but also geographic variation in the genetic and environmental contribution to patterns of phenotypic variation.

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14. Nestlings were measured in the field on a minimum of 4 days. All variables were transformed to logs before analysis. For each individual, separate regressions of the logs of bill length, bill depth, bill width, wing length, and central toe length on log tarsal length were calculated. For each measurement the predicted log value at log tarsus = log 20 was obtained. Univariate F tests of data for unmanipulated nestling populations in the Everglades and Tallahassee showed that at a tarsal length of 20 mm the ratio of bill depth to tarsus (Everglades 0.201, Tallahassee 0.220), a ratio of bill length to tarsus (0.492, 0.463), and a ratio of toe to tarsus (0.741, 0.693) were different at $P = .005$. The ratio of wing to tarsus in Minnesota nestlings (1.501) was higher than in Colorado nestlings (1.378), $P = .005$, as was the ratio of toe to tarsus (0.745, 0.693), $P = .01$. Numbers in parentheses above are the antilogs of the mean predicted log value at log tarsus = log 20.
15. The methods of analysis proposed (*11*) permit tests of the differences in shape. Shape variables are ratios or proportions. If the original data follow a lognormal distribution, their logs follow a normal distribution, and parametric statistics can be used. Tests of shape differences can be performed on ratios transformed to differences between logs. In measurements of study skins of adults from the Everglades (66 males, 70 females) and Tallahassee (18 males, 12 females), the most highly significant univariate shape differences ($P < .01$) were higher ratios of bill depth to tarsus for Tallahassee females and lower ratios of bill length to tarsus and toe to tarsus for Tallahassee males ($P < .001$). For adults from Minnesota (18 males, 5 females) and Colorado (13 males, 10 females) there were higher sample ratios for wing to tarsus in Minnesota, but the differences were not significant ($P = .07$ for males and $P = .13$ for females). Within localities adult females weigh only about 65 percent of the weight of males. Sexual size differences are also apparent in nestlings, but when nestling measurements were standardized to a tarsus of 20 mm, within-locality nestling shape did not differ between the sexes.
16. Clutches of three eggs each were transported intact during the last half of incubation. After eggs in foster nests were removed and replaced with equivalent-sized clutches of transplanted eggs, foster mothers accepted and incubated the new eggs.
17. Log-transformed variables at log tarsus = log 20 (*14*) for normal nestling populations were entered into two separate canonical discriminant function analyses, one for the Florida comparison and one for the Colorado-Minnesota comparison. This log shape procedure computed equations for axes (Fig. 1) that maximized differences between groups. These axes are better discriminants than are any of the shape variables taken singly. The most important correlations between the axis in Fig. 1A and the original shape variables are ratios of bill depth to tarsus (.45) and bill length to tarsus (−.24); for Fig. 1B, the ratio of wing length to tarsus was −.78, and that of toe to tarsus was −.64. The Colorado-Minnesota axis is plotted in increasingly negative units of discrimination.
18. Apparent differences in Fig. 1 between scores along the discriminant axes for normal groups and control groups are more a result of the fact that the CDF axes are determined by the normal groups than a result of experimental error. When the control groups were used to differentiate the populations, and normals were plotted on those axes, the normals were less well differentiated than the controls. The biological result of the experiment is expressed in the differences between the scores for control and transplant groups.
19. All changes reported in Table 1 are in the direction predicted by differences among adults except ratios of toe to tarsus in Tallahassee. Even differences that are not significant at the univariate level make significant contributions to the canonical discrimination.
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Recognition of H-2 Types in Relation to the Blocking of Pregnancy in Mice

Abstract. *Inbred BALB/c females were mated and subsequently exposed in a divided cage to "stimulus" males or females whose H-2 type was similar or dissimilar to the stud male's. The incidence of pregnancy blocking was considerably higher when stud and stimulus males differed in H-2 type than when they did not. Similar results were obtained with urine samples of H-2 identical and nonidentical males. Females exposed after mating to other females whose H-2 type differed from the stud male, under the same experimental conditions, also showed an appreciable incidence of pregnancy block. It is therefore concluded that chemosensory recognition of H-2 types affects the reproductive hormonal status of the pregnant female.*

Genes of the major histocompatibility complex (MHC), best known for their importance in transplantation and the immunologic handling of chemical information, also participate in a variety of other biological features (*1*), including chemosensory recognition.

