are visible in measurements of layers 1, 2, and 3 (Fig. 2). Although other interpretations are possible, one is that the decrease is due to spatial frequency inhibition, such as has recently been implicated in psychophysical (*15*) and physiological (*16*) studies. That is, the decrement in 2DG uptake between columns may be due to the inhibition (by the cells tuned to the high spatial frequency test pattern) of those cells tuned to lower spatial frequencies in neighboring spatial frequency columns.

Orientation slabs are made up of columns of cells tuned to the same orientation (Fig. 3A), and spatial frequency slabs are made up of columns of cells tuned to the same spatial frequency. How, then, are the orientation and spatial frequency "slabs" related to each other? Preliminary 2DG evidence indicates that these slabs run in somewhat different directions across the cortical surface. Thus the autoradiographic pattern from a cat shown all spatial frequencies at a single orientation has a slablike appearance (Fig. 3A). The autoradiograph from an animal shown a single spatial frequency at a single orientation, however, is more dotlike (Fig. 3B), reflecting the intersections of spatial frequency and orientation slabs. Preliminary accounts of these intersection results have appeared (*17*).

The results indicate that striate neurons tuned to particular spatial frequencies are anatomically arranged in columns, perpendicular to the cortical surface. High spatial frequency columns are confined to the central striate cortex, and low spatial frequency columns extend peripherally, as one would predict from the well-known falloff in acuity with eccentricity. The evidence is compatible with an orderly intersection of spatial frequency and orientation slabs, and a coextensive [and possibly random (*6*)] intersection of ocular dominance slabs. Functionally, this cortical arrangement could form an anatomical substrate for a local, two-dimensional spatial frequency by orientation analysis of information in the visual world.

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References and Notes

1. C. Blakemore and F. W. Campbell, *J. Physiol. (London)* **203**, 237 (1969); K. K. De Valois, R. De Valois, E. W. Yund, *ibid.* **291**, 483 (1979); L. Maffei and A. Fiorentini, *Vision Res.* **13**, 1255 (1973); D. G. Albrecht, R. L. De Valois, L. G. Thorell, *Science* **207**, 88 (1980).
2. S. A. Talbot and W. H. Marshall, *Am. J. Ophthalmol.* **24**, 1255 (1941); D. Whitteridge and P. M. Daniel, *J. Physiol. (London)* **159**, 203 (1961); R. J. Tusa, L. A. Palmer, A. C. Rosenquist, *J. Comp. Neurol.* **177**, 213 (1978).
3. E. T. Rolls and A. Cowey, *Exp. Brain Res.* **10**, 298 (1970).
4. D. H. Hubel and T. N. Wiesel; *J. Physiol. (London)* **165**, 559 (1963); *Proc. R. Soc. London Ser. B* **198**, 1 (1977).
5. M. P. Stryker, D. H. Hubel, T. N. Wiesel, *Soc. Neurosci. Abstr.* **3**, 1852 (1977).
6. D. H. Hubel, T. N. Wiesel, M. P. Stryker, *J. Comp. Neurol.* **177**, 361 (1978).
7. L. Maffei and A. Fiorentini, *Vision Res.* **17**, 257 (1977).
8. I. I. Thompson and D. J. Tolhurst, *J. Physiol. (London)* **300**, 57P (1980).
9. L. Sokoloff, C. Reivich, C. Kennedy, M. H. Des Rosiers, C. S. Patlack, K. D. Pettigrew, O. Sakurda, M. Shinohara, *J. Neurochem.* **28**, 897 (1977).
10. A. L. Humphrey and A. Hendrickson, *Soc. Neurosci. Abstr.* **10**, 315 (1980); J. C. Horton and D. H. Hubel, *ibid.* p. 315.
11. M. Wong-Riley, *Brain Res.* **171**, 11 (1979).
12. R. L. De Valois and P. L. Pease, in *Methods in Physiological Psychology*, R. F. Thompson, Ed. (Academic Press, New York, 1973), p. 95.
13. J. A. Movshon, I. D. Thompson, D. J. Tolhurst, *J. Physiol. (London)* **283**, 101 (1978).
14. R. C. Collins, *Brain Res.* **150**, 487 (1978).
15. K. K. De Valois, *Vision Res.* **17**, 1057 (1977); D. J. Tolhurst and L. P. Barfield, *ibid.* **18**, 951 (1978).
16. K. K. De Valois, in *Frontiers in Visual Science*, S. J. Cool and E. Smith, Eds. (Springer-Verlag, New York, 1978), p. 277; ——— and R. B. H. Tootell, in preparation.
17. R. B. H. Tootell, M. S. Silverman, R. L. De Valois, paper presented at the annual meeting of the Optical Society of America, Sarasota, Fla., 29 April to 3 May 1980; M. L. Silverman, R. B. H. Tootell, R. L. De Valois, *Invest. Ophthalmol. Visual Sci.* **19/4** (Suppl.), 225 (1980); I. D. Thompson, and D. J. Tolhurst, *J. Physiol. (London)* **300**, 58P (1980).
18. This work was supported by grants EY0014-12 and BNS78-06171 from the National Institutes of Health. We thank E. Switkes and L. G. Thorell for advice and technical assistance during this study.

