The Cortical Correlate of Pattern Vision[1]

Wolfgang Köhler and Richard Held

Swarthmore College, Swarthmore, Pennsylvania

BOTH PHYSIOLOGISTS AND PSYCHOLOGISTS are convinced that psychological facts are directly related to certain brain processes, which determine the various characteristics of these facts. Such processes are called the cortical correlates of the phenomena in question. No actual demonstration of cortical correlates has so far been possible, and their nature has remained a matter of speculation. In the case of vision, it is true, operations of the cortex are not entirely unknown. When the organism is in a relaxed condition, the visual area of the brain, but not this area alone, exhibits the alpha rhythm, an electric oscillation of about 10 cycles per second. Since this rhythm is most pronounced when the eyes are closed, and is disturbed by visual facts, nobody regards it as the correlate of these facts as such. A few electric waves are also observed when the visual cortex is thrown into action by stimulation of the eyes; and some waves may again occur when stimulation is discontinued. But such on- and off-effects cannot be related to vision in general, because they accompany only its beginning and its end.

Many believe that cortical function is essentially of the same type as peripheral function; in other words, that nerve impulses which arrive in the cortex merely give rise to further impulses which travel in cortical fibers. This thesis meets with a serious difficulty: large masses of cortical cells tend to operate as though each were taking account of what the others are doing. Thus, Gerard (*2*) suggested that, quite apart from impulses which are transmitted in fibers, brain action may involve fields which spread through the tissue as a continuum. Later he and Libet showed that parts of the brain remain functionally interrelated even when all connecting fibers have been severed, or when their synapses are blocked by drug action (*3, 4, 8*). In the meantime, psychological evidence had led to the assumption that, when the level of activity in adjacent parts of the visual cortex differs, a direct current flows around the contour at which they are in contact (*5, 6*). An investigation of so-called figural after-effects in vision strongly supported this assumption (*7*). Just like Gerard's fields, the currents in question were supposed to spread through the brain as a volume conductor. This is not a bold assumption. The short-lived current of a nerve impulse flows through the surrounding medium no less than through the active stretch of the fiber, although in general discussions about the operations of the nervous system the fact is sometimes ignored. Again, since the alpha rhythm of human subjects is commonly registered when the electrodes are attached to the surface of the head, this activity of brain cells must also have fields which spread in the tissue as a continuum. Electric displacements which readily penetrate skull and scalp are not, of course, restricted to special conductors *in* the brain.

In the theory of visual perception, we cannot be satisfied with the general hypothesis that, when a subject sees objects or patterns, corresponding parts of his visual cortex are pervaded by direct currents. If it is assumed that such currents determine certain characteristics of the visual field, it will be necessary to show more specifically how these characteristics can be derived from the behavior of the cortical flow. But this is by no means an easy task. We therefore decided to postpone further theorizing until we had better evidence to support the main hypothesis, and tried to find such evidence in direct physiological tests.

Although later it will be necessary to take records from the brains of animals whose skulls have been opened, recording from the intact heads of human subjects appeared to us more convenient in a first exploration. This procedure had to give results if the size of the postulated potentials could be assumed to be comparable to the amplitude of the alpha rhythm. As our main instrument, we used the breaker type d-c amplifier constructed by the General Motors Company (*10*); the amplified current was registered with a photoelectric recorder of the General Electric Company. The subject was seated in a shielding cage. We used electrodes of the silver-silver chloride type. Usually, one electrode was placed slightly above the occipital protuberance, where the foveal region of the visual cortex is located, and the second electrode was attached to the vertex. Under these conditions, the vertex electrode was connected with the grounded parts of the amplifier and the shielding cage. Steady potentials appearing in the absence of visual stimulation were eliminated by a balancing circuit.

All currents which spread in the nervous system tend to reduce their own intensity by immediate polar-