Mice have been found to show natural mating preferences according to their H-2 (MHC) haplotypes, generally with a bias in favor of matings between H-2 dissimilar rather than H-2 identical pairs (*2*). The inference that H-2 haplotypes determine individual odor phenotypes that mice can sense has been confirmed by use of a Y maze in which mice were trained to distinguish the scents of congenic mice (*3*), or their urine (*4*), that differed genetically only at the H-2 region of chromosome 17, or parts of this region.

In the mouse and other species, constituents of urine and glandular secretions, acting through neuroendocrine channels, have striking effects on such reproductive phenomena as the timing of reproductive maturity and the estrous cycle (*5*). Another instance of olfactory induction of a reproductive hormonal response, and one in which recognition of individual identity appears to be involved, is "pregnancy block" (the Bruce effect). Pregnancy block refers to termination of pregnancy before implantation of the embryo (before day 6 of gestation in the mouse) after exposure of the female to an unfamiliar male, particularly of a strain different from the stud male; soiled bedding or urine of a strange male has the same effect (*6*). Administration of prolactin or progesterone can forestall blocking (*7*), which is therefore viewed as the result of a neuroendocrine imbalance inimical to implantation.

The female's recognition of a strain difference between the stud and unfamiliar males implies that pregnancy block is a means of genotype selection, at least under laboratory conditions (*8, 9*). The particular question addressed in the work reported here is whether sensory distinction of H-2 haplotypes by the female is an appreciable factor in the blocking of pregnancy.

These studies were conducted under uniform conditions of isolation to reduce interference from extraneous airborne odors (*10*). Virgin BALB/c females

(MHC type H-2^d), about 2 months of age, were paired with stud males and examined daily. When a vaginal plug was seen, the female was transferred to a second cage. Twenty-four hours later, the female was moved to a divided cage with a perforated central screen, on the other side of which was a "stimulus" mouse, or urine in a petri dish; the screen allowed only limited contact of the female with the stimulus mouse, and no contact with urine. After 3 days, the test female was returned to the second cage and was monitored for return of estrus by visual inspection of the external genitalia. Females that neither returned to estrus within 7 days nor gave birth within 21 days were classed as pseudopregnant. Blocked pregnancies and blocked pseudopregnancies are considered to be endocrinologically equivalent (*11*).

The stud males and the stimulus mice in the divided cage were typed homozygous H-2^b and H-2^k segregants of the congenic cross (B6-H-2^k × B6)F_2 (*12*). Use of congenic F_2 segregants instead of the genetically equivalent congenic strains serves to confirm cosegregation of H-2 and individual recognition and has the added advantage that F_2 segregants share their total environment, being born of uniform F_1 parents and reared in the same families. The stimulus mouse or urine donor was (i) the stud male once again; (ii) an F_2 male genetically identical to the stud male (that is, syngeneic); (iii) an H-2 dissimilar F_2 male (that is, congenic), H-2^b if the stud was H-2^k, and vice versa; or (iv) an F_2 segregant female of the same or congenic H-2 type with respect to the stud male.

Study 1 of Table 1 shows that the incidence of blocking was considerably greater when the H-2 type of the second male was different from that of the stud (58 percent, group C) rather than the same (12 percent, group B). The difference in incidence between group D (25 percent), in which there was no male in the divided cage, and the combined incidences for groups A (stud) and B (syngeneic) approaches significance ($P < .07$) and suggests that the presence of a male per se tends to preserve pregnancy (*13*).

Generally, in studies of pregnancy block, the novel male to which the inseminated female is exposed has not been recently mated, whereas the stud male, to which the female is again exposed for control purposes, has been recently mated. Since mating influences testosterone levels, a difference in recent mating experience might possibly influence the propensity of the male to induce blocking, regardless of the male's identity (*8, 14*). This does not concern groups B and C of study 1 because neither the syngeneic nor the congenic males had been recently mated. Nevertheless, the point was pursued further in study 2.

