limit.) With the possible exception of the osmotic effect, I can think of no way the central nervous system could develop anything like this pressure difference across 2 μ in 1 msec. The electroosmotic flow of water cannot be swamped out by other factors.

The flow of water in the interstitial space would not have an effect upon cells if it remained entirely interstitial. However, wherever current crosses a cell membrane, the membrane will appear as a source or sink of water flow relative to the interstitial space. A transmembrane electroosmotic effect in cell membranes has often been postulated (*12*). If this transmembrane electroosmosis were exactly equal to the effect in the interstitial space, there would be no net result; the water would move in a circle without generating any pressure. Since these two electroosmotic effects have a different physical basis, it is unreasonable to assume that the two would be equal. The synaptic membrane will be a source or sink of water and some pressure must be exerted on the membrane.

The example of an excitatory synapse was used intentionally, since excitatory and presumably inhibitory postsynaptic membranes have current densities higher by several orders of magnitude than any other parts of the central nervous system. During an action potential in a postsynaptic cell, the mean transmembrane voltage in the postsynaptic cell is about -10 mv. This potential is approximately the so-called "equilibrium potential" of an EPSP at which the excitatory postsynaptic membrane generates no current (*13*). Therefore, if a postsynaptic excitatory membrane is activated simultaneously with an action potential in the postsynaptic cell, much less current will flow across the postsynaptic membrane than was calculated for the subthreshold case above. Conversely, current density across a postsynaptic inhibitory membrane will be much larger if the postsynaptic cell *does* have an action potential simultaneously with activation of the postsynaptic inhibitory membrane, because the transmembrane potential will be further from the so-called "equilibrium potential" of the inhibitory postsynaptic membrane (*13*). (However, I know of no data from which to estimate the magnitude of inhibitory synaptic density.)

The mechanism can now be shown to perform an integrative function in the central nervous system. Let us coin the term "unsuccessful synaptic event" to refer to the following cases: (i) an excitatory postsynaptic membrane is activated and no action potential occurs in the postsynaptic cell, and (ii) an inhibitory postsynaptic membrane is activated and the postsynaptic cell *does* fire. Let us use the term "unsuccessful synapse" to refer to a synapse which usually has "unsuccessful synaptic events." The "success" of a particular synaptic event will then depend mostly upon the timing of the particular presynaptic input relative to other presynaptic inputs to the postsynaptic cell, that is, the central excitatory state of the postsynaptic cell at the time the particular presynaptic action potential arrives.

Since it takes many excitatory synapses firing closely together in time to fire a postsynaptic cell, the magnitude of the postsynaptic effect of any single synaptic event will have relatively little influence in determining its own "success." As shown above, the current flow and consequently the electroosmotic and osmotic effects are greatest with "unsuccessful" synaptic events. Even though there seems to be no way to predict just what these effects on synapses will be, the end result would be similar. For if the effect increases the efficacy of an "unsuccessful" synapse, it will tend to make the synapse more "successful," especially if the same thing is occurring simultaneously at other synapses on the same postsynaptic cell. If it decreases the efficacy of an "unsuccessful" synapse, it tends to destroy it as a synapse. So no matter what the effect, "unsuccessful" synapses will tend not to survive; they may either become "successful" or be eliminated as synapses. "Unsuccessful" synapses are unstable. "Successful" synapses are not affected, and are stable. Therefore, the proportion of the total synapses which are "successful" is maximized.

On psychological grounds Hebb and Milner (*14*) have proposed and developed the idea that learning might be due to synaptic efficacy increasing whenever a presynaptic excitatory fiber fires simultaneously with its postsynaptic cell. The electroosmotic effect and possibly the osmotic effect provide just such a mechanism, including a functional generalization to postsynaptic inhibitory synapses.

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15. Supported by NIH grant NB 04352-01.

23 December 1963

Albinism and Water Escape Performance in the Mouse

Abstract. *Observation of six inbred strains of mice in a water escape test revealed that albino strains perform markedly slower than non-albino strains. Performances of F_1, F_2, and backcross offspring of selected crosses between these strains indicated that there is an association between the homozygous condition for albinism* (cc) *and slow performance in the water escape test.*

This report presents evidence for an association between albinism and water escape performance in the mouse (*Mus musculus*). Albinism in the mouse is due to the homozygous recessive condition of the *c* allele at the *C*-locus in linkage group 1 (*1*).

Our measure of behavior (escape from water) is a quantitative character displaying continuous variation. It seems reasonable to assume that many loci are involved because behavioral characteristics are physiologically complex and undoubtedly are influenced by a variety of genes (*2*). However, such a character may be influenced by domi-

Table 1. Summary of performances in the water escape test.

