apparently approaches zero dose and zero response.

In Fig. 2 the ratio of tumors to animals in each of the eight lowest dosage groups is plotted against dosage in the above-described units. The tumors represented in this graph are the sum of the malignant bone tumors and the reticular tissue tumors reported in *Argonne Natl. Lab. Rept. No. 5597* and the sum of the sarcomas, giant cell tumors, and epidermoid cancers reported in *Argonne Natl. Lab. Rept. No. 5841* by Finkel *et al.* (*3*). Since some animals had more than one type of tumor, the resultant ratio in two of the groups was greater than 1.0. The points on this graph also appear to represent a direct linear relationship between dosage and response which approaches zero dose and zero response.

When presented in this way, the results of Finkel's work can thus be used not only as an argument against the stand taken by Brues (*2*) but can be used to support the views of the United Nations Scientific Committee on the Effects of Atomic Radiation (*4*) and of Lewis (*5*), which are that there may be no threshold for radiation injury, and that the dose-response curve may be straight, extending to zero dose and zero response.

As noted above, in Figs. 1 and 2 only the eight groups of animals having the lowest doses have been used. The four high dosage groups, which were not used, do not continue on the straight line exhibited by the eight lower dosage groups. This alteration of the curve at high radiation levels may be attributed to the fact that at high levels there is considerable "wastage" of radiation. That is, much of the radiation energy is absorbed by dead or dying tissue. Energy which is absorbed by dead or dying tissue is not likely to produce tumors or to shorten life.

In all experience with radiation-induced neoplasms, a latent period between irradiation and resultant neoplasms has been observed. This latent period has been thought to be shortened by larger radiation doses. In Finkel's experiment (*1*) there was an initial whole body radiation dose followed by chronic radiation, primarily to bone. Under these conditions, the longer-lived (low-dose) groups might be expected to exhibit proportionately more neoplasms by virtue of having lived farther past an average latent period. However, this effect might be counteracted by a shortened latent period in the high-dose (shorter-lived) groups.

Without the knowledge to assess the importance of these three factors—initial radiation dose, chronic radiation dose, and possibly variable latent period—one must consider that the linear response suggested in Fig. 2 may be merely fortuitous. However, it gives no comfort to those who would interpret this data as demonstrating a threshold for radiation-induced neoplasia.

In both Fig. 1 and Fig. 2, uncertainties in the values for the points near zero dose as well as uncertainties in the average lifetime of the controls and per cent of tumors in controls are sufficiently great that little reliance can be placed on the exact position or shape of the curves as they approach zero dose.

There are, no doubt, other informative methods of presenting the data from this excellent experiment. In a more recent publication Finkel has presented the data somewhat differently (*6*). This presentation indicates, among other things, an apparent independence of Sr^{90} dose and latent period of resultant tumors.

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11 March 1960

Weber Ratio for Visual Discrimination of Velocity

Abstract. As an approximation based on various experiments reported in the literature, the least detectable difference in speed ($\Delta \omega$) varies in direct proportion to the speed (ω) over a range from 0.1 to 20 degrees of visual angle per second. The constancy of the Weber ratio ($\Delta\omega/\omega$) aids in understanding how men react to velocity in various situations.

Need for information on the Weber ratio has recently been stressed in research on traffic dynamics. Chandler, Herman, and Montroll (*1*) have reported that drivers react mainly to relative velocity rather than to relative distance. This finding provides an experimental basis for models of vehicular interaction which may be applied to multiple collisions on modern superhighways and to other traffic problems.

Fortunately, a rather extensive literature has accumulated on visual discriminations of velocity. Plotting of data from the literature yields a useful generalization. The inference may be applied not only to the dynamics of moving vehicles, but also to other interactions of men with machines.