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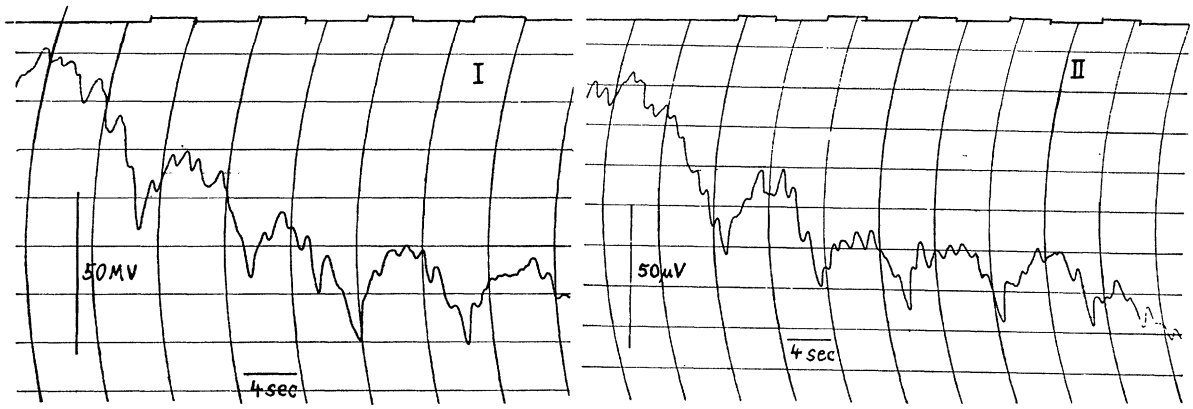

FIG. 1. Record I, subject S, four responses to four exposures of a bright moving object. Record II, subject S, five responses to five exposures of a moving object.

ization of the tissue.[1] We tried to minimize this difficulty by showing the subject bright objects that were slowly moving rather than stationary. Actually, it is more difficult, although not impossible, to obtain responses also in the latter situation. The objects did not move with a very high speed; we have sometimes used velocities of only 3° of visual angle per second. The records we will show here were taken with retinal speeds that varied from about 6° to 12°. It has been reported that moderately bright objects give better on-effects than very intense objects. It is our experience that objects which do not differ too strongly from their background are most likely to give good results. The reason is probably that the advantage which arises from working with a moving object is lost if the object, or rather its current, is strong enough to polarize parts of the visual area before the stimulus actually reaches these parts. We have used moving strips of white or gray cardboard, seen against a dark background in a fairly well illuminated room, as well as moving bars of light projected on a screen under conditions of lower general illumination. Of the records to be shown in this report, only the first, the second, and the fifth have been taken in the latter situation. The objects always had a vertical orientation, and moved in the horizontal direction.

When studying the on-effects of the rabbit's visual cortex, Bishop once remarked that "the variety in the records taken under as nearly constant conditions as we are able to maintain would be discouraging in experiments on any other structure than the cerebral cortex . . ." (*1*). This statement also applies to our records, which often show irregularities of unknown origin. But we should have to regard these records with suspicion if there were no such irregularities. Even in a very calm subject, processes are bound to occur which are not related, or related only indirectly, to the fact that an object moves in his visual field. We have taken records from 13 subjects altogether. All have given responses, although results have been more satisfactory with some than with others. The curves we will now discuss show responses of four different individuals.

When Record I (Fig. 1) was taken, the object moved four times in succession across a screen, in the middle of which a faint fixation mark was given. Both electrodes were placed in the median plane of the head, one in the region of the visual cortex, the other near the vertex. In examining this record, one has to keep in mind that it is written on very slowly moving paper (cf. the length of 4 sec given below the record). It will be seen that there are four responses corresponding to the four marks on top, which indicate the time and the length of the exposures. The responses are maximal in the middle of the exposures, i.e., when the object passes the fixation mark and, in the visual cortex, the place of the occipital electrode. The total length of the four exposures with the intervals between them is about half a minute. During this period the base line has drifted considerably. It is nevertheless obvious that all responses are deflections downward. With the connections of our arrangement, this means that, when the object moves across the fovea, the surface of the cortex under the occipital electrode is positive in relation to the vertex. The size of the responses amounts to slightly more than 25 μv. The small waves which the curves exhibit represent the subject's very slow and steady pulse. It appears in almost all his records, but is disturbing only with some positions of the electrodes.

Record II is a repetition of the same experiment, with the same subject, but with five successive exposures. Although in this case the base line has begun to drift before the exposures, the five responses are

[1] To be exact, not only is the tissue polarized; its polarizability also grows.