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Competition Between Ant Species: Outcome Controlled by Parasitic Flies

Abstract. *Experimental evidence demonstrates that the parasitic phorid fly* Apocephalus *shifts the competitive balance between the ant species* Pheidole dentata *and* Solenopsis texana *by interfering with the defensive behavior of* Pheidole dentata *major workers (soldiers). This represents one of the first examples of a parasite affecting competitive interactions among terrestrial animals in natural communities. Similar complex interactions are probably common in many ant communities.*

Although several theoretical (*1*) and laboratory (*2*) investigations suggest that parasites and parasitoids may alter biotic interactions among host species, their role in organizing natural communities has received little experimental study. I now present evidence that the outcome of competition between two species of ants is altered by the presence of a species of fly that is parasitic on one of the ant species. These results are significant in that the effects of higher trophic levels on interactions among terrestrial animals have seldom been investigated in natural communities (*3*), and past studies on interactions among ant species have served as a principal source of documentation for general competition theory (*4*, *5*). Most of the studies have been comparative rather than experimental, and the effects of disturbance, parasitism, and predation have not been investigated. When competition among species involves direct behavioral interactions, as is often the case in ants (*5*), alterations of these interactions arising from the presence of parasites or predators may lead to rapid shifts in community organization.

Wilson (*6*) investigated defense behavior in laboratory colonies of *Pheidole dentata*, a myrmicine ant species found

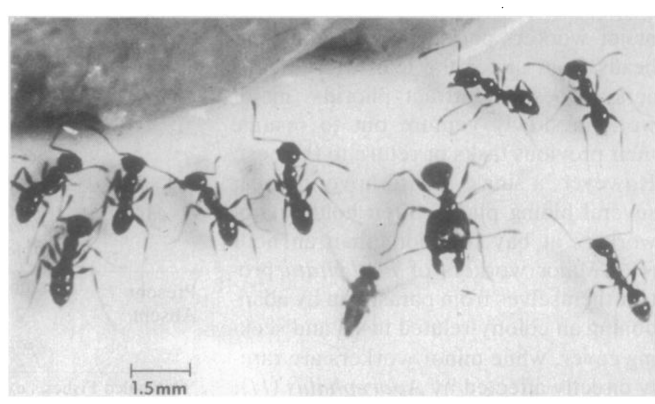

Fig. 1. Parasitic phorid fly, *Apocephalus*, hovering near major worker of the ant *Pheidole dentata*. Within seconds after this photograph was taken, the fly attempted to oviposit on the major worker.

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in woodlands of the southern United States. Like most other members of this genus, *P. dentata* has a dimorphic worker caste, with large (major) and small (minor) workers, but no workers of intermediate sizes. In most instances *P. dentata* defends its nesting and foraging areas by recruiting minor workers to the vicinity of intruding ants. However, if the intruders are fire ants of the genus *Solenopsis*, foraging minor workers recruit major workers instead. These major workers are more efficient than minor workers at eliminating small exploratory forces of *Solenopsis* and presumably reduce the chance of a massive invasion of food and nest sites. Wilson termed this preferential recruitment of major workers enemy-specific alarm-recruitment and suggested that the evolution of this behavior is a response to intense nest and food site competition between *P. dentata* and the very aggressive, rapidly recruiting, and larger colonies of *Solenopsis*.