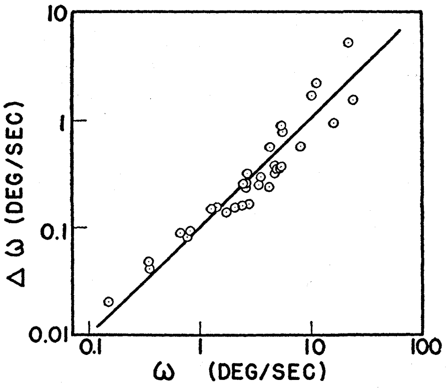

Fig. 1. The differential threshold ($\Delta \omega$) as a function of angular speed (ω). Experimental points are the thresholds as measured in eight experiments (*5*). A least squares solution for the intercept constant yielded the straight line with unit slope; $\log_{10} \Delta \omega = -1.00 + \log_{10} \omega$.

Graham (*2*) has emphasized the importance of expressing extent in terms of the visual angle subtended at the eye. Similarly, it is advantageous to use angular units for velocity. Expression of speed in units of visual angle per second makes it easy to compare measurements which experimenters have made from different distances of observation. In addition, angular speed has advantages for experimental design since its use facilitates the recognition and control of major variables. These and other methodological considerations have been reviewed recently (*3, 4*).

Visual sensitivity to velocity is indicated by the differential threshold, which may be defined as

$$\Delta \omega = \omega_2 - \omega_1 \qquad (1)$$

where ω_2 is a uniform angular speed an observer discriminates, according to a specified criterion, from the constant rate of motion ω_1. The differential threshold has been of continuing interest since the turn of the century; in eight papers (*5*), scientists have reported measurements over a wide range of speeds.

The difference thresholds are plotted against the angular speed in Fig. 1. The straight line of unit slope represents a constant Weber ratio $\Delta\omega/\omega$. Solution for the intercept constant by least squares yields the plotted equation

$$\Delta \omega = (0.10)\, \omega \qquad (2)$$

As a very rough approximation, Fig. 1 shows that the differential threshold increases in direct proportion to the angular speed of the stimulus. Discrepancies result from variations in procedures and from nonrandom effects of major variables. A recent report (*4*) has presented a rationale for interpreting the discrepancies.

The Weber ratio provides a convenient measure by means of which velocity discriminations may be compared with other sensory discriminations and with performances in tracking and predicting. As indicated by Fig. 1 and the least squares solution, the best estimate of $\Delta\omega/\omega$ for an unspecified ω is 0.10. This value is of the same order of magnitude as the Weber ratio for a loudness of 100 db at 1000 cy/sec and for cutaneous pressure at 5 gm/mm^2 and for smell of rubber at 200 olfacties (*6*).

Speed of target motion seems to have the same effect on tracking error as it has on the differential threshold, that is, tracking error increases as a linear function of speed (*7*). In addition, the discrimination of a 10-percent difference in speed agrees with the error a tracker makes when he follows a target which moves at a constant speed but suddenly disappears (*8*). The Weber ratio is also clearly related to predictions of future positions of a moving object (*9*).

Research on tracking and predictive behavior indicates the need to consider the effects of parameters other than speed. It may be anticipated that $\Delta\omega/\omega$, like other Weber ratios, is approximately constant only within a restricted range of stimulus variation, and that the systematic effects of major variables other than speed will become apparent in future experiments. The present report serves to indicate the potential utility which may result from appropriate experimental analyses of the Weber ratio for visual discriminations of velocity.

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Complementation at the Maroon-like Eye-Color Locus of Drosophila melanogaster

Abstract. Two "allelic" *Drosophila melanogaster* mutants which are deficient in xanthine dehydrogenase can complement one another in heterozygotes. This complementation is due to the production of small amounts of xanthine dehydrogenase, enough of which is present to restore the normal eye color. However, not enough of the enzyme is present to produce normal amounts of the enzyme products, or to reduce the accumulation of the enzyme substrates to levels found in wild-type flies.