Genotype	N	Escape time (sec.)		Escape time (Log. trans.)	
		Mean	S.D.	Mean	S.D.
A (albino)	46	99.5	64.63	4.79	1.02
BALB/c (albino)	48	149.8	125.74	5.30	1.43
C3H/Bi	36	39.3	22.41	3.21	0.89
C57BL/1	36	29.8	15.13	2.75	0.91
DBA/8	81	44.3	47.82	3.36	0.80
JK	36	44.6	24.44	3.58	0.81
A × BALB/c	49	112.2	89.54	4.77	1.22
A × C3H/Bi	20	28.4	20.22	2.53	0.90
A × DBA/8	43	34.1	14.93	3.10	0.85
C3H/Bi × DBA/8	20	20.0	10.44	2.26	0.82
(A × DBA/8) × (A × DBA/8)	56	49.3	44.11	3.63	0.96
Albino	11	62.7	25.90	4.39	0.81
Non-albino	45	46.1	44.69	3.45	0.91
A × (A × DBA/8)	25	47.9	22.11	3.65	0.80
Albino	11	56.4	22.61	4.06	0.73
Non-albino	14	37.2	16.79	3.32	0.70
DBA/8 × (A × DBA/8)	25	39.3	30.51	3.32	0.91

nant or recessive alleles at single major loci, as well as by the action of polygenes. Moreover, environmental variation may contribute to the observed continuous variation.

The subjects used in this experiment were derived from six strains of laboratory mice, all of which have been inbred for more than 30 generations by brother-sister mating. Our findings are based upon 521 animals distributed across genotypes in the manner indicated in Table 1. All subjects were reared and housed under the same conditions and were tested in early adulthood (75 to 125 days of age) with age distributions approximately the same for all genotypes.

The water escape test was conducted in a circular galvanized iron container, 26.7 cm high, 43.2 cm in diameter, and filled to a depth of 8.9 cm with tap water at 27° ± 1°C. A wire-mesh escape ramp 10.2 cm wide was mounted on the wall of the container at approximately an 80° angle so that it was 3.2 cm from the wall at the water surface. Each subject was given four trials with an interval between trials of 15 to 20 minutes.

A trial was begun by placing the animal in the water facing the wall opposite the escape ramp. The subject was returned to its home cage when it was out of the water and had all four feet on the ramp, and the experimental measure was the time (in seconds) required to swim to the escape ramp and emerge from the water. A correlation between means and standard deviations of escape times was eliminated by transforming the score on individual trials to common logarithms.

Initial observation of water escape performance in six strains of inbred mice revealed that the two strains of albino mice were very much slower in escaping from the water than any of the four non-albino strains (*3*). Moreover, the non-albino strains did not differ as much between themselves as the slowest of the four non-albino strains differed from the fastest of the two albino strains. These findings suggested that the *c* allele might be a gene of major effect on water escape, and this hypothesis led us to collect further data which are summarized in Table 1.

Three hybrid crosses between strains A (albino), C3H/Bi and DBA/8 resulted in offspring that exhibited heterosis in performance [escape from water faster than the faster of the two parent strains: A × C3H/Bi: $t_{54} = 1.80$, $p < .01$; A × DBA/8: $t_{122} = 1.69$, $p < .10$; C3H/Bi × DBA/8: $t_{99} = 5.48$, $p < .001$ (*4*)]. Heterosis suggests the existence of nonallelic interaction within a polygenic system. In the two crosses involving the albino strain (A × C3H/Bi and A × DBA/8), however, the similarity of the offspring to the non-albino parent is also consistent with the possibility of a single factor which, when recessive, contributes to slow escape from water.

To further investigate the likelihood that there is such a factor, and that it is associated with the albino locus, we examined the performance of the F_2 generation of the A × DBA/8 cross. The albino mice recovered (segregated) in the F_2 generation were significantly slower than non-albino F_2 animals from the same cross ($t_{54} = 3.14$; $p < .005$); this supports the hypothesis of an association between water escape behavior and albinism. In addition, examination of the offspring from the backcross between the A × DBA/8 (F_1) and the A strain revealed a comparable difference between albino and non-albino subjects ($t_{23} = 2.56$; $p < .02$).

One further comparison was made to explore the relationship of homozygosity for albinism to water escape behavior. For this comparison the A (albino) and BALB/c (albino) strains were crossed. These two strains have been reproductively isolated for more than 60 generations of inbreeding and they are known to differ on a variety of characters (*5*). Thus, we know that they differ in genotype in spite of their identity at the *C*-locus. The hybrids of this cross exhibited some of the usual manifestations of heterosis or hybrid vigor, such as increased litter size, low infant mortality, and greater average weight at weaning (Table 2). In the water escape test, however, they failed to display significant behavioral heterosis.

Our inference, then, is that the recessive gene for albinism is also a recessive gene for slow water escape behavior. These data in no way suggest that albinism is the only factor that does or could make a "major gene" contribution to phenotypic variance in water escape behavior; indeed, any one of a number of heritable factors could make such a contribution. However, the magnitude of the contribution from this single genetic locus is sufficient to be discernibly expressed even in the presence of hybrid vigor resulting from heterozygosity at other loci.

The passivity of albino mice and rats is well known among behavioral investigators and the behavior of albino strains has frequently been reported as discontinuous with the performance of

Table 2. Heterosis in the offspring of a cross between albino strains.

