predicted on the assumption that the animals injected with puromycin would be less fearful. Here then is further evidence that puromycin interferes with the consolidation of conditioned fear. Whether its effects on retention in goldfish are still more general remains to be demonstrated in experiments with different dosages, different loci of injection, and different tasks.

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Hormone-Mediated Nutritional Control of Sexual Behavior in Male Dung Flies

Abstract. *Male* Scatophaga stercoraria *must prey on other Diptera before they display sexual behavior, develop the accessory cells of their ejaculatory ducts, and achieve full elongation of the testes. The corpus allatum also becomes enlarged after predation and is necessary for the onset of sexual behavior and development of reproductive organs. The complex diet consumed during predation apparently activates the corpus allatum, and the hormone released acts independently on organ growth and sexual behavior.*

It is widely stated that male insects require no special nutrition for reproduction, but vitamin E recently has been shown to be necessary for normal spermiogenesis in the cricket *Acheta domestica* (*1*), and spermatophore production in the bug *Rhodnius prolixus* ceases after long periods of starvation (*2*). Deprivation of food has also been shown to reduce development of male internal reproductive organs in several insects (*3*), yet the influence of nutrition on male sexual behavior apparently has not been examined.

In the predatory yellow dung fly, *Scatophaga stercoraria* (L.) (Diptera, Anthomyiidae), I have found that both sexes generally must be sexually mature to be attracted to cattle dung, on which both insemination and oviposition occur, and a period of predation on small Diptera in pastureland vegetation is prerequisite to sexual maturity. Laboratory studies revealed that males, maintained from emergence on sucrose and water, never attempted to copulate with females; at first they ignored or avoided them, and after several days they ate them. Males having access to *Musca domestica* L. from emergence continued to avoid or ignore females for about 4 days before abruptly starting to copulate with them; ability to copulate sometimes preceded ability to inseminate by as much as 1 day. The onset of sexual behavior did not require the presence of females; sexual responses could be elicited by other males or by inanimate objects.

Comparison of dissections of ten prey-supplied and ten prey-deprived males 8 days after emergence with dissections of ten newly emerged males revealed that deprivation of prey did not prevent spermiogenesis. But the testes of prey-deprived males were not so elongated as those of prey-supplied males (*t*, 2.89; d.f., 18; $P < .01$; two-tailed test), though testes of the former were much longer than those of newly emerged males. The accessory cells that surround the ejaculatory duct (measured as the greatest diameter of the ejaculatory duct) were slightly smaller in prey-deprived males than in newly emerged males (*t*, 3.10; df., 18; $P < .01$; two-tailed test), whereas in prey-supplied males the accessory cells were far larger than those in newly emerged males. Similarly, the corpora allata of prey-supplied males were usually much larger than those of prey-deprived males of similar age, or those of newly emerged males.

These observations suggested that in male *Scatophaga* the corpora allata might control both development of accessory cells and sexual behavior as in the locusts *Schistocerca gregaria* (*4*) and *Locusta migratoria* (*5*); the corpora allata might also control the rate of spermiogenesis. Furthermore the apparent nutritional activation of the corpora allata in male *Scatophaga* closely resembles the case in female insects, in which corpora allata hormone, as well as available yolk precursors, is necessary for vitellogenesis; it is released in response either to gut expansion (*6*) or to the presence of nutrients in the gut or hemolymph (*7, 8*).

To demonstrate the role of the corpora allata in male sexual maturation in *Scatophaga*, seven males were allatectomized within 4 hours of emergence, with fine forceps through a neck incision; then each was allowed access to ten *Musca*, the dead being replaced daily, in a 340-cm^3 predation carton, with water and sucrose available. Sham-operated and unoperated controls were each divided into prey-supplied and prey-deprived groups. Eight days after emergence all males were tested for response to females in the presence of dung (but pairs were separated before insemination could occur); they were then dissected for measurement of the ejaculatory ducts, testes, and corpora allata.

Predation rates were roughly the same in all three prey-supplied groups, but none of the seven allatectomized or 13 prey-deprived males attempted to copulate with females, whereas all six sham-operated, prey-supplied males attempted copulation, as did five of the ten unoperated, prey-supplied males. The diameters of ejaculatory ducts of allatectomized males were all a little larger than those of 17 prey-deprived controls (including four not used in mating tests) (*t*, 9.25; d.f., 22; $P < .01$; two-tailed test), but were much smaller than those of all but two of the prey-supplied controls.

The mean length of testis of allatectomized males was not significantly greater than that of prey-deprived controls (*t*, .90; d.f., 22; $P > .03$; two-tailed test), but was significantly shorter than that of prey-supplied controls (*t*, 3.61; d.f., 21; $P < .01$; two-tailed test). Examination of the retrocerebral complexes of allatectomized males showed that in all instances the corpora allata had been mainly or completely removed, while the corpora cardiaca and hypocerebral ganglia remained intact. The corpora allata, measured as the product of the long and short diameters in sagittal view, were all larger in 14 prey-supplied controls than in seven prey-deprived controls (I used only preparations in which accurate measurements could be made). Two prey-supplied controls had corpora allata almost as small as those of prey-deprived controls; these males had failed to copulate and were the ones having ejaculatory ducts unusually small in diameter.

