trast, TOH activity in the locus coeruleus was markedly depressed in the IOH patients. Enzyme activity was at or below blank values (0.2 pmole mg$^{-1}$ hour$^{-1}$) in each locus from the IOH patients, whereas mean activity was $11.8 \pm 5.98$ pmole mg$^{-1}$ hour$^{-1}$ in the control group (Table 1). Thus, TOH activity was at least 50 times lower in loci coeruleus of IOH patients. In control patient 2 activity in all brain areas was also at blank levels, but this subject died with disseminated lupus erythematosus and had multiple areas of brain necrosis (Table 1).

Nigrostriatal TOH activity was depressed only in patient B with IOH, and this patient had Parkinsonian symptoms and nigrostriatal neuronal loss (Table 1). In the other patients with IOH, none of whom had significant extrapyramidal dysfunction or histopathological changes, nigrostriatal TOH activity was within the normal range.

In our observations there is a remarkably good correlation between the histological and biochemical abnormalities. The results suggest that noradrenergic neurons of the central as well as the peripheral nervous system are severely affected in this degenerative neurological disease. Our results also suggest that different noradrenergic neurons are affected differently in IOH. In the IOH patients, DBH activity was undetectable in sympathetic ganglion neurons, whereas TOH activity was normal. Conversely, in the locus coeruleus TOH activity was undetectable, whereas DBH activity was normal. Dopamine $\beta$-hydroxylase and tyrosine hydroxylase are thus altered in a nonparallel fashion in these two