Table 1. Mean scores of cells of known phenotype when tested against specific antiserums.

Phenotype	Mean score
Pooled anti-A serum	
A	29.5
AF	31.9
AD	14.8*
Anti-D serum	
D	48.0
DF	53.8
AD	27.3*

* $P < 0.01$.

when tested against a panel of rabbit cells containing all our previously identified antigens, reacted strongly with cells that had antigens *A* and *D* and did not react with cells that were homozygous for *A, D,* or *F* or with cells that were heterozygous for *AF* or *DF*.

Matings were made to include all combinations of blood groups controlled by this locus; antigen *I* consistently appeared only when, as a result of segregation, the genes for *A* and *D* occurred in the animal. In all, 223 animals in our colony were typed, and of these 63 were found to be type *ADI*. In no case did *I* appear when neither *A* nor *D* was present. In no case was antigen *I* missing when both *A* and *D* were present. As the result of our attempts to maintain lines of inbred rabbits, we had available at least three generations of animals showing segregation for the genes Hg^A and Hg^D. The complete pedigree, shown in Fig. 1, indicates the relationships that must exist for the appearance of *I*.

In studying the effect of genotypes on the reactivity of cells, we compared the relative titers of various typing serums as they reacted with cells with antigen combinations resulting from the *Hg* allelic series. Anti-*A* was titrated against cells of animals of phenotypes *A, AD,* and *AF*; anti-*D* was titrated against cells of animals of phenotypes, *D, AD,* and *DF*. The scoring method suggested by Race and Sanger (*4*) was used to measure the titer of the typing serum. In every case the score for the *AD* cells was significantly ($P < 0.01$) lower than that for the other antigenic types (Table 1).

This finding, also reported in part by Joysey (5), is consistent with the concept that the interaction of genes Hg^A and Hg^D results in the formation of three products that perhaps involve a common substrate somewhere in the process of action so that the amount of antigens *A* and *D* is diminished. No attempt will be made at this time to give a physiological explanation of the reaction beyond the statement that two genes have clearly given rise to three antigens. The following genetic hypotheses may be rejected as inconsistent with the data: recessivity, and linkage between the *Hg* series and a gene giving rise to antigen *I*. The interaction postulated for the existence of human *f* may be similar to our findings, but *f* is dependent on *c* and *e* being on the same chromosome. In our example, Hg^A and Hg^D cannot be on the same chromosome.

The rare occurrence in offspring of cellular antigens that do not occur in either parent has been reported by Irwin (*6*), Thompsen (*7*), Boyd and Alley (*8*), and more recently by Rendel, Sorensen, and Irwin (*9*) and Levine *et al.* (*10*).

Our findings described here are of interest in three areas. First, the appearance in the rabbit offspring of antigens that are not present in either parent is one of a few cases in mammals. The use of blood groups in paternity cases is based on the premise that a child cannot have an antigen that is not present in either parent. Although the findings in the rabbit cannot, of course, be extrapolated to human blood groups, it is possible that such a phenomenon as that reported here may occur in human beings.

The second area of interest is that of the gene-antigen relationship. Since we have shown that two genes can give rise to three detectable antigens, the one gene-one antigen relationship obviously does not hold true for all situations.

Third, there have been several theories proposed on the mechanism for selective value of heterozygotes. The findings reported here support the theory of Rendel (*11*) and Haldane (*12*), among others, that the heterosis effect may be due to the fact that the products of the interaction of two alleles may be more effective than the product of either homozygote.

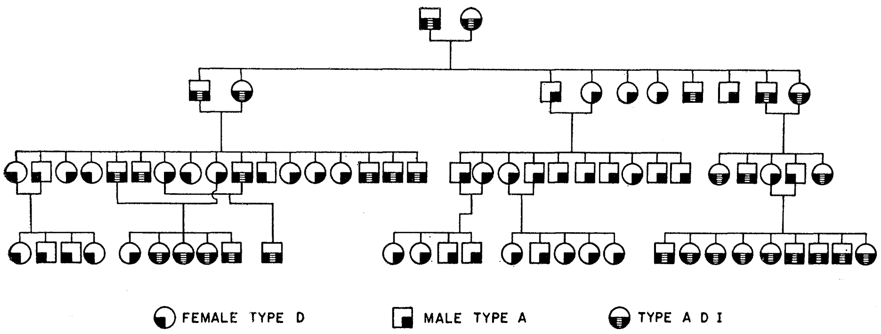

Fig. 1. Pedigree of a family of rabbits showing the inheritance of antigens *A, D,* and *I.*

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References and Notes

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Efficacy of Striatal Shocks in Avian Conditioned Behaviors

A cursory investigation has shown that electric stimulation of the striatum of the pigeon can serve as a conditioned stimulus in both classical and instrumental situations. In three pigeons, silver-wire electrodes spaced 1.5 mm apart and insulated except at the tips were implanted in one hemisphere of the forebrain and affixed firmly to the skull. Leads were brought through the skin to allow direct connection with a stimulator. Such preparations could be maintained indefinitely without danger of infection or other complications. Post-mortem gross examination, correlated with histologic study of other specimens, suggested that the electrode tips were placed in the neostriatum intermediale just below tractus fronto-occipitalis (*1*). When delivered to this region, a very brief 60-cy/sec pulse of about 2 v produced discrete and highly consistent turning of the head in the direction opposite to the side stimulated. If the voltage was very slightly reduced, there was no observable response. If the voltage was very slightly increased, the result was "startle" in two birds, and indiscriminate jerking and struggling in the third.