My observations in a central Texas woodland indicate that *P. dentata* and six other common ant species are attacked by parasitic flies belonging to the family Phoridae (*7*). Interactions between ants and phorids in the field suggest that each phorid species is usually specific to one ant species or caste. In particular, the undescribed species of *Apocephalus* (*8*) associated with *P. dentata* may hover over all workers moving along a recruitment trail, but attempts to oviposit only on major workers (Fig. 1) (*9*). The caste specificity of *Apocephalus* is reflected in the different behavioral responses of minor and major workers to the presence of this phorid. Although minor workers occasionally snap at hovering *Apocephalus*, they usually continue their foraging or defensive tasks. In contrast, major workers immediately seek refuge in the leaf litter or attempt to return to the nest. If *Apocephalus* pursues a retreating major worker, the ant takes more pronounced evasive action, involving sudden stops, rapid turns, and a speedier retreat. Once under cover, major workers periodically extend their heads from under the leaf litter. If this action does not attract phorids, major workers slowly venture out to resume their previous tasks or return to the nest. However, a single phorid hovering near several hiding places often holds major workers at bay for more than an hour (*10*). Major workers of *P. dentata* protect themselves from parasitism by abandoning all colony-related tasks and seeking cover, while minor workers are rarely directly affected by *Apocephalus* (*11*).

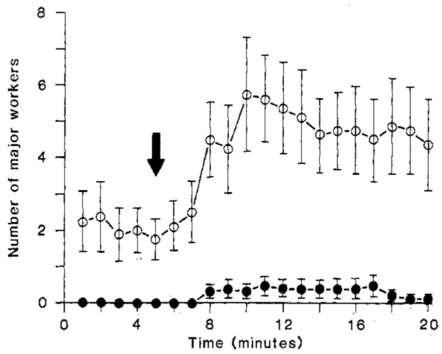

Fig. 2. Responses of *Pheidole dentata* major workers to the addition of *Solenopsis texana* (●) in the presence and (○) in the absence of the phorid *Apocephalus*. Arrow indicates the time of addition of *S. texana*. Values are means ± standard errors.

Since *Apocephalus* can "stampede" major workers, the mere presence of phorids may neutralize the alarm-recruitment against *Solenopsis*. To test this hypothesis, I performed a series of field experiments in semideciduous woodland at the University of Texas Brackenridge Field Laboratory in Austin, Texas. Ants were attracted to tuna fish placed on cards (12.7 by 10.3 cm) situated on the surface of the leaf litter. Only colonies of *P. dentata* exhibiting strong recruitment trails and maintaining more than 20 workers on cards were used in the experiments. For the first 5 minutes of each experimental session, I recorded the maximum number of major workers on the card during each minute. Next, I added 20 to 30 workers of *Solenopsis texana*. The intensity of alarm-recruitment provoked by *S. texana* was measured by counting the maximum number of *P. dentata* major workers on the card every minute for the next 15 minutes.

Table 1. Seasonal shift in the outcome of confrontations between *Pheidole dentata* and *Solenopsis texana*. Confrontations were observed along two transects of 50 tuna fish baits each. A species was scored as having control of a bait if it outnumbered all species present by at least ten workers. A change in control of a bait was scored if one species dominated that bait at time 1 and another species dominated the bait at time 2. Two hours separated times 1 and 2. Dominance changes were tallied for 22 observation periods along the transects. *Apocephalus* was absent during the observation periods of 7, 9, and 10 November 1976, and 6, 8, and 23 April 1977. *Apocephalus* was present during the observation periods of 28 May 1976; 3 June 1976; 19 and 23 July 1976; 14 August 1976; 30 May 1977; 2 June 1977; 9, 10, 13, and 17 July 1977; 18 August 1977; and 14, 16, and 18 September 1977. The small number of changes in the outcome of confrontations when *Apocephalus* was absent was primarily due to the lower activity level of *S. texana*. This reduced the number of encounters between *P. dentata* and *S. texana*.

Apocephalus	*Solenopsis* over *Pheidole*	*Pheidole* over *Solenopsis*	Total observed
Present	27	4	31
Absent	2	4	6
	$P = .0129$*		

*One-tailed Fisher's exact test.

In the absence of *Apocephalus*, *P. dentata* responded to *S. texana* by significantly increasing the average number of major workers on cards from two or three to more than six within 3 to 5 minutes ($P = .016$, two-tailed Walsh test for matched pairs). The number of major workers remained at this high level for the duration of the experimental period. Although alarm-recruitment of major workers in *P. dentata* is specifically directed at enemy ants of the genus *Solenopsis* (*6, 12*), the intensity of alarm-recruitment provoked by the addition of *S. texana* was sharply reduced when *Apocephalus* was near the experimental card or along recruitment trails. In this situation, there was no significant increase in the number of major workers recruited to the area of the bait after the addition of *S. texana* ($P > .05$, two-tailed Walsh test for matched pairs). The presence of *Apocephalus* even reduced the number of major workers at baits during the 5-minute control period ($P < .05$, two-tailed Mann-Whitney *U* test) (Fig. 2).

