ered more digestible than triglycerides). It seems likely that the odoriferous short-chain acids also serve some purpose, such as a feeding stimulant or to identify the locations of cells, but we have no evidence on this point. The microbial production of this odor in Anthophoridae has often been assumed (*1*), but we isolated no odorifactant yeasts or other such microorganisms from cells or provisions.

Analyses of the Dufour's gland contents of related species, *A. bomboides* Kirby and *Clisodon furcata terminalis* Cresson, reveal that they also contain triglycerides. In contrast, the cell linings of many other species of *Anthophora* and related genera are thin transparent films (*5, 6*) and probably not used as larval food. Most of the secretion may be deposited instead in the provision, which often has a cheesy or rancid odor similar to that of *A. abrupta*. The use of a glandular secretion as larval food indicates a high level of specialization in these solitary bees, comparable to the production of royal jelly by honey bees.

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Binocularity in the Cat Visual Cortex Is Reduced by Sectioning the Corpus Callosum

Abstract. *In the normal cat, most cells in area 17 can be binocularly driven. Sectioning the corpus callosum results in a significant reduction in binocularly driven cells. Normal binocular vision is thus dependent on the corpus callosum.*

Integrating information from the two eyes is essential for binocular single vision and for binocular depth perception. The neural substrate for this integration is assumed to be cells that receive binocular input. In the visual pathway from the retina, information from each eye remains segregated in separate laminae of the lateral geniculate nucleus, and binocular cells first occur in the visual cortex. It has always been assumed that convergence of the input from cells in two adjacent lateral geniculate laminae onto single cortical cells is the primary means of achieving binocular integration (*1*). We have found that the corpus callosum also plays an important role in this system of binocular integration.

The corpora callosa of 11 adult cats were sectioned (*2*). In one sham-operated control animal, the skull was opened and the right hemisphere retracted to expose the corpus callosum, but no lesion was made. Between 6 and 51 days after surgery, extracellular recordings were made from single neurons in area 17 of the left hemisphere (*3, 4*). Recordings were made from the medial bank of the lateral gyrus to ensure sampling across ocular dominance columns. Receptive fields were classified as simple (types I and II) or complex, and each of these types was further subclassified as hypercomplex if the unit did not respond to long lines (*5, 6*).

Ocular dominance was estimated according to the 1 to 7 scale of Hubel and Wiesel (*7*). The receptive field size and location of each cell was marked on a tangent screen, and its position relative to the optic disks and vertical meridian was measured. We used a fiber optics system to project the retinal landmarks onto the tangent screen (*8*). After the final recording sessions, each animal was killed, the brain sectioned, and completeness of the lesion confirmed. Fourteen cells were recorded from the sham-operated cat, 66 cells from normal cats, and 304 cells from cats in which the corpus callosum had been sectioned (CCX cats). Of the 304 cells recorded in the CCX cats, 29 were not responsive to visual stimulation and 10 were geniculate afferent fibers. These 39 units have not been included in the data analysis. The ocular dominance distribution of the remaining 265 cells recorded in CCX cats is shown in Fig. 1. Sixty-three percent of the cells responded to input from one eye only (ocular dominance groups 1 and 7), and 40 percent of all neurons were driven only by the contralateral eye. The distribution of cells driven by the left or right eye was not random but was clustered, suggesting a columnar organization (*9*). In the sham-operated cat, only 16 percent of the cells were monocularly driven; this proportion did not differ from that of the five normal cats, and the data were thus combined (Fig. 1). In this normal ocular dominance distribution, only 20 percent of the cells are monocularly driven. The ocular dominance distribution in cats with corpus callosum section is significantly different from normal [χ^2 (3) = 45.5, $P < .001$].