Genotype	No. of litters	Litter size		Litter size at 22 days of age		Weight at 22 days of age	
		Mean	S.D.	Mean	S.D.	Mean	S.D.
A	175	6.200	2.295	3.720	2.559	9.593	1.464
BALB/c	133	7.038	2.390	6.233	2.620	10.762	1.413
A × BALB/c	28	7.964	2.743	6.714	3.029	11.075	1.247

other strains (*6*), suggesting that albinism may influence not only escape from water but other forms of behavior as well. Previous investigations have revealed an inability of the A strain to learn a running response in a test of avoidance of electric shock, and a tendency toward low activity (freezing) and a high rate of emotional defecation in a stressful or aversive situation (*7*); our water escape test is also a measure of an active response to aversive stimulation. All these findings together suggest that albinism may be associated in a general way with activity, or with responsiveness to aversive stimuli.

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3. The vigor or persistence of swimming may have been the major determinant of test performance, although some animals did learn to escape very rapidly by orienting toward the escape ramp immediately upon being placed in the water. The fast performance of C3H/Bi, a blind strain, indicates visual stimuli were of little importance.
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22 January 1963

Courtship Sound Production in Two Sympatric Sibling Drosophila Species

Abstract. *Courting males of* Drosophila persimilis *produce a pulsed "vibration sound," with frequency of oscillation and pulse repetition rate markedly different from that of* D. pseudoobscura. *These differences probably contribute to reproductive isolation. Flight frequency is the same in both species. Brief "preliminary sounds" are common and the same in both species. Males with large parts of both wings removed produce nearly normal vibration sounds, and normal preliminary sounds.*

The range of *Drosophila persimilis* extends along most of the western coast of the United States and is almost entirely contained within the more southerly and easterly extending range of *D. pseudoobscura.* Compared with *D. pseudoobscura, D. persimilis* is generally found in cooler, more moist habitats and is relatively more active in the morning and less active in the evening. The two species have somewhat different food preferences. However, there is wide overlap in the natural occurrence of the two species; copulating intraspecific pairs of the two can be collected simultaneously from the same food source (*1*). Hybrids are extremely rare in natural populations (less than 1/1000). Though hybrids occur in the laboratory, partial sexual isolation persists. Thus there must be isolating factors effective at close range.

Differences in courtship acts are of special interest in this context. Vibration of one or both wings is a very common act in *Drosophila* courtship. In *D. persimilis* and *D. pseudoobscura,* as in *D. melanogaster* (*2*), this vibration is accompanied by the production of a train of sound pulses. Each pulse consists of two to seven almost sinusoidal oscillations, with amplitude decreasing from about the second oscillation (see Fig. 1). The frequency of oscillation and the pulse repetition rate differ markedly in the two species (see Table 1). No consistent differences between the two species were observed in the number of oscillations per pulse or the amplitude of oscillation.

The differences in the frequency of oscillation are not directly related to differences in the frequency of wing beat during flight, since these frequencies are the same in the two species and differ from the frequency of oscillation in "vibration sounds" produced by either species. The frequency of the wing beat during flight was determined stroboscopically for three 7-day-old males of each species. The range for *D. persimilis* was 185 to 215 cy/sec and for *D. pseudoobscura* was 185 to 219 cy/sec at 24° to 26°C. Reed *et al.* (*3*), using 3-day-old virgin females of several strains of each species, found that at 20°C, the wing beat of *D. persimilis* averaged 174 cy/sec and that of *D. pseudoobscura* averaged 182 cy/sec.

Shorey (*2*) found that the temperature in his closed recording cell increased by ¼° to ½°C per minute, and that the pulse repetition rate increased by 1.4 per second with each degree centigrade in the range of 25° to 30°C. My observations on the two species were made roughly in alternation on any given day of recording, so that both species were exposed to about the same range of recording conditions. Room temperature was kept within 24.5° to 26.5°C, and when a new pair of flies was put in the observation chamber, the air in the chamber mixed freely with room air. No trends were seen in pulse repetition rate in several records taken over a period of about 3 minutes. Thus, while cell temperature was not recorded it is virtually certain that the species differences in pulse repetition rate (and also frequency of oscillation) cannot be ascribed to variations in temperature.

The observed properties of courtship sounds are presumed to be characteristic of large portions of the natural populations of these species, since they were consistent for three strains of *D. persimilis* and two strains of *D. pseudoobscura* collected in widely different parts of California. Three of these strains had been kept in the laboratory for only two generations, one for four, and one for about 16 generations.

The second very commonly observed courtship sound (designated "preliminary sound") often directly preceded vibration, though sometimes it was not immediately followed by any courtship activity. It often occurred when the male was tapping the female prior to beginning vibration. I was unable to observe any movement which was correlated with the production of this sound. The sound may occur singly or in series, somewhat more rapidly than one sound per second. The tone of the sound is not pure and the oscilloscope shows a rather irregular waveform of about 4 cycles at 430 to 500 cy/sec.

The third courtship sound was comparatively rare. It occurred when males flicked both wings, usually as they approached a female from a distance. The sound produced by one flick is a burst of about seven oscillations of irregular waveform at about 155 cy/sec. Both males and females have been seen to flick both wings without producing detectable sound.