two with New Hampshire X Barred Rock chicks, the third with Barred Rock chicks. Birds in each experiment were assigned at random to one of three groups. Birds in group 1 were exposed to the model during the critical period for imprinting. Birds in group 2 were exposed to the model for the same length of time but after the critical period for imprinting. The exposure period of group 3 covered that of both group 1 and group 2.

From Table 1 it can be seen that the birds in groups 1 and 3 were within 4 inches of the model during about half the observations. Birds in group 2 followed hardly at all. Most of them remained at the opposite end of the box from the model, although two birds in this group scored about half the mean for the other groups (13.1 and 12.9).

Birds imprinted within the critical period (groups 1 and 3 combined) trod much more than those imprinted outside the critical period ($\chi^2 = 10.6$, $p < .01$), and the difference between group 1 and group 2 is also significant ($p = .002$, Fisher's exact test).

Of the 19 birds which exhibited sexual behavior, 18 trod only their training model. The remaining bird trod the training model 12 of 13 times.

Most of the birds which exhibited sexual behavior did so within the first minute of the first test, although one did not start until the second test on day 20. Typically, a bird would tread the model several times during each of the first few minutes of the test, and then sporadically toward the end of the session. Non-treaders in groups 1 and 3 did not differ significantly in their following scores from the treaders (26.9 for treaders and 26.8 for non-treaders). However, the one bird in group 2 which trod the model had a high following score (13.1). There were no observable differences in behavior between the different strains or replications.

Birds in groups 1 and 2 were exposed to the model for the same length of time, and differences can therefore be attributed only to the different times at which the models were introduced into the boxes. The two groups differed also in the length of time between their last exposure to the model and the sex tests, but it is unlikely that this variable caused the difference in behavior since birds of group 2, which had seen the model only 2 days before the sex tests, did *not* tread, and group 3 birds, having the same interval between last exposure and sex tests, *did* tread. Under the conditions of this experiment, experience during the critical period for following is of particular significance in determining the sexual object (*4*).

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3. Testosterone propionate used in this experiment was supplied by the Schering Corp., through the courtesy of Dr. E. Henderson.
4. This research was done in partial fulfilment of the requirements for the M.A. degree at Queen's University, and was supported by a grant (APA-37) from the National Research Council of Canada to Dr. P. H. R. James.

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Alimentary Responses Evoked from Forebrain Structures in Macaca mulatta

Abstract. Previous work on the mechanisms of hunger-satiety in mammals has led to the localization of these functions in the lateral and ventromedial hypothalamic areas. The present work indicates that portions of the frontal lobe, temporal lobe, cingulate gyrus, septum, and thalamus are involved as well.

The results of numerous experiments on alimentary mechanisms in the past 25 years (*1*) have led to the proposal that hunger and satiety are critically dependent on discrete, mutually antagonistic centers located in the hypothalamus. This evidence has provided strong support for the concept of diencephalic control of basic physiological needs and has had an important influence on theories relating to a variety of visceral functions.

The possibility that the mechanisms of hunger-satiety are somewhat less discretely organized than is implied by this concept of hypothalamic control has been suggested recently by at least two different lines of evidence. First, sexual behavior, which in the past has also been closely linked with the hypothalamus, is now known to have components—for example, penile erection—which can be elicited by stimulation from many areas outside as well as inside the hypothalamus (*2*). Second, that alimentary mechanisms may resemble sexual mechanisms in having a widely dispersed neural representation in the forebrain has been suggested by recent experiments implicating the orbital cortex and the amygdala in various forms of alimentary behavior (*3*).

The following experiment (*4*) was undertaken to search for those areas in the forebrain of the monkey (*Macaca mulatta*) from which food and water intake could be directly modified by electrical stimulation. The brains of 8- to 12-lb rhesus monkeys were explored stereotactically with movable electrodes while the unanesthetized animal was confined temporarily in a primate chair (*5*). Food and water were always present, and the animal could obtain them directly without using its hands. The electrode was advanced through the brain in 1-mm steps, and at each locus the behavior evoked was studied for its relationship to alimentation. Over 5800 loci distributed among 220 tracks in 15 animals have been explored in this fashion. The stimulating electrode consisted of Teflon-coated, stainless-steel wire 0.005 inch in diameter, bare at the tip for 0.5 to 1.0 mm. A large stainless-steel screw inserted into the skull served as an indifferent electrode. The stimulus was usually a 50-cy/sec, 1-msec unidirectional pulse. The stimulating electrode was the cathode, with threshold current intensities for the behavior patterns to be described ranging from 0.05 to 0.5 ma per pulse. Reconstruction of the electrode tracks was aided by utilizing measurements of imped-

Table 1. Number of points (N) which were stimulated and the number which yielded alimentary effects.

