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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18. We do not have a large sample of normal data at these degrees of eccentricity and have therefore used the data of J. R. Wilson and S. M. Sherman [*J. Neurophysiol.* **39**, 512 (1976)] for comparison.
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.

27 August 1979

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*).

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		+		

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 m³) 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 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*).

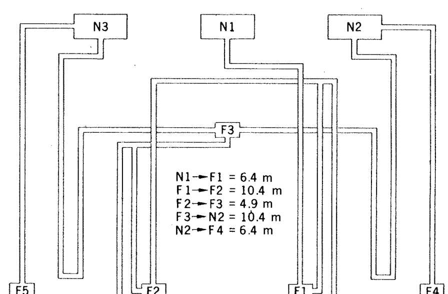

Fig. 1. Arrangement of nest boxes, food boxes, and runways comprising "Tube City." All booty was placed in F3 prior to opening the nests each day.

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Other factors, including mechanical disturbance, defense against predators, and overcrowding, may also cause colonies to change nests (*12*). Finally, even our overfed laboratory colonies eventually emigrated. When we examined the contents of the abandoned bivouac, we found large amounts of uneaten booty in various stages of decomposition. It is thus possible that chemical products of booty decay may also promote emigrations. Nevertheless, it seems clear that food scarcity is a principal cause of emigrations in *N. nigrescens*. And, given recent evidence that changes in the alimentary condition of ant larvae can produce corresponding changes in the level of adult arousal (*13*), the link between food abundance and brood excitation seems equally clear-cut for army ants.

Longitudinal field studies on *N. nigrescens* by Schneirla and Mirenda (*14*) show that the emigration frequency of nomadic colonies ranges between 74 and 88 percent. Because this corresponds best to the behavior of our underfed laboratory colonies, we are led to the conclusion that nomadic raids rarely bring in enough booty to satiate the larval broods. According to Mirenda's study (*7*), this situation is exacerbated by the very occurrence of emigrations, which take valuable time away from foraging. Perhaps the key to understanding the relationship between foraging and emigrations in *N. nigrescens* is Wilson's (*15*) principle of stringency—that time-energy budgets evolve to fit periods of greatest ecological stringency. The large number of species of *Neivamyrmex* in tropical America suggest a neotropical origin for this genus. Given the intense competition among army ant species, selection favored colonies that frequently shifted foraging areas. When food is abundant and competition reduced, as it is in southeastern Arizona, colonies are unable to suspend emigrations because of constraints imposed by the mechanisms suited to more severe conditions.

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8. Booty consisted of termites and pupae of ant species belonging to the genera *Formica*, *Camponotus*, *Acanthomyops*, *Pheidole*, and *Trachymyrmex*.
9. The arrangement of the nests and runways was dictated by an additional study (in preparation) on the relation between booty location and emigration direction.
10. That these results are not an artifact of the laboratory is shown by Mirenda's field study (*7*), in which artificially fed nomadic colonies did not emigrate for up to five consecutive days.
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Do the Two Eyes Constitute Separate Visual Channels?

Abstract. *A two-interval forced-choice procedure was used to study monocular detection of a briefly presented low-contrast sine-wave grating pattern. Uncertainty about which eye was stimulated degraded detection performance for stereoblind observers but not for normal ones. These results relate to selective monocular suppression, stereopsis, and other forms of binocular interaction and suggest the level at which inputs to the two eyes are combined neurally.*

Some question has always existed about the extent to which the two monocular images are separately processed, in terms of their spatial content, before being combined binocularly. This question bears directly on issues relating to binocular interaction, such as stereopsis, suppression, and single vision. According to one school of thought, a more or less complete analysis of monocular form precedes stereopsis and fusion. This hypothesis, which asserts that the two eyes constitute separate visual channels, was championed early by Sherrington (*1*) and has been expressed in more contemporary writings as well (*2*). Alternatively there is the viewpoint that information from the two eyes is integrated earlier in visual processing, prior to stages involving more refined analysis such as pattern recognition. Julesz (*3*) is a proponent of this view, and there are those who believe that cortical neurophysiology provides support for this single channel position (*4*). We have attempted to evaluate these two alternatives with a detection uncertainty paradigm.

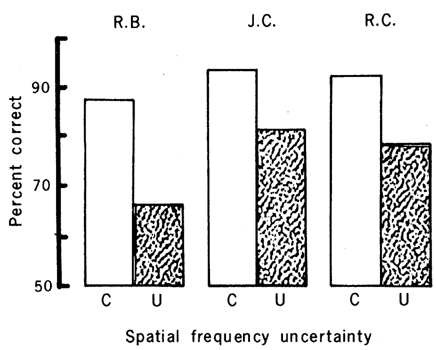

Fig. 1. Detection on a two-interval forced-choice procedure of a sinusoidal grating presented binocularly under conditions of spatial frequency certainty (*C*) and uncertainty (*U*) for three observers. Each score is based on 200 trials and represents combined data for 1 cycle/deg and 4 cycle/deg. For each observer, values for 1 and 4 cycle/deg differed by less than 5 percentage points. Before each block of trials, observers were exposed to the stimuli used for that block at easily observable contrast, thus ensuring that for the certainty conditions the observer knew the properties of the stimulus.

Our experiments capitalized on the fact that uncertainty about the spatial or temporal characteristics of a stimulus can degrade detection. This effect has been demonstrated on a variety of tasks in both audition (*5*) and vision (*6*). An example of the effects of uncertainty is illustrated by Fig. 1. These values were obtained in a two-interval forced-choice experiment; the observer's task was to indicate in which of two successive 1-second intervals (each defined by a tone) a vertical, sinusoidal grating pattern was presented. The grating was generated electronically on a cathode-ray tube (CRT) and presented binocularly. Details of the apparatus are given elsewhere (*7*). Observers viewed one of two 5° by 7° CRT displays separately with each eye. The vertical sinusoidal grating pattern which served as the stimulus was presented on both CRT's and had a total du-

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