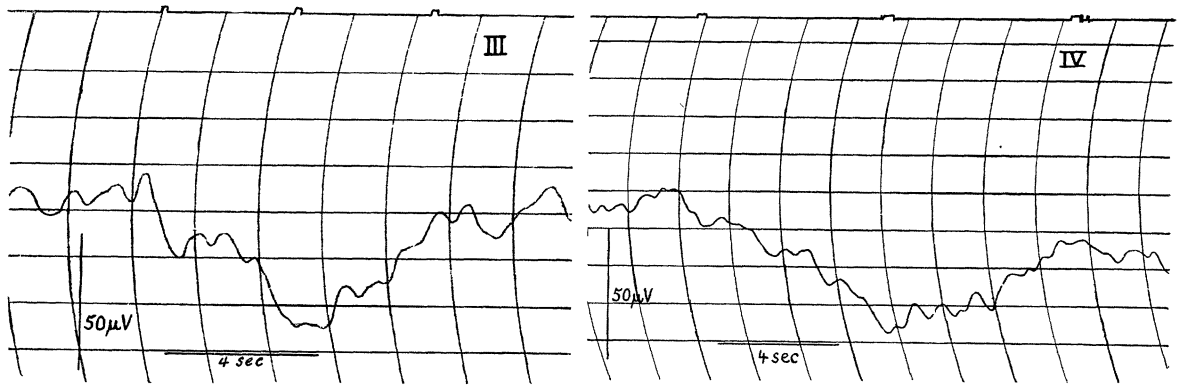

FIG. 2. Record III, subject M, one response to a longer exposure. Record IV, subject M, response to one exposure (12 sec).

again clearly discernible. They have the same polarity as those of Record I, and also almost the same size.

In Records I and II, responses give the impression of being short waves, merely because the records are written on very slowly moving paper and because the extension of the movement is restricted. Records III and IV (Fig. 2), taken from another subject, but with the same position of the electrodes, show reactions to single exposures of objects when the extension of the movement approximates 100° of visual angle, and when the paper of the recorder moves three times as fast as in Records I and II. In both records, there is an almost immediate response when the object begins its movement far in the periphery of the field (cf. the first mark on top). The deflection, which is again positive, grows as the object approaches the fixation mark; it becomes maximal near or at this point (second mark on top), and it gradually decreases as the object moves toward the end of its course (third mark). In Record IV, which is taken with a more slowly moving object, the total time of the exposure amounts to 12 sec. During this period, a current of constant polarity flows from the head into the amplifier. Its greatest intensity corresponds to about 40 μv. The fact that the deflection begins when the object moves at a distance of almost 50° from the fovea deserves particular attention. If such responses actually issue from the visual cortex, parts of this area seem to be interrelated by currents across very considerable distances.

Record V (Fig. 3), taken from a third subject, differs from Records I–IV mainly by the fact that the slowly responding galvanometer (of the recorder) used in the preceding experiments is now replaced by a much faster instrument. The response time of this instrument is .04 sec. As a result, Record V is covered with comparatively rapid oscillations, which the slower instrument could not register. The major positive deflection, which reaches its maximum (about 50 μv) at the fixation mark, is nevertheless perfectly obvious. In the present case, the response is restricted to the middle of the exposure (about 30° of visual angle). This happens occasionally, even if, with the same subjects, other responses extend from the beginning to the end of a wide exposure field. The variation may be related to differences in the attitude of the

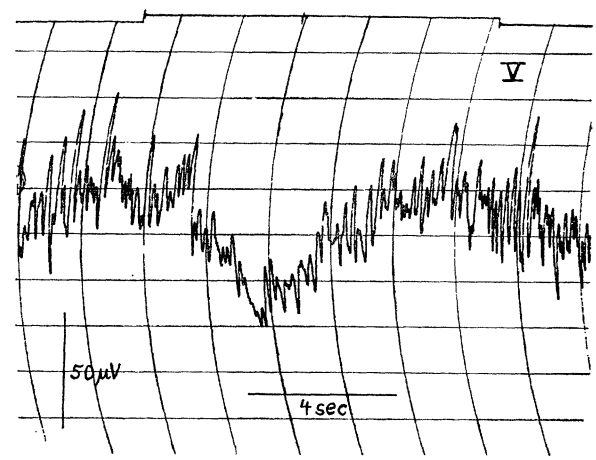

Fig. 3. Record V, subject R, response to one exposure, with alpha waves.

subjects who, while they fixate, may either concentrate on the fixation mark or follow the object with their attention.

When counting the faster oscillations in the periods before or after the exposure, one finds that their frequency is almost 10 cycles, the average frequency of alpha. In our experiments, this rhythm is never really suppressed when the visual environment remains more or less constant for some time. But changes, such as the movements of our experimental objects, tend to disturb the rhythm, at least for a while. Thus, in this record, the frequency, the amplitude, and the regularity of the oscillations appear to be affected during the exposure, particularly during its central part.