Figure 2 shows the ocular dominance distribution in CCX cats for simple type I and type II cells and for complex cells, with receptive fields more than 4° from the area centralis. We have excluded

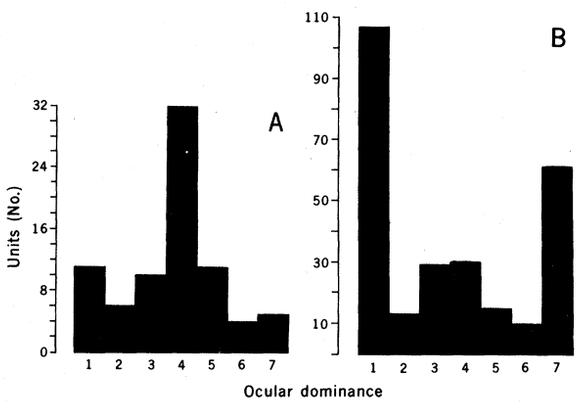

Fig. 1. Ocular dominance histogram compiled from single unit recordings in area 17 of five normal and one sham-operated cat (A) and 11 cats in which the posterior corpus callosum had been sectioned (B). In normal cats, 80 percent of cortical neurons can be binocularly activated (ocular dominance columns 2 to 6) compared with 37 percent in CCX cats.

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units with receptive fields within the central 8°, since most units recorded within this central region are monocularly driven (*4*, *10*). Only 24 percent of the simple cells and 53 percent of the complex cells in the CCX cats were binocularly driven (Fig. 2). In normal cats, 63 percent of the simple cells and 93 percent of the complex cells were binocularly driven. Thus, removal of callosal input significantly reduces the numbers of binocularly driven simple and complex cells. However, the proportion of cells that are simple or complex is not altered by the surgery (*11*).

The possibility that the corpus callosum may play a limited role in binocular integration has been suggested by other data. There is behavioral evidence of a loss of binocular depth discrimination for objects on the vertical meridian in a human subject with corpus callosum section (*12*). In addition, most corpus callosum fibers have receptive fields close to the vertical meridian (*13*). Unilateral ablation of areas 17 and 18 in the cat has been reported to result in a decrease in binocularity of cells in the opposite intact area 18 (*14*), and this effect is most apparent close to the representation of the vertical meridian. All of these findings suggested to us that, after the corpus callosum is sectioned, binocularity in cells with fields close to the vertical meridian might be lost. Our data show, however, that the influence of the corpus callosum in binocular integration extends over a much wider area of the visual field. The receptive field position of cells we recorded from ranged from the vertical meridian to more than 20° peripheral; we observed a significant loss of binocularity, not only close to the vertical meridian but also in cells with receptive field centers lying between the 10° and 20° meridians (Table 1).

The percentage of monocularly driven cells in normal cats is not uniform across the visual field (Table 2). Sectioning the callosum more than doubles the percentage of monocularly driven cells at 5° to 9° from the vertical meridian and more than triples it at 10° to 19°. [Since a high proportion of cells located within 4° of the area centralis are monocularly driven (*4*, *10*) the effects of callosal section are less pronounced in this region.] Thus corpus callosum section resulted in a loss of binocular convergence between 10° and 20° from the vertical meridian. The mechanisms by which the corpus callosum confers this binocularity are not yet fully understood (*15*).

Our data showing that the corpus callosum is essential for normal binocularity have implications for the developing visual systems, since it is well established that early monocular suture or surgical induction of strabismus result in a predominance of monocularly driven neurons in the primary visual cortex (*16*) and that these manipulations also alter the connections of the corpus callosum (*17*). The correlation between the loss of binocularity and altered callosal connections, together with our evidence on the importance of the callosum for cortical binocularity, suggest that disrupting the normal development of callosal connections may play an important role in the loss of binocularity that follows early deprivation.

Table 1. Ocular dominance distribution of cells recorded in cats with corpus callosum section as a function of distance of the receptive field from the vertical meridian.

