induction, effect upon				
new detector	2%	"	,,	,,
After 15 minutes muto-induction and 15 mi-				
nutes recovery	0%	,,	,,	,,
After 15 minutes muto-induction and 30 mi-				
nutes recovery	1.8%	,)	"	,,

Perhaps 30 minutes is too short a time for recovery of yeast, the generation time of which must have been at least one hour under the condition of the experiment.

This phenomenon itself can be at least partially explained by the experiences with secondary radiation (see p. 45).

Practically all these facts had been discovered, before it was found that in certain cell-free solutions, the same effect can be obtained (see p. 44). This does not alter the explanations materially, however. It only means that secondary radiation need not be connected with life processes. It is brought about by some unknown influence of ultraviolet rays which induce certain chemical reactions in cells or complex organic substances.

In their latest publication (1934a), WOLFF and RAS point out that mitogenetic rays become polarized by reflection like common light does, and that apparently, polarized mitogenetic rays have an enormously greater biological effect. When mitogenetic rays fall upon any cell, it seems highly probable that at

Protoplasma - Monographien IX: Rahn

least part of this radiation will be reflected from the cell walls, and thus will become polarized. It is not possible, at the present moment, to foresee all the consequences of such polarisation.

D. INTENSITY OF THE MITOGENETIC EFFECT

It has already been stated repeatedly that the intensity of the effect is not proportional to the intensity of the radiation. One very simple reason for this is the usual method of recording the results. The "induction effect" as the increase in the exposed yeast over that of the control, expressed in percentages of the latter cannot possibly be used as quantitative measure, as explained on p. 79.

The error of this method of recording results becomes most evident when applied to physical measurements. If the number of impacts induced by biological radiations is expressed in percentage of the stray radiations of the surroundings, it is utterly meaningless from a quantitative viewpoint because this stray radiation (the background radiation) can be greatly altered by shielding the instrument with iron or lead. This does not affect the intensity of the biological radiation at all. The "mitogenetic effect" as used especially by the Russian investigators has no quantitative value whatever. It is not surprising that it was never possible to use it for measurements of intensities.

The customary way of comparing intensities is to compare the minimal time of exposure (threshold time) required to give definite mitogenetic effects. This method has been used repeatedly by the Russian workers, and recently also by WOLFF and RAS. Examples may be found in Table 12 p. 44, Table 46 p. 145, and Table 49 p. 157. However, there are physical reasons to warn against quantitative conclusions from threshold times. It has been pointed out above (p. 24) that, with photographic plates, the reciprocity law (double intensity means half as long exposure) does not hold with very low intensities.

All previous measurements of intensities have become practically meaningless since WOLFF and RAS (1934a) showed that mitogenetic rays may easily become polarized, and that polarized rays have an enormously much stronger biological effect than the ordinary radiations of this type.

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E. RETARDATION THROUGH RADIATION

It seems quite probable that an overdose of radiation might produce the opposite effect of mitogenesis, and prevent or retard mitosis. GURWITSCH called this phenomenon mitogenetic depression which, really, is a self-contradictory term; it should be "depressed mitogenesis". Observations of this kind have been recorded rather frequently, but the circumstance that different detectors sometimes give opposite results, warns against hasty conclusions.

As early as 1928, SUSSMANOWITSON irradiated onion roots biologically for 12 hours and longer, together with control roots exposed only during the last 2.5 to 3 hours. She observed a decrease of mitoses in the exposed side of the root as compared with the opposite, shaded one. This was interpreted as "exhaustion" by too much radiation. Strong physical light produced the same depression in a few minutes.

It must be remembered, however, that with roots as detectors, we have no real controls; a difference between the two sides of the root may mean stimulation on one side, or retardation on the other side, or both. In this case of over-exposure, there may have been retardation through over-exposure, or it may mean no effect through over-exposure, and stimulation (through secondary radiation) on the shaded side.

We must therefore turn to other detectors which permit absolute controls, i. e., to unicellular detectors. The yeast bud method appears to be the one by which "depression" is observed most easily. But it is just these retardations by the yeast bud method which are frequently contradicted, in the same experiments, by parallel measurements of the actual cell increase. Table 34 shows SALKIND's experiments (1933) with rat blood radiation. With exposures of 2.5 minutes and longer, the percentage of buds showed a decrease against the controls, the actual number of cells, however, is larger than that of the controls. This can only mean that the yeast bud technique fails to indicate the true growth rate (see p. 69).