Structure	N	Effect		
		Intake	Ejection	Vomiting
Lateral hypothalmus	67	28	3	0
Posteror hypothalmus	79	34	9	0
Septum	75	4	5	18
Medal preoptic area	85	14	14	0
Anterior cingulate gyrus	200	33	2	0
Olfactory tubercle–diagonal band–substantia innominata	75	16	21	23
Amygdala	142	3	38	63
Midline thalmus	88	24	6	3
Ventralis anterior	102	0	24	59

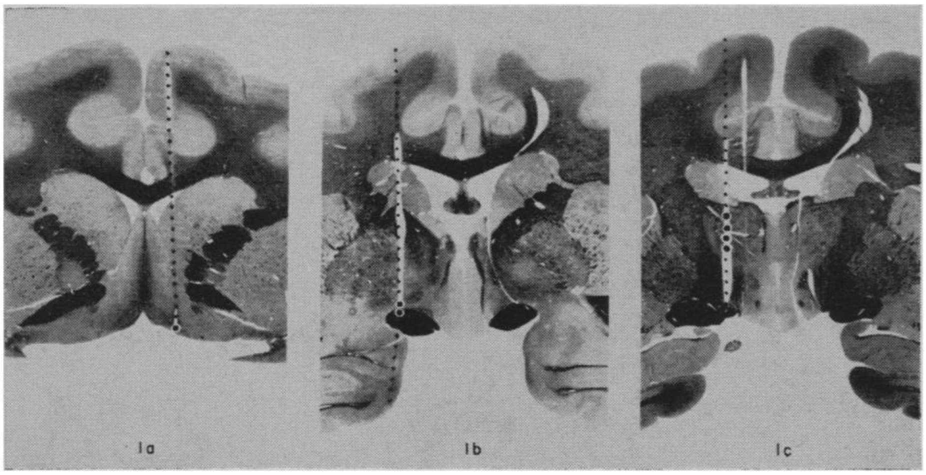

Fig. 1. The loci stimulated are indicated by the columns of dots. Responses of the types indicated for *a*, *b*, and *c* headings were evoked from those loci marked with large dots. Portions of the electrode channel can be seen in each case. Myelin stain. Frontal sections. *a*, Food intake from diagonal band of Broca. *b*, Food ejection from substantia innominata. *c*, Vomiting from nucleus ventralis anterior.

ance changes in the tissue surrounding the electrode tip taken during exploration as the electrode was advanced through the brain (*6*). For example, in the track illustrated in Fig. 1*a*, entries into cortex, corpus callosum, ventricle, caudate, and ventral subarachnoid space (exit from the brain) produced characteristic impedance changes and could therefore be identified during exploration. The measurements obtained plus the terminal position of the electrode allowed reconstruction of the track in five segments, each depending on a slightly different scale of expansion. Much of the distortion introduced by histological processing can be corrected in this manner.

This report deals only with those structures listed in Table 1 (column 1), for which all electrode placements have been analyzed histologically. Food and water intake in sated animals have been elicited from 62 hypothalamic and 94 extrahypothalamic placements in 13 animals. The number of effective loci are indicated in column 3 of Table 1. Figure 1*a* illustrates one such point in the diagonal band. If near-threshold currents were used there was usually no evidence of strong emotion or excitement; indeed, little was seen to suggest the nature of the point if food and water were removed. The effects of stimulation were apparently rapidly dispelled, for ordinarily, at the cessation of stimulation, ingestion and swallowing of food and water ceased, and food remaining in the mouth or buccal pouches was ejected spontaneously. Normal food preferences—for example, fruit over laboratory chow—could usually be demonstrated when ingestion was elicited from extrahypothalamic loci. Although food and water intake were obtained together from some of the hypothalamic and extrahypothalamic points, this overlap was small and, when it did occur, a clear preference for one or the other was usually observed (see *7*).