Table 1. Incidence of pregnancy blocking in relation to the H-2 types of stud and stimulus mice. A mouse or a urine sample was placed in the second compartment of the divided cage housing the inseminated BALB/c female. All stud and stimulus mice were homozygous F_2 segregants from the congenic cross B6-H-2^k × B6 (*12*). Stud males (mates of the BALB/c test females) were *H-2*^{b} or *H-2*^{k} in roughly equal numbers; the results were similar and the data have been combined. Statistical analysis was performed by the χ^2 test.

Group	Stimulus	Test females			
		Total	Returned to estrus*		P
			N	Percentage	
		Study 1			
A	— Stud male	73	8	11	
B	Syngeneic male†	76	9	12	<.001
C	Congenic male‡	76	44	58	
D	None	40	10	25	
		Study 2			
A	Stud male	47	7	15	
B	Syngeneic male	58	5	9	<.001
C	Congenic male	55	26	47	
		Study 3			
A	Syngeneic female	62	12	19	<.025
B	Congenic female	63	25	40	
		Study 4			
A	Syngeneic male urine§	64	21	33	<.01
B	Congenic male urine§	65	40	62	

*Return of estrus returning within 7 days of mating signified that pregnancy or pseudopregnancy was terminated. †Genetically identical to the stud male. ‡Genetically identical to the stud male except for H-2 type. §Fresh urine, 0.5 ml, was placed in a 3.8-diameter petri dish with gauze; the petri dish and contents were replaced twice daily.

In study 2, the syngeneic and congenic stimulus males were mated with a female at the time the test female was mated with the stud male. Thus the recent mating experience of all stimulus males was similar. The incidence of blocking was 47 percent for congenic males (group C), 9 percent for syngeneic males (group B), and 15 percent for stud males (group A). Clearly, recent mating experience is not a significant factor in the context of these studies.

We have reasoned elsewhere (*15*) that the chemosensory input upon which pregnancy block depends may include two categories of information concerning the strange mouse, one relating to sex (male pheromone), and another to genotypic identity (H-2 in the present case). Study 3 was undertaken to indicate whether both sorts of information are essential or whether H-2 disparity of stud and stimulus mice alone might induce pregnancy block. This was tested by using syngeneic and congenic stimulus females in place of males. Blocking incidence was significantly higher for congenic stimulus females (40 percent, group B) than for syngeneic stimulus females (19 percent, group A), suggesting that MHC signals alone can cause pregnancy block, although probably less effectively than when accompanied by male pheromone.

The efficacy of urine in inducing H-2–related pregnancy block was tested in study 4, in which urine samples from male donors took the place of the males themselves in the divided cage. The incidence for congenic male urine donors was 62 percent (group B) as compared with 33 percent for syngeneic donors (group A). These incidences for urine from congenic and syngeneic donors are higher than for congenic and syngeneic stimulus mice, which may be due to absence of a companion mouse, as noted above.

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12. All stud and stimulus mice, serially numbered for individual identification, were drawn from four groups of H-2 homozygous segregants of the cross (B6-H-2^k × B6)F_2, typed serologically by the cytotoxicity test on lymph node cells, comprising 38 H-2^b males, 41 H-2^k males, 41 H-2^b females, and 32 H-2^k females (B6 = C57BL/6, MHC type H-2^b).
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Insulin Elicits Ingestion in Decerebrate Rats

Abstract. *Insulin administered to rats reliably elicits ingestion of food. To determine whether the neural mechanisms sufficient to control insulin-elicited ingestion are located in or caudal to the forebrain, decerebrate rats were treated with insulin and ingestive responses were measured. Insulin treatment produced hypoglycemia that was comparable, in magnitude and duration, in control and decerebrate rats. Decerebrate and control rats ingested significantly more sucrose solution while hypoglycemic than while normoglycemic. In contrast, insulin did not augment the water consumption of either group. These data indicate that neural systems caudal to the forebrain are sufficient to control ingestive consummatory behavior through the integration of metabolic signals generated by insulin treatment and taste afferent input from the oropharynx.*