Distance	Ocular dominance distribution						
	1	2	3	4	5	6	7
0° to 4°	65	9	14	20	9	7	23
5° to 9°	35	2	8	6	3	3	25
10° to 19°	3	0	2	3	2	0	11
> 20°	4	2	5	1	1	0	2

Table 2. Percentage of cells monocularly driven in normal cats and in cats with corpus callosum section (CCX) as a function of receptive field distance from the vertical meridian.

Distance	CCX (%)	Normal (%)
0° to 4°	60	48
5° to 9°	73	29
10° to 19°	67	17
> 20°	40	44 (*18*)

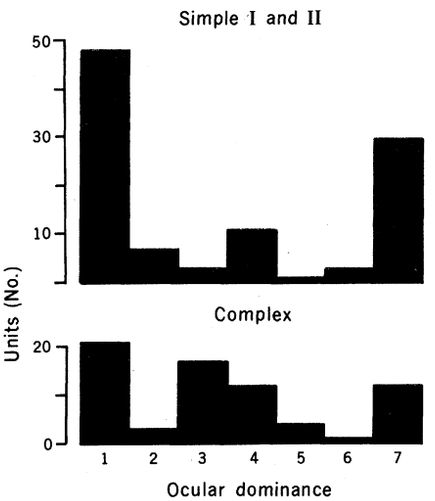

Fig. 2. Ocular dominance histograms of simple types I and II and complex cells with receptive fields located outside the central 4° of vision. The majority (76 percent) of simple cells were activated by only one eye after callosum section, whereas 53 percent of complex cells could be driven by visual stimuli presented to either eye.

Note added in proof: Our more recent experiments indicate that the loss in binocularity varies with cortical layer, and maximum loss of binocularity occurs 5 to 7 weeks after surgery.

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fibers have identified some units whose receptive fields are not adjacent to the vertical midline of the visual field. Although anatomical data indicate that the callosal projection is confined to the region of area 17 which represents the 2° of visual space adjacent to the midline, there may also be a sparse projection to areas representing more peripheral parts of the visual field. (ii) Alternatively, the appropriate information may be relayed indirectly to area 17 from another visual cortical area. It is known that neurons in other visual areas (18, 19, and lateral suprasylvian areas) have axons that project through the corpus callosum to regions in the contralateral hemisphere, which in turn project to area 17 [L. J. Garey, E. G. Jones, T. P. S. Powell, *J. Neurol. Neurosurg. Psychiatr.* **31**, 137 (1968)].
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19. We thank M. Waldron, M. D. Mulcahy, and P. Merle for excellent technician assistance. Supported by NIH grants EY-2088-01 to N.B. and EY02488-01 to E.H.M. and N.B. and by NSF grant BNS77 24923 to N.B.

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Army Ants on the Move: Relation Between Food Supply and Emigration Frequency

Abstract. *Underfed colonies of* Neivamyrmex nigrescens *in the laboratory emigrated on 62 percent of the nomadic days, as compared with only 28 percent for overfed colonies. Because the emigration frequency in the field is similar to that of underfed colonies, nomadic raids may not bring in enough food to satiate the larval broods. Since emigrations take time away from raiding, the food-related mechanism underlying emigrations may have evolved under more stringent ecological conditions.*

It is commonly believed that nomadic behavior in army ants evolved as an adaptation that enables group-predatory colonies with large, synchronous broods to regularly exploit new feeding areas (*1, 2*). This idea is supported by the fact that the nomadic phase in many species coincides with the period of larval development and ends when the larvae cease feeding prior to pupation (*3*). Nevertheless, ever since Schneirla's pioneering studies on the neotropical genus *Eciton* and on nearctic colonies of *Neivamyrmex nigrescens*, a controversy has existed concerning the proximate relation between the amount of captured booty and the frequency of emigrations to new nests (*4*). Schneirla first emphasized the role of callow and larval excitation and maintained that colony emigrations were not related to the amount of food in the nest (*1*), but later, after studying the paleotropical genus *Aenictus*, conceded that short-term variations in colony excitation may indeed depend upon the "alimentary condition prevalent in the brood" and that emigrations are likely to begin soon after food has run low (*5*).