Food ejection in hungry animals has been evoked from 12 hypothalamic and from 110 extrahypothalamic placements in ten animals. Column 4 of Table 1 indicates the number of effective loci. Figure 1*b* illustrates one such point in the substantia innominata. (The ejection elicited from the second point, in the optic tract, is believed to have resulted from current spread). The ejection pattern is a short latency response consisting of cessation of chewing, transfer of the contents of the buccal pouches into the mouth, and then expulsion of the food with the tongue. This pattern appears to be similar to that previously described by Delgado and Wyrwicka (*8*). If near-threshold currents are used, stimulation of ejection points may produce observable effects only if the animal has food in its mouth at the onset of stimulation. A low-preference food or food in the front of the mouth is more readily ejected than a high-preference food or food in the buccal pouches or anterior pharynx. As with evoked ingestion, the effect rapidly dissipated after the stimulus was terminated, for the ejected food, if made available, was usually reingested after a few seconds. Ejection often occurred without vomiting or gagging and, under these circumstances, was only rarely accompanied by signs of emotional disturbance. (Indeed, in a preliminary study of the motivational properties of this behavior pattern, 7 of 12 ejection points were found to motivate self-stimulation and only 1 point motivated behavior leading to escape from stimulation.) Interaction studies have indicated that ejection and intake points are mutually antagonistic, since simultaneous threshold stimulation of one of each type results in a net cancellation of effects.

Gagging and vomiting have been evoked from 166 placements in 11 animals. The number of effective loci are given in column 5 of Table 1. Figure 1*c* illustrates one track passing through the nucleus ventralis anterior. The latency of this response is considerably longer than that for food ejection, and the response is usually prolonged for several minutes after cessation of the stimulus. Surprisingly, food ejection failed to accompany the gagging in slightly less than half the placements, the animal pouching the food until it appeared to feel well enough to continue eating.

The present data suggest that the neural substrate for ingestion, ejection, and vomiting is distributed over extensive areas of the primate forebrain and has representation not only in the hypothalamus, but in other parts of the limbic system as well as in the thalamus. Additional studies are necessary to determine whether the hypothalamic components of this system possess motivational, autonomic, or other properties which would differentiate them from the extrahypothalamic components. However, it is clear that studies of alimentation confined to the hypothalamus serve to characterize only part of a larger forebrain system.

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Reflexive Selection: A Possible Answer to an Old Puzzle

Abstract. With the color vision and learning abilities of birds and teleosts now proved, it appears possible that the hitherto puzzling massive variation in color and pattern of certain species, distributed through at least five phyla, is not the result of the mere free play of mutation but represents a protective variation and is the product of what may be called reflexive selection.

Animal species in which variation in color and pattern is so great that virtually no two individuals look alike have long presented an evolutionary puzzle. For such species it is impossible to designate one form as "wild-type" and others as mutants. In marked contrast stand most species with their rigorous uniformity, as, for example, the common eastern robin, *Turdus migratorius*, in which every individual among countless thousands will show a white spot on each outer corner of the tail when in flight. In contrast also are the commonly recognized polymorphic species such as the eastern gray squirrel, *Sciurus carolinensis*, with its two color phases, or the well-studied ladybird beetle, *Adalia bipunctata*, and *Drosophila pseudoobscura*, where only a limited number of forms occur and do not necessarily coexist in time and place.

The kind of variation discussed here is well exemplified by the common North Atlantic brittlestar, *Ophiopholis aculeata*, among echinoderms, and the little coquina or butterfly clam, *Donax variabilis*, among mollusks. In *Ophiopholis* the variation in color and pattern occurs on both the body disc and on the arms. The colors range from reds and purples to browns, near blacks, light yellows, deep yellows, oranges, and pinks. The disc may be some solid color with or without a conspicuous colored border. Instead of a continuous border there may be a large colored spot on the disc at the base of each arm. Or the disc itself may show a single central spot or group of spots with or without a colored border or peripheral spots. The disc may bear a large five-pointed star, or it may be mottled or finely speckled. Every combination and permutation of these designs and colors, and many more besides, can be found. The variation of colors and patterns on the arms is as great as it is on the disc and is independent of the design on the disc. The not surprising result is that out of hundreds of individuals collected at low tide in about an inch of water in a single cove on the coast of Maine it is not possible to find two exactly alike (see Fig. 1).