Feeding is elicited when metabolic fuels are insufficient to meet the energetic demands of the organism. This compensatory ingestive behavior can be triggered by insulin treatment. Receptors located in the forebrain that are responsive to decreased glucose utilization brought about by the action of large doses of insulin are thought to mediate this feeding behavior (*1*). Several lines of evidence suggest that the lateral hypothalamus (LH) is the site of these forebrain receptors. Intravenous administration of insulin alters the activity of LH neurons (*2*). Also, destruction of these putative receptors by LH lesions abolishes insulin-elicited feeding (*3*). Analogously, supplying these receptors with glucose by way of cannulas implanted in the LH blocks insulin-elicited feeding (*4*).

Recent findings, however, indicate that under special circumstances rats with LH lesions will feed in response to insulin treatment (*5*). While these data suggest that the critical receptors or pathways mediating insulin-elicited feeding are not in the LH area alone, they do not specify the neural systems sufficient to control this feeding response. These systems could reside in hypothalamic tissue not damaged by the lesions, in other forebrain tissue, or in sites caudal to the forebrain.

Evidence also suggests that neural controls of ingestion are represented at more caudal levels of the nervous system. Decerebrate rats have normal discriminative responses to taste (*6*) and there is evidence (*7, 8*) that such decerebrate rats increase their ingestion of sucrose solution in response to food deprivation. Furthermore, microinfusions of an antimetabolic analog of glucose (5-thioglucose) restricted to the fourth ventricle of intact rats elicit feeding (*9*). It remains unclear, however, whether both the energy deficit signal and the resultant compensatory food intake are mediated by hindbrain mechanisms alone, or whether hindbrain signals are relayed to the forebrain which then initiates ingestion. The purpose of the present study was to determine whether, in isolation of the forebrain, integrative mechanisms complete within the caudal brainstem are sufficient to regulate sucrose ingestion in response to the energy deficit signals evoked by insulin treatment.

Sprague-Dawley male rats (320 to 350 g) served as subjects. Brains were transected in the supracollicular plane with a hand-held spatula. Decerebration was performed in two stages with a 7-day period separating the first and second stages (*10*). Rats so treated do not spontaneously eat or drink, nor do they effectively thermoregulate. Therefore, these decerebrate rats and control rats were maintained exclusively on three 12-ml, tube-fed meals daily (*11*). Body temperature of the decerebrate rats was closely monitored and maintained between 32° and 36°C by warming or promoting evaporative cooling by wetting the fur. With the use of these procedures rats can survive transection for 1 to 2 months. The rats were housed in individual cages and maintained on a normal cycle of light and darkness.

The ingestive responses of the aphagic rats was assessed by fitting both the decerebrate (N = 12) and control (N = 20) animals with two intraoral fistulas through which taste stimuli could be delivered. Three rats from each group were also implanted with intravena cava cannulas (*12*) to facilitate blood withdrawal. The distal end of the venous cannula was anchored to the top of the skull adjacent to the intraoral fistulas. In the first experiment, control (N = 11) and decerebrate (N = 6) rats were treated with regular insulin (10 U/kg; Iletin, Lilly) or saline (0.9 percent). Subsequently, in a second experiment, six decerebrate and nine control rats were treated with 5 U of insulin per kilogram of body weight. Intake and plasma glucose testing occurred a minimum of 2 weeks after complete decerebration.

Insulin elicits spontaneous feeding in normal rats when blood glucose levels fall below 70 mg/100 ml (*13*). To determine the optimal time for the intraoral intake tests, we monitored plasma glucose concentrations after insulin treatments. Rats were tube-fed their morning 12-ml meal and 1 hour later were injected subcutaneously with either physiological saline (0.9 percent) or regular insulin (10 or 5 U/kg in a volume of 1.0 ml/kg).