One pigeon was trained to flex its leg in response to striatal stimulation. The unconditioned stimulus, an electric shock to the skin on the thigh, evoked a clearly unilateral leg flexion. A 0.75-sec striatal shock just sufficiently intense to evoke a headturning response was given immediately before the leg shock. Thirty reinforced trials per day were given, with two additional nonreinforced striatal test shocks. Anticipatory flexions began to appear on the fourth day of training and continued during the subsequent 5 days of training and testing. The flexion response failed to appear to a test shock given 2 months later, but reappeared on the second day of retraining. The electrodes were in the right forebrain, and the right thigh was shocked.

That cues arising out of head movement were not operative is suggested by the following observation. Conditioned flexion was not established in three pigeons given 200, 400, and 600 trials when a bright light, toward which the birds turned their heads, was substituted for the striatal shock. Whether the striatal shock evoked a sentient response, such as an aura, or a motor response, such as an adversive movement, cannot be specified. It is interesting to note that investigation of this area, under Nembutal, with a 5-micron glass microelectrode showed many tonically active units (which were diphasic and initially negative with respect to the indifferent electrode), but no units responsive to leg shock. It was necessary to penetrate below this area, probably to tractus thalamo-frontalis medialis of the forebrain bundle, to find fiber activity. In this region, a good primary response with a latency of about 14.5 msec was recordable following leg shock. A reflex discharge from leg movement subsequent to the leg shock was also found. The lesser amplitude and pure positivity of this response suggested that it was somewhat removed from the point of recording.

Two birds were trained to peck at one of two simultaneously presented visual figures when a striatal shock or external light was presented in order to obtain food reward. Twenty trials were given daily until a criterion of 16 consecutive correct responses was attained. One pigeon was required to peck a black triangle after striatal shock and horizontal black lines after bright light. This subject reached the criterion performance level in 113 trials and maintained a very high level of performance during the 160 trials of overtraining. The other bird, given the reverse task, attained the criterion in 86 trials. The light and shock were presented in random sequence, and the visual figures appeared randomly to the right or the left of each other in a discrimination apparatus that has been described in detail elsewhere (*2*).

Usually, a pigeon requires about eight training trials before it discriminates perfectly between the two figures used in the customary discrimination procedure. Thus, this far more complex task was mastered in only 10 times the number of trials. Acquisition of the two discriminatory-conditioned responses appeared at about the same rate, possibly signifying that the striatal stimulation was also operating on the sensory side. An auditory signal presented after learning did not evoke pecking; hence the mere lack of light or the presence of some stimulus other than light was probably not sufficient to produce the "striatal-conditioned response."

If purely motor effects resulted from the striatal stimulus, the instrumental discriminative response is in line with previous observations, but the classical leg conditioning is not (*3*). Ancillary experiments indicated that movement-produced cues were not operative in this situation. It therefore appears that the neostriatal stimulation gave rise to a sentient response that was more efficacious than the peripherally evoked sensory response in the nonreward situation, and was equally efficacious in the instrumental-discriminative situation.

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Chinese Walls of New Cave, Carlsbad Caverns National Park

Speleothems—Moore's proposed term for cavern formations (*1*)—are as variable as the caverns and caves in which they form. Although I have seen many types of speleothems in Carlsbad Caverns National Park, New Mexico, there are none that challenge one's imagination more than the Chinese Walls (Figs. 1 and 2) of New Cave (once known as Slaughter Cave).

Fig. 1. View of several feet of the Chinese Wall. Two levels of terracing shown. Size is indicated by the pocketknife in the foreground between the walls.

Fig. 2. Close-up view of a small section of the Chinese Wall. Gravel-size accretions are in the foreground. Scale is indicated by the pocketknife in the foreground.

Unlike most speleothems, these walls have no apparent pattern other than that of growing vertically. There are no shelves of minerals or water lines that might indicate water levels. The trace of the meandering tops of the walls curve or furl as often in one direction as in another. Some furlings are so well developed that they nearly form vertical tubes. Only one characteristic seems to have any consistency: the degree of furling apparently increases with the amount of vertical growth. Unlike retaining dams (*2*) and embaying walls of Carlsbad Caverns, the Chinese Walls do not overhang or obviously grow toward any particular direction. Tests made on small sections indicated that these walls are able to withstand more than 100 pounds of compressive pressure to each inch of trace. The furling course of the trace probably accounts for the strength that has preserved it from vandalism. When I last observed it in 1951, only a few small pieces had been broken from the wall.

To complicate their study still further, free, gravel-like accretions cover the flat floors between the walls. These accretions have a rough, granular surface (Figs. 1 and 2) and should not be considered to be cave pearls. Apparently they are in place, since no stream channels or gravels were noted.

Many speleologists would consider the meandering and furled walls to be just "rimstone." Although they apparently did "rim" pools of water at one time, they definitely differ from any of the rimstone I have seen in Carlsbad Caverns. The trace of that in the former is very irregular, whereas the traces of the latter are often gently arching for a distance of several feet. It is my opinion that the Chinese Walls of New Cave should be considered a special type of "furled retaining wall."

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