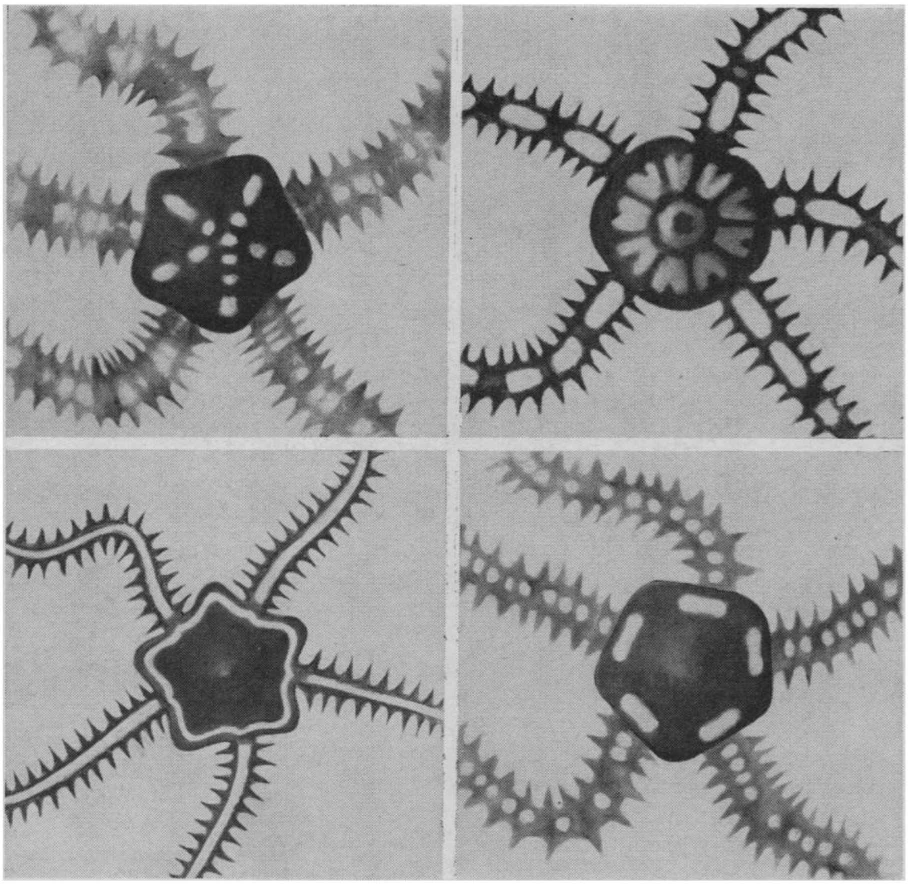

Fig. 1. Four individuals of the same species of brittlestar, *Ophiopholis aculeata*, showing variation in pattern.

In *Donax* the shells range from white to yellow, orange, green, pale blue, lavendar, deep purple, red, pink, and brown. These colors, or lack of color, are sometimes uniform over the entire shell but are usually combined in various ways and the colors themselves are found in concentric rings following the growth lines of the shell and as bands of color radiating out from the umbones so that a plaid-like effect is produced. The statistical possibilities for variation are again enormous, and diligent search through hundreds of individuals is required to find two that are the same.

Massive diversity of this kind is usually dismissed as the result of the free play of meaningless mutation in the absence of selection on the assumption that the colors and patterns have a selection value of approximately zero, being neither positive or negative in effect. Even in the familiar cases of polymorphism mentioned earlier there is "little or nothing," according to E. B. Ford (*1*), "to show what are the advantages that are opposed to one another" in maintaining the condition.

However, in the case of massive variation the possibility presents itself that it is the variation as such which is adaptive, giving a measure of protection against predators. *Donax variabilis*, for example, lives in enormous numbers on beaches from Maryland to Texas, migrating daily with the surf up and down the beach (*2*) where it is eaten by various species of sandpipers (*3*). Brittlestars are known to be eaten by teleosts and are probably eaten by birds also (*4*). Birds and teleosts are now known to possess color vision as well as the ability to learn (*5*). Consequently, if all brittlestars or all co-