Many cases have now been reported in which "allelic" genes can complement each other in heterozygotes or in heterocaryons to produce a wild-type phenotype. Such complementation has been reported for some eye-color alleles in *Habrobracon* (*1*) and for some wing mutants (*2*) and the bithorax cluster (*3*) in *Drosophila.* The data indicate that restoration of proteins is involved, since, in *Neurospora,* glutamic dehydrogenase is found in heterocaryons of allelic mutants lacking this enzyme (*4*), while a similar situation exists for allelic mutants lacking adenylsuccinase (*5*). This is a report of a similar phenomenon which we have found in *Drosophila melanogaster* between "allelic" mutants which lack xanthine dehydrogenase.

Mutants deficient in this enzyme comprise two loci, maroon-like eye-color (*ma-l*) (*6*) and rosy eye color (*ry*), which are located on the first and third chromosomes, respectively (*7*). As a result of the deficiency of xanthine dehydrogenase, *ma-l* and *ry* mutants accumulate the enzyme substrates (hypoxanthine and 2-amino-4-hydroxypteridine), and show no trace of the products (uric acid and isoxanthopterin) formed from these compounds (*8*). Xanthine dehydrogenase has been purified from wild-type flies by using charcoal, ammonium sulfate, and calcium phosphate gel, and no activity could be detected in purified extracts of the mutants (*9*). In this report we are concerned solely with the *ma-l* locus.

In general, the chromatographic methods followed those described by Hadorn and Mitchell (*10*) and others; the enzymatic techniques followed those described by Glassman and Mitchell (*9*). The amount of xanthine dehydrogenase in the various stocks was determined as follows: Flies were homogenized (40 mg/ml) in a Kontes "Duall" glass tissue grinder in 0.1*M* Tris buffer at *p*H 8. An amount of charcoal (Norite-A) equal to the weight of the flies used was added to remove inhibitors, and after 30 minutes the solution was centrifuged at 20,000*g* for 20 minutes. One milliliter of the supernatant was placed in the fluorometer cuvette with 0.02 ml of $10^{-3}M$ methylene blue and 0.05 ml of $5 \times 10^{-4}M$ 2-amino-4-hydroxypteridine. The increase in fluorescence due to the formation of isoxanthopterin was detected in a Turner model 110 fluorometer using a primary filter with principal transmission at 360, and a Turner 2A with a Farrand interference filter transmitting at 416 mμ for a secondary filter. The red eye pigment was estimated by measuring the fluorescence directly on the paper (*11*). The other compounds were estimated visually.

The locus involved in this investigation is on the right end of the X-chromosome between Beadex wing (Bx^3) and suppressor of forked bristle (*su-f*) (*12*). The mutants are *ma-l*, induced by x-rays by Oliver (*7*), and the bronzy allele of maroon-like eye color ($ma\text{-}l^{bz}$), originally called bronzy by M. O. Fahmy, who induced it with phenylalanine mustard (*13*). The "allelism" of these mutants is based on their biochemical similarity, on the lack of complete complementation, and on the fact that no crossovers were observed in approximately 5000 progeny (*12*). This number is low, however, and does not rule out the possibility that these mutants are psuedoallelic; indeed, because they are complementary one might expect

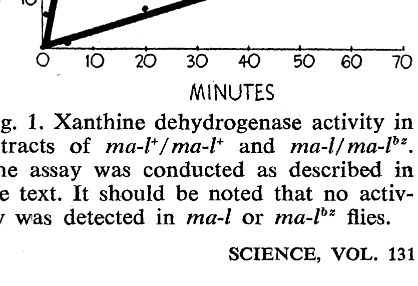

Fig. 1. Xanthine dehydrogenase activity in extracts of $ma\text{-}l^{+}/ma\text{-}l^{+}$ and $ma\text{-}l/ma\text{-}l^{bz}$. The assay was conducted as described in the text. It should be noted that no activity was detected in *ma-l* or $ma\text{-}l^{bz}$ flies.