Behavioral observations during the experiments suggest that *Apocephalus* directly interferes with alarm-recruitment in *P. dentata*. After encountering *S. texana* on the experimental card, several minor workers ran swiftly back to the nest along the recruitment trail. *Apocephalus* never interfered with the progress of these workers. Within 2 to 3 minutes of the arrival of minor workers at the nest, major workers left the nest and attempted to follow the recruitment trail to the bait. When present, phorids almost invariably intercepted these major workers and chased them into hiding before they arrived at the experimental card. Thus the attenuation of alarm-recruitment in the presence of *Apocephalus* is the result of collective responses of individual major workers.

Since *Apocephalus* interferes with alarm-recruitment of major workers, this phorid may affect competitive interactions between *P. dentata* and *S. texana*. Ant species are active from early April until mid-November and parasitic phorids are active from early May until mid-

October. I therefore tested this hypothesis by examining seasonal variation in the outcome of confrontations between the two ant species at tuna fish baits (Table 1). In the absence of *Apocephalus*, *P. dentata* dominated most confrontations with *S. texana*; in the presence of phorids the outcome in most of the confrontations was reversed. Thus *Apocephalus* seasonally shifts the competitive balance between *P. dentata* and *S. texana* at large food sources.

Complex interactions among hosts, parasites, and competitors, similar to the ones described here, may be more common in ant communities than is generally realized (*4*). Such complex interactions may have profound effects on community organization and coexistence patterns. Parasitic phorids have been observed in all warm temperate woodlands in which careful searches have been conducted. In Texas, *Camponotus pennsylvanicus*, a common aggressive dominant ant species inhabiting many woodlands in the eastern United States, rapidly leaves baits at the appearance of the phorid fly *Apocephalus pergandei*. Baits abandoned by *C. pennsylvanicus* are normally quickly occupied by a variety of ant species, including *P. dentata*, *S. geminata*, and *Crematogaster punctulata* (*13*). Pasture and woodland nests of *S. geminata*, a fire ant native to the southern United States, are apparently heavily parasitized by several species of phorid flies (*14*). My observations in Austin, Texas, indicate that the presence of the phorid *Pseudacteon antiguensis* can prevent normal foraging behavior of *S. geminata* by forcing workers to assume defensive postures (*15*). In contrast, the notorious imported fire ant, *Solenopsis invicta*, appears free of phorid parasites in the United States, despite the diverse array of phorid flies this species and its close relatives support in South America (*16*). This freedom may partly explain the high densities of *S. invicta* and its competitive dominance over *S. geminata* in the southeastern United States.

