

minial branches of the conduction system constitute the false tendons. These procedures have been successful in four dogs and one monkey.

The potentials from the region of the A-V node proper require a detailed and critical study, which is not within the compass of the present paper. They have varied markedly in certain respects. At times an electrode in this region records a local auricular depolarization followed by nodal depolarization, but at other times the former is lacking. Moreover, the records thus far do not permit any statement regarding the nature of A-V nodal delay or the mechanism of activation of the node.

An electrode a few millimeters from the A-V node records a small potential, usually biphasic, of about 2-msec duration and 5-mv amplitude (Fig. 1). This potential appears about 10 msec after the last sign of auricular activity and precedes the earliest sign of ventricular activity by about 40 msec. The potentials from the intraventricular false tendons containing the preterminal branches of the conduction system have similar characteristics, but precede earliest myocardial ventricular activity by only a few milliseconds (Fig. 2). If the direct distance between electrodes near the node and the false tendon is divided by the time required for impulse transmission, the calculated conduction velocity falls between 1.4 m and 1.7 m/sec. Since the impulse does not follow a straight path, the actual velocity must be greater. Thus, it appears that the conduction rate in the more central part of the system is nearer the 2.0 m/sec rate calculated for transmission in the false tendon (2) than the 1.0 m/sec found (4, 6) in the lining of most of the ventricular wall. When this system is stimulated in either a forward or a retrograde direction, the transmission time is identical to that during the spontaneous beat. There is no appreciable delay between activation of the terminal portions of the conducting system and activation of the ventricular musculature.

This work (7) is being continued with the hope that the difficult problem of the nature of A-V nodal delay and excitation will ultimately be understood.

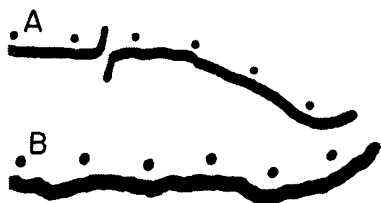


Fig. 2. Activity in false tendon of monkey. (A) Records from electrode that pierced false tendon in lower left ventricular cavity. Biphasic potential at left is from false tendon. Negative potential at right is caused by activity proceeding away from left cavity. (B) Simultaneous Lead II ECG. Time pips 5 msec. Biphasic potential on A has peak-to-peak value of 8 mv; it is followed in 7.5 msec by negative cavity deflection on that channel. ECG on B, 2.5 msec later, shows negative (Q) deflection followed by positive deflection.

References and Notes

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6. This velocity is found with stimulation. Normally the endocardium is excited at many points simultaneously by the branched purkinje system. Thus, the apparent velocity is high.
7. Aided by a grant from the Washington State Fund for Biology and Medicine, and by a grant, H-1315, from the National Heart Institute.

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Dosage Effect of Multiple *Dt* Loci on Mutation of *a* in the Maize Endosperm

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The mutability of certain alleles at the *A* locus on chromosome 3 in maize is affected to a remarkable degree by the gene *Dt* located on chromosome 9 (1). The mutations produced are changes of *a* to *A* that can be expressed, when the appropriate complementary genes are present, as long, slender, purple sectors of (*Aa*) cells surrounded by otherwise green or brown (*aa*) plant tissue and as frequent small purple or red (*Aaa*) dots on the colorless (*aaa*) aleurone of the seed.

In an effort (2) to find other genes similar to *Dt*, 98 strains of maize from Central and South America were tested. Included were 1 from Argentina, 5 from Bolivia, 6 from Brazil, 17 from Colombia, 2 from Costa Rica, 11 from Ecuador, 4 from Guatemala, 7 from Honduras, 4 from Mexico, 7 from Nicaragua, 31 from Peru, and 3 from Venezuela. The test consisted of backcrossing *Aa* heterozygotes, to an *a^m dt* tester and examining the ears produced for colorless seeds with red or purple dots (reversions). The *a^m* allele in the stock used is extremely sensitive to the action of *Dt* (3), and therefore it provides an excellent indicator of the presence of possible weak expressions of *Dt*. Two of the races tested gave positive dotting: a Brazilian yellow flint variety called Cateto and a purple aleurone race from the Peruvian coastal village of Huarney.

A number of investigations were made for the purpose of locating and characterizing these two possible *Dt* genes. Tests for their allelism with *Dt₁* and with each other showed that they are independent loci. They were, therefore, designated *Dt₂* (from Brazil) and *Dt₃* (from Peru). Preliminary linkage data from the original backcross indicate that *Dt₂* is linked to *Y* (*Y* produces yellow endosperm and *y* white) on chromosome 6 with 26-percent recombination. Linkage data are not yet available for *Dt₃*. An effort was made, using the x-ray induced deficiency method (4), to confirm the location of *Dt₂* and to place both *Dt₂*

and Dt_3 in their proper positions on the chromosome map. Two plants, one deficient for Dt_2 and the other for Dt_3 , were obtained. Cytological examination revealed that the first had lost all the long arm of chromosome 6, except for the three heavy-staining proximal chromomeres, and that the second was deficient for the terminal end of the long arm of chromosome 7, including all the material beyond the heterochromatic knob that commonly occurs on this chromosome.