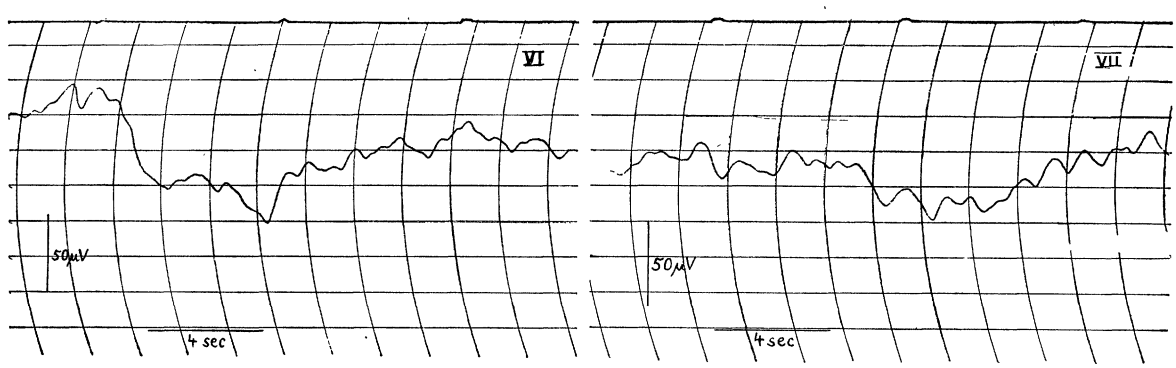

FIG. 4. Records VI and VII, subject M, asymmetrical responses with movements in opposite directions.

If the faster oscillations of Record V are alpha waves (or modified alpha), they represent, of course, one phase of what the cortex is actually doing while an object moves across the field. Strictly speaking, it would therefore seem desirable always to allow these oscillations to appear in our records, and thus to use a galvanometer, the response time of which is short enough for the purpose. We have nevertheless taken many records with our slower galvanometer (response time 0.5 sec), because the behavior of the slower potentials is sometimes more strikingly revealed when they are not covered with alpha. The following records, excepting XI, are taken with this instrument. After all, most records of alpha are taken under conditions which virtually eliminate the steady potentials of the brain. The fact that the slow instrument must also slightly distort steadier potentials can be ignored in a first exploration, which is not yet concerned with details.

Only a small central zone of the human retina seems to be represented in the parts of the visual cortex which lie, on both sides of the median fissure, directly under the skull. But localization within this zone is assumed to be specific; retinal cells on the left side of the central meridian are connected with cortical tissue in the left hemisphere, and cells on the right side with tissue in the right hemisphere. Just the opposite relations obtain, of course, between positions of outside objects and the locations of their cortical counterparts. We tried to decide whether the behavior of the currents here under investigation agrees with such facts. For this purpose, the occipital electrode was placed slightly to the right or the left of the median plane, while the second electrode remained attached to the region of the vertex. It seemed possible that the moving object would affect the occipital electrode more strongly when its cortical counterpart moved in the hemisphere corresponding to this electrode's position. We were thus led to the following four tests.

Records VI and VII (Fig. 4): In both tests the occipital electrode is placed on the right side of the median plane. With a movement of the object from left to right, i.e., retinally from right to left, the first half of the record ought to show a stronger response (VI). With the opposite direction of the movement, this asymmetry must be reversed (VII). Records VIII and IX (Fig. 5): In both tests the object moves left to right, i.e., retinally from right to left. With the occipital electrode on the left side of the median plane, the second half of the record must show a stronger response (VIII). With the electrode on the right side, the opposite must happen (IX). In such experiments, responses are expected to show a more specific shape, in spite of disturbances, and in spite of the fact that the impedance of the skull may vary from one part of the crucial region to another. We have nevertheless often obtained the predicted results. Records VI–IX may serve as examples. The asymmetries agree with our predictions.