Real retardation by biological radiation can be measured only by decrease in the growth rate. The measurement of the actual number of cells permits of only one interpretation; a smaller increase than in the control can only signify a retardation

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Length of			Induction Effect obtained						
Exposure				by yeast buds	by yeast cells				
7 s	econds			3; 3					
15	,,			23; 41; 30	1; 7; 12; 13				
30	,,			17; 20; 28; 30; 35	47;69				
1.5	minutes			5; 9; 13					
2.5	""				46; 50; 57; 69; 74; 123				
5	,,		•		22; 22; 40; 43; 109; 120				
				-24; -25; -28; -28;					
10	"				73				
2 0	**								

Table 34. Induction Effects from Intermittent Radiation of Rat Blood, as Measured by the Relative Increase in Yeast Buds, and by the Increase in Total Cells

of the growth rate. Such cases are also reported. WOLFF and RAS (see p. 77) consider it the normal reaction after continued irradiation. In his analysis of this phenomenon, SALKIND (1933) observed that with prolonged irradiation, the depression did not increase. A more detailed investigation revealed a certain periodicity; after stimulation followed depression, but after depression, if radiation continued, again stimulation could be observed, (Table 35). This was the case with physical as well as biological senders. In each instance, as well in the experiment of Table 34, irradiation was applied intermittently. No *definite* periodicity could be found in SALKIND's data.

GURWITSCH as well as WOLFF and RAS (1933 c) have verified this observation of several maxima at widely different exposure times while between these maxima, no mitogenetic effects were obtained.

A striking parallel exists between this effect and that of the photographic plate, as may be seen by the following quotation from NEBLETTE (1930).

"Reversal by Light: With a short exposure to light we get a latent image which on development yields a negative. If the exposure is lengthened considerably, the image becomes positive instead of negative when developed, while still further exposure will produce a second negative, and it is probable that the cycle may be repeated indefinitely, although

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	Percei	itage In	crease over Control Cultures					
Source of Radiation	Line Carbon Arc	2350Å 1(orCu) Light	Agar Culture of Yeast		Serum Albu- min in gastric juice			
Experiment No	I	II	I	п	I	II		
Exposed for 18 seconds	+48	- 8						
2 minutes .	— 8		+20	+27	+43			
5 ,,	i.	+ 1	+94	+ 6	+85	+80		
8 "	+ 8	+28	- 6		+ 2	-23		
10 "			+38	+39	+77	38		
. 12 "	13			11	+17			
15 "	+37	-2		+37	+ 7	+37		
18 "	40	+30			16	+88		
30 ,,						+79		
40 ,,						+40		

 Table 35. Periodicity of the Mitogenetic Effect Measured by the Increase in Cell Numbers with Yeast

owing to the enormous exposures required, no one has been able to go past the second negative stage. The reactions which result in reversal are still obscure."

GURWITSCH (1932, p. 219) gives some examples where, after too long an exposure, the effect was not at once harmful, but was delayed for a short time, acceleration being noticeable followed by a distinct retardation. He calls this "secondary depression".

F. ADAPTATION TO GRADUAL INCREASES IN INTENSITY

When the intensity of radiation is gradually increased from below the threshold to a value which would produce a strong effect under usual conditions of exposure, no induction takes place. This has been demonstrated most simply in experiments on mutual yeast irradiation (GURWITSCH 1932, p. 263). An experiment was started with two yeast agar blocks mounted 6 cm. apart, on the movable substage of a microscope. This distance is too far to produce a mitogenetic effect. Very slowly, the two blocks were made to approach one another, until after 5 to 8 minutes, they were very close together; they remained in this position for some

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time. The total irradiation time corresponded to that of another set with the same yeast culture which had been placed in the final position at the start. While this latter set showed increases of 40 to 50% over the controls, the yeast of the equally long exposed, but gradually nearing agar blocks paralleled the controls. The time required for this slow approach must be about 5 to 6 minutes. When it is reduced to 3 minutes, the regular mitogenetic effect is observed.

The same phenomenon was obtained when an elliptical disk was rotated between two yeast agar blocks. This disk was mounted so that in rotation, it gradually exposed the two agar blocks to each other, and gradually shaded them again. This was sufficient to prevent induction.

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