Since the corpora allata might control the onset of sexual behavior indirectly, through development of reproductive organs, the ejaculatory ducts and testes of newly emerged males were removed through incisions in the abdomen; these males were then allowed ten *Musca*, which were restored daily. Six days after emergence only one male survived, which then attempted to copulate with females; one testis had not been removed from this specimen. Of ten males deprived of ejaculatory ducts and both testes after sexual maturity, six continued to attempt copulation for as long as 1 day later, when all had died.

These experiments hinted that the corpora allata hormone acts independently both on development of reproductive organs and on sexual behavior. This suggestion was substantiated by implantation of two retrocerebral complexes (containing corpora allata, corpora cardiaca, and hypocerebral ganglia) of sexually mature and well-fed males into the thorax of each of seven newly emerged males. By 11 days after emergence, all three surviving prey-deprived recipients of implants displayed sexual behavior, while none of the six unoperated prey-deprived controls did. None of the recipients of implants had ejaculatory ducts nearly as large as those that normal prey-supplied males have at the onset of sexual maturity, and insemination was not achieved; but the mean duct diameter of the seven recipients (including those dying 5 to 7 days before the mating test) was greater than that of the controls (t, 2.95; d.f., 10; $P < .01$; one-tailed test), and the differences in length of testis showed a similar relation (t, 1.87; d.f., 10; $P < .05$; one-tailed test).

Possibly the act of feeding stimulates production of corpora allata hormone in *Scatophaga* males, but such stimulation has not been found in female insects of other species. Studies of the influence of deprivation of prey in *Scatophaga* males showed that hunger is manifested through both increase in prey killed relative to time and increase in tissue consumed per unit of prey. Thus, when males were allowed to prey on only three *Musca* daily from emergence, they consumed more tissue from each prey, so that development of reproductive organs and onset of sexual behavior were only slightly more retarded than in males allowed ten *Musca* daily. This finding suggests that the amount of complex diet consumed, rather than the number of prey killed, controls the rate of sexual maturation.

It is also unlikely that gut expansion triggers corpora allata activation in insects that feed frequently (*7*): In *Scatophaga,* imbibition of sucrose solutions has no effect on sexual maturation even though the abdomen becomes distended by the engorged diverticulum; the tissues of consumed prey move straight to the midgut, but do not cause it to become greatly enlarged. It appears rather that food in the gut or metabolites in the hemolymph act indirectly on the corpora allata through the central nervous system [as Johansson (*7*) has proposed for the female milkweed bug *Oncopeltus fasciatus*], or that metabolites in the hemolymph act directly on the corpora allata, as Strangways-Dixon (*8*) has proposed for the female blow fly *Calliphora erythrocephala.*

Thus it appears that *Scatophaga* males are nutritionally anautogenous in the full physiological sense ascribed to many female insects, whereas, in most male insects so far studied, the males are autogenous because the corpora allata are activated spontaneously at emergence or are unnecessary for sexual maturation. The corpora allata hormone may control a switch mechanism allowing sexual responses to females, and associated sexual behavior. Although the hormone could act by blocking a nervous inhibitor of the behavior, the whole nervous mechanism would lie within the thoracic ganglion, for decapitated mature males respond sexually to females on contact, whereas decapitated immature males do not.

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Responses of Human Somatosensory Cortex to Stimuli below Threshold for Conscious Sensation

Abstract. *Averaged evoked responses of somatosensory cortex, recorded subdurally, appeared with stimuli (skin, ventral posterolateral nucleus, cortex) which were subthreshold for sensation. Such responses were deficient in late components. Subthreshold stimuli could elicit sensation with suitable repetition. The primary evoked response was not sufficient for sensation. These facts bear on the problems of neurophysiological correlates of conscious and unconscious experience, and of "subliminal perception."*

Previous studies have indicated that the first appearance of any evoked potential in sensory cortex, elicited by a stimulus to skin or sensory nerve, coincides with the threshold for some report of subjective sensation by the human subject (*1*). A similar relationship was reported for the threshold of sensory discrimination in the cat, upon stimulation of a cutaneous nerve (*2*). Such conclusions were based upon recordings made with electrodes on the scalp or situated epidurally. This provides a relatively diffuse lead from unresponsive as well as responsive cortex (see, for example, *3*). It has been demonstrated in monkeys that localized responses recorded with cortical surface electrodes may be essentially indetectable with scalp electrodes (*4*); we have found this to be true in man (see also *3*). In the present work, the recording electrode is placed subdurally, directly on the pia-arachnoid surface of somatosensory cortex (postcentral gyrus). In addition, the stimulus to the skin or to ventral posterolateral (VPL) nucleus of thalamus is so located as to elicit a sensation within the same somatic area as that in which the sensation was subjectively felt when the recording site on somatosensory cortex was stimulated directly. With such relatively precise localization it has be-