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References and Notes

1. K. R. Barbehenn, *Biotropica* **1**, 29 (1969); H. Cornell, *Am. Nat.* **108**, 880 (1974); B. R. Levin, F. M. Stewart, L. Chao, *ibid.* **111**, 3 (1977); M. P. Hassell, *The Dynamics of Arthropod Predator Prey Systems* (Princeton Univ. Press, Princeton, N.J., 1978); P. Price, *Evolutionary Biology of Parasites* (Princeton Univ. Press, Princeton, N.J., 1980).
2. T. Park, *Ecol. Monogr.* **18**, 265 (1948); S. Utida, *Ecology* **34**, 301 (1952); L. Chao, B. R. Levin, F. M. Stewart, *ibid.* **58**, 369 (1977); K. Steinwasher, *ibid.* **60**, 884 (1979).
3. J. H. Connell, in *Ecology and Evolution of Communities*, M. L. Cody and J. M. Diamond, Eds. (Harvard Univ. Press, Cambridge, Mass., 1974), p. 460; R. K. Colwell and E. R. Fuentes, *Annu. Rev. Ecol. Syst.* **6**, 281 (1975).
4. E. O. Wilson, *The Insect Societies* (Harvard Univ. Press, Cambridge, Mass., 1971).
5. ———, in *Man and Beast*, W. Dillon and J. F. Eisenberg, Eds. (Smithsonian Institution Press, Washington, D.C., 1971), p. 183; D. C. Culver, *Ecology* **55**, 974 (1974); D. H. Morse, *Am. Nat.* **108**, 818 (1974).
6. E. O. Wilson, *Science* **190**, 798 (1975); *Behav. Ecol. Sociobiol.* **1**, 63, 141 (1976).
7. My observations were made at the University of Texas Brackenridge Field Laboratory in Austin between April and November 1976–78. I have made similar observations in Brazoria and Hardin Counties, Texas.
8. R. H. L. Disney, personal communication. Voucher specimens are deposited in both the author's and Dr. Disney's collections.
9. Specificity of phorids was determined by the number of ant species to which the flies were attracted and what species or castes elicited oviposition attempts. *Apocephalus* was attracted to more than 160 tuna fish baits occupied by *P. dentata* and to only two baits occupied by other species; both of the latter were within 10 cm of *P. dentata* workers. I have observed more than 50 oviposition attempts by *Apocephalus*. All of these attempts were directed at major workers of *P. dentata*. In no case were they directed at minor workers of *P. dentata* or the workers of other ant species.
10. Continuous observations for 2 hours on three separate occasions indicate that major workers stay in their hiding places as long as phorids remain within 10 to 15 cm of the hiding places. Repeated spot checking at 1- and 2-hour intervals on more than 100 separate occasions yielded similar conclusions.
11. Behavior of minor workers is never altered by the presence of one or two *Apocephalus*. However, minor workers may temporarily leave the area of a bait if five or more *Apocephalus* are present. This occurs in only 4 to 18 percent of the instances when *Apocephalus* are present. The response of the minor workers in these instances appears to be a generalized response to disturbance rather than parasite avoidance.
12. Laboratory experiments by D. Meyer demonstrated that colonies collected in Austin, Texas, respond by alarm-recruitment only in the presence of *Solenopsis*. Furthermore, addition of *Monomorium minimum*, a species of similar size and behavior to *S. texana*, did not provoke alarm-recruitment during field experiments concurrent with the ones described in my report.
13. D. H. Feener, personal observation, Brazoria County, Texas.
14. T. Borgmeier, *Stud. Entomol.* **6**, 1 (1963).
15. D. H. Feener, in preparation.
16. R. N. Williams, J. R. Panaia, D. Gallo, W. H. Whitcomb, *Fla. Entomol.* **56**, 259 (1973); R. N. Williams and W. H. Whitcomb, *Proc. Tall Timbers Conf. Ecol. Anim. Control Habitat Manag.* **5**, 49 (1974).
17. I thank D. Meyer for help in the field and laboratory, E. Evans, L. E. Gilbert, S. P. Hubbell, D. A. Mackey, P. Mason, P. L. Mitchell, M. Singer, D. Waller, and P. Ward for comments on an earlier draft of this paper, and P. L. Mitchell for help in collecting ant colonies. Supported in part by a Bess Heflin fellowship, the University of Texas, Austin. This is a publication of the University of Texas Brackenridge Field Laboratory, Austin.

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Individual Hippocampal Mossy Fiber Distribution in Mice Correlates with Two-Way Avoidance Performance

Abstract. *Mice systematically bred for randomization of their genotype show large individual differences when performing a two-way avoidance task (shuttle-box learning). Their behavioral scores correlate strongly* ($r = -0.80$, $P < .01$) *with the number of mossy fibers synapsing on basal dendrites of hippocampal pyramidal neurons, poor avoiders having relatively more such terminals. This confirms previous findings showing that rat and mouse strains known for genetically dependent poor avoidance learning have extended intra- and infrapyramidal mossy fiber projections.*

Recently we found evidence (*1*) confirming a previous hypothesis that variations in mammalian learning behavior are associated with genetically dependent variations in the connectivity of limbic and cortical areas (*2*). In mouse and rat strains characterized by high or low inherited performance levels in a two-way avoidance test, we observed that the poorly avoiding strains had more mossy fiber terminals on the basal dendrites of pyramidal neurons in regio inferior of the hippocampus as compared to the well-performing strains (*1*). Here we report for the first time that such a correlation occurs in individual mice of variable genotype: each animal was first tested for two-way avoidance, and then morphometrically for hippocampal mossy fiber distribution.

For the morphometry, we used Timm's silver sulfide stain for visualization of heavy metals, which are associated with synaptic enzymes (*3*). Where specific classes of synapses are arranged in laminae or clusters, as in the hippocampus, populations of synapses forming terminal fields are seen as colored bands or patches (Fig. 1, C and D). Most prominent among these populations are the clusters of the darkly staining giant boutons of the mossy fibers. These fibers originate from the granule cell layer in the fascia dentata and synapse predominantly on the proximal parts of the apical dendrites of the pyramidal neurons, forming a prominent band in Timm-stained sections: the suprapyramidal mossy fibers. A smaller projection occurs within or below the pyramidal layer on the proximal parts of the basal dendrites: the intra- and infrapyramidal (IIP) mossy fibers (*4*). Their presence is variable and genetically dependent (*5*). With-