We now report an empirical study of the relation between booty supply and emigration frequency. We have reared colonies of *N. nigrescens* through complete nomadic-statary cycles in the laboratory, and have been able to control the amount of food available to a nomadic colony to a degree that is impossible to achieve in the field. Our study shows that overfed colonies emigrate less frequently than colonies given little food. Because most of the booty captured by a nomadic colony is consumed by the larvae, we conclude that the hypotheses of food level in the nest and brood excitation are complementary rather than antithetical.

The apparatus for this study consisted of three wooden nests (each 1 m^3) filled halfway with soil, rocks, and small sections of split logs collected in the field. The nests were interconnected with 75 m of Lucite tubing (3 cm in diameter) containing a sand substrate (Fig. 1). We used four colonies that were collected early in the nomadic phase. Two colonies (77N-7 and 77N-10) comprised the underfed group and were given 0.5 g of booty each night (*6, 7*); the remaining two colonies (77N-4 and 77N-6) comprised the overfed group and were given 6.0 g each night (*8*). For all colonies, booty was always placed in food box 3 (F3 in Fig. 1) prior to nest opening in the evening (*9*). Because the nests were too heavy to move, the exit tubes were reconnected after each emigration to make the new nest lead directly to F1. In addition, after each emigration, the old nest box was emptied and filled with new substrate materials. Finally, to simulate the field condition in which army ants typically raid over new substrate each night, we redistributed the sand in the tubes by shaking them each morning. Every third day we emptied the tubes and filled them with fresh sand.

Table 1. Emigrations (+) for underfed and overfed colonies of the army ant *Neivamyrmex nigrescens*.

Nomadic day	Underfed colonies		Overfed colonies	
	77N-7	77N-10	77N-4	77N-6
3			+	+
4		+	−	−
5	−	+	−	−
6	+	+	−	+
7	+	−	−	−
8	+	−	−	−
9	−	+	−	+
10	+	+	−	−
11	+	+	+	−
12	−	−	−	−
13	+	−	−	−
14	+	+	+	−
15	+	−		+
16		+		

Table 1 shows the frequency of emigrations for the two colonies in each group. Of the two underfed colonies, colony 77N-7 emigrated on 8 out of 11 nomadic days, and colony 77N-10 emigrated on 8 out of 13 days. In the overfed group, by contrast, colony 77N-4 emigrated on only 3 out of 12 nomadic days, while colony 77N-6 emigrated on 4 out of 13 days. Perhaps most striking was the fact that overfeeding kept colony 77N-4 from emigrating for seven consecutive days, and kept colony 77N-6 in the same nest for up to five consecutive days (*10*). Overall, for the two underfed colonies combined, emigrations occurred on 62 percent of the nomadic days; in the overfed group, the emigration frequency was reduced to 28 percent ($\chi^2 = 7.8$, $P < .01$).

Although our laboratory study represents a quantitative controlled analysis of the relation between food abundance and emigration frequency, we are not ready to conclude that food quantity alone is sufficient to account for all aspects of emigration behavior in army ants. Many species of ants shift nest site when environmental conditions become unfavorable, and food scarcity can effectively make a nest unsuitable (*11*).

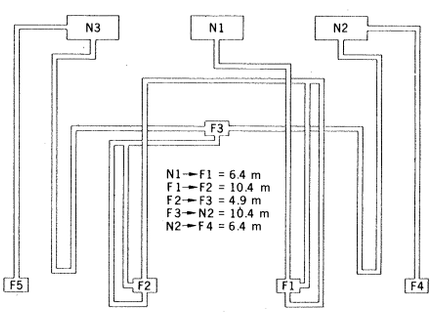

Fig. 1. Arrangement of nest boxes, food boxes, and runways comprising "Tube City." All booty was placed in F3 prior to opening the nests each day.

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