From the afore-mentioned facts it can be reasoned that, since Dt_2 is included in a deficiency of the long arm of chromosome 6 and is linked with 26-percent recombination to Y (Y is located very near the centromere), it must be approximately 26 crossover units distal to Y or near the gene Pl . Comparable data are not available for an accurate placement of Dt_3 .

The behavior of both Dt_2 and Dt_3 is similar to Dt_1 in that all three cause a and a^m to mutate at comparable frequencies and in a fashion characteristic of the a allele involved. Similarly, there is an exponential increase in response to each when their respective dosages are increased from one to three in the endosperm.

A preliminary comparison of Dt_1 and Dt_2 was made using the offspring from the cross of $aa, Dt_2 Y/dt_2 y, Dt_1 dt_1$ by homozygous $a, dt_2 y, dt_1$. Ears were obtained that had seeds of the noncrossover classes; yellow Dt_2 (two doses), yellow $Dt_2 Dt_1$ (four doses), white Dt_1 (two doses), and white nondotted plus the recombination classes white Dt_2 , white $Dt_2 Dt_1$, yellow Dt_1 and yellow nondotted. The four-dose seeds have 10 times as many reversions as the two-dose seeds of either the Dt_2 or the Dt_1 types, thus allowing identification of the two-dose class.

Even though crossing over between Dt_2 and Y is high, sizable differences in dotting frequency and character between Dt_1 and Dt_2 should be demonstrated in a comparison of the two-dose yellow seeds with the two-dose white ones. Reversion counts of 53 seeds revealed that the average dot number for yellow seeds was 6.04 ± 3.5 and for the white seeds was 5.73 ± 3.4 . Such a slight variation in dot number coupled with an apparent lack of differences in the character of the reversions observed on these sib seeds

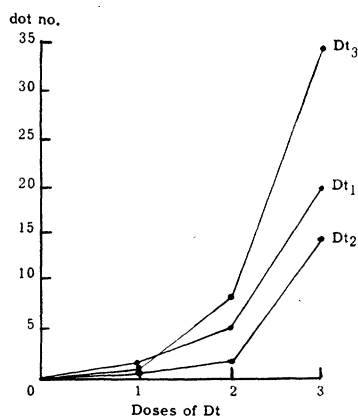


Fig. 1. The effect of one to three doses of Dt_1 , Dt_2 and Dt_3 from selfed $aa Dt Dt$ ears.

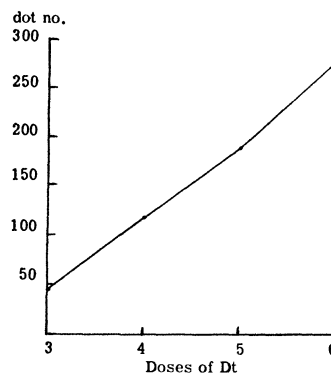


Fig. 2. The effect of the combined dosage of Dt_1 and Dt_2 on dot frequency.

provide some justification for considering Dt_1 and Dt_2 as equivalent, and for attributing the differences in dot number among the three unrelated Dt cultures listed in Fig. 1 to genetic modifiers.

Since Dt_1 , Dt_2 and Dt_3 have similar dosage relationships, experiments dealing with their combination for higher doses have distinct possibilities. It should be possible in the 3N maize endosperm to get up to nine doses of Dt with these genes. At present only the data from the addition of Dt_1 and Dt_2 are available. Seeds with three, four, five, and six doses of Dt were obtained from the cross of $aa, Dt_2 Y/dt_2 y, Dt_1 Dt_1$ by $aa, Dt_2 y/dt_2 y, Dt_1 Dt_1$. These dots on each seed were counted, the seeds were sorted for Y and y , and adjustments for crossing over were made.

As can be seen by the data presented in Fig. 2, the frequency of dotting increases with increasing Dt dosage up to six doses, even though it is not clear whether the curve is an exponential one, a linear one, or one represented by the part of a sigmoid curve that lies near the point of inflection. Data from the addition of Dt_3 , which will permit the study of seven, eight, and nine doses of Dt , should extend the curve to a point that will indicate which type of curve we have.

Significantly, the character of the reversions produced does not change when their frequency is altered. The dots at all dosage levels have the same size, shape, and color intensity. This is quite different from the behavior of other mutable loci-mutator combinations, such as McClintock's $Ds-Ac$ system (5) and the $bz-M$ system (6), in which changes in dosage of the mutator not only cause a change in frequency but also in size of the sectors produced.

References and Notes

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2. This work was supported by a grant from the U.S. Atomic Energy Commission, contract AT(11-1)-73, project No. 4. This paper is Journal Series Paper No. 1493 approved by the director of the Missouri Agricultural Experiment Station.
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