One can go still farther in the same direction. If both electrodes are placed in the crucial occipital region, one on the left, and the other on the right side of the median plane, the cortical counterpart of the visual object will move first nearer one electrode, and then nearer the other. Under these circumstances, the resulting records ought to be diphasic; two deflections in opposite directions ought to follow each other. The difficulties inherent in such experiments are still greater than those involved in experiments VI–IX: visual potentials must be much weaker when the electrodes are placed so near each other, and responses will seldom appear to be convincingly diphasic if the curves in question show a major drift. Nonetheless, results are sometimes perfectly clear. For instance, in Records X and XI (Fig. 6), taken when the object moved from the right to the left, and when the left electrode was "active," a positive (downward) deflection during the first part of the exposure is followed by a negative deflection in the second half. With the connections used in our experiments, this is the expected sequence. The deflections are, of course, quite small (cf. the calibration).

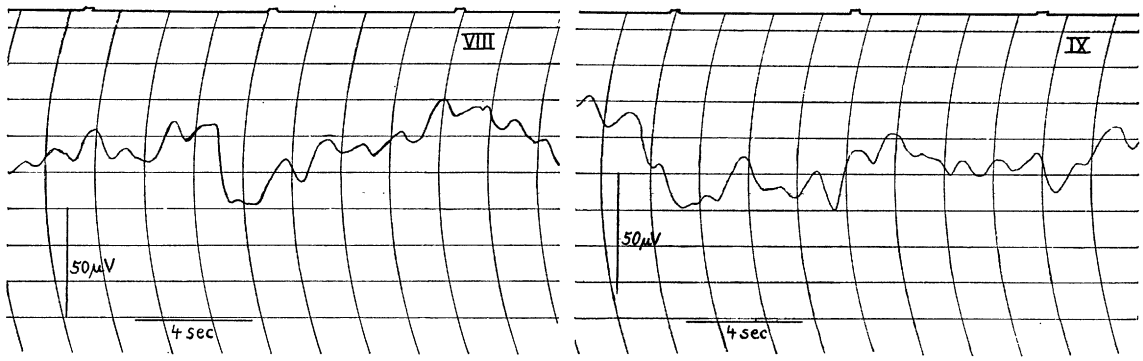

FIG. 5. Records VIII and IX, subject S, asymmetrical responses with different positions of the active electrode.

All our records have this in common: they seem to show that active parts of the visual area are surface-positive in relation to less active parts of the cortex; and that, therefore, when bright objects appear in the visual field the cortex is pervaded by currents which flow in corresponding directions. Libet and Kahn, Jr. recently obtained relatively steady potentials from other regions of the cat's cortex, but found no such responses in the visual area when the eyes were stimulated (*9*). We do not know what conditions of stimulation were used in these experiments. The negative result would contradict our findings only if the authors had also worked with moving objects of very moderate brightness.

In the meantime, the question arises whether our records are actually related to visual facts as such. It might, for instance, be suggested that such responses merely accompany eye movements, or that they represent psychogalvanic reflexes. Comparison with records obtained during eye movements and with the known characteristics of psychogalvanic reflexes has led us to the conclusion that these suggestions are not acceptable. Professor Gerard has called our attention to the possibility that vascular reactions might be associated with cortical fields. Obviously, this possibility will have to be examined; but, at the present time, the electric phase of vascular reactions does not seem to be sufficiently known for the purpose.

If the responses of our records should prove to be visual currents, our next question would refer to the origin of these currents in the visual system. As a radical answer, it might be held that responses such as these need not be interpreted in terms of steady potentials; when registered with a slowly reacting instrument, synchronized nerve impulses of considerable frequency would give similar curves. We hesitate to follow this interpretation. There is no question that, after Berger's discovery of alpha, numerous attempts have been made to find electric oscillations which accompany vision. The instruments used in such experiments have generally been well adapted to the purpose. If synchronized nerve impulses (or, rather, their fields) actually spread through skull and scalp while we see, the fact would probably have been discovered years ago. To be sure, further tests may be desirable.

It seems to us a more plausible assumption that the currents of our records represent the fields of impulses which are thoroughly nonsynchronized. It has been argued that if, from each part of a bright retinal image, nonsynchronized impulses arrive in a corre-

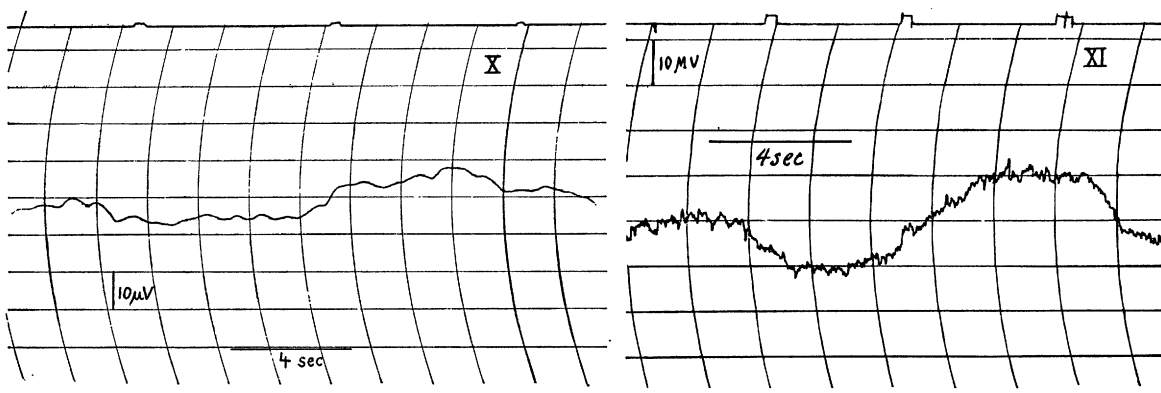

FIG. 6. Records X and XI, subjects M and E, diphasic responses.

sponding part of the visual cortex, the statistical result would be an approximately steady potential and an equally steady flow through and around the cortical counterpart of the image. If this is otherwise good reasoning, we have no cause for objection. The conclusion agrees with our own thesis. Elsewhere, we have given a derivation of steady potentials in the visual area, which refers to the much debated chemical action of nerve impulses (*5, 6, 7*). We need not choose between these two possibilities; the distribution of the resulting flow would be about the same in both cases, and this, from a psychological point of view, is the main issue.

More generally speaking, our results must be interpreted with some caution, just because they are related to important problems. The occurrence of direct currents in the cortex would probably have consequences in various parts of neurophysiology. In psychology, access to the cortical correlate of pattern vision would immediately affect the theory of psychophysical relations—and would affect first of all, the theory of perceptual space.

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TECHNICAL PAPERS

The Mutagenic Mode of Action of Formalin

C. Auerbach

Institute of Animal Genetics,
Edinburgh University, Edinburgh, Scotland

In 1946 Rapoport (*5*) reported that formalin, when mixed with the food of *Drosophila melanogaster* in sublethal concentrations, produces a high frequency of mutations. In the one experiment for which full data were given, the percentage of induced sex-linked lethals was 5.92. Kaplan (*2*) confirmed this finding, and similar results were obtained in this laboratory with a wild-type (OrK) stock. Rapoport attributes the mutagenic effect of formalin to a chemical reaction between the chromosomes and the CO group of the aldehyde. It seems rather unlikely that formalin as such would reach the chromosomes of the germ cells under the conditions of these experiments. Two other possibilities have to be considered. First, formalin might react with the food to produce a new mutagenic compound. Since formalin is added to the food while the agar is still well pourable, this reaction would take place at a temperature of about 60° C. Second, it also seems possible that a mutagenic substance is formed not in the food, but in the body of the fly either during digestion or in the germ cells.

In order to obtain information on this point, the effect of formaldehyde vapor on *Drosophila* was tested. A positive result with this method would prove that formaldehyde as such is a mutagen, which would make it at least probable that it is the effective agent in the feeding experiments also. A comparison of the effects of formaldehyde vapor on male and female germ cells in various stages of development should help to decide whether the action on the chromosomes is direct or mediated by the cytoplasm; for in the latter case female germ cells and spermatogonia should be more affected than mature spermatozoa. The OrK stock which had given 3–6% sex-linked lethals in previous feeding tests with formalin was used. Young adult ♂♂ and ♀♀ were exposed to formaldehyde vapor in the first series. Exposures lasted from 30 to 60 min, and the biologically effective dose was measured roughly by the survival rate during exposure and the first few hours afterwards. This does not take account of the fact that flies often die during the subsequent days. In all tests, ♀♀ survived in a larger proportion than ♂♂. In order to test germ cells which at the time of exposure had been at different stages of development, the treated ♂♂ were given fresh ♀♀ every fifth day, the treated ♀♀ were put on fresh food every fifth day, and mutation rates were recorded separately for the different broods. The untreated mates for both sexes were taken from the Muller-5 stock. Table 1 gives a short summary of the results.

The OrK stock used for these experiments has been tested repeatedly over the past few years. Sex-linked lethals in the ♂♂ arise at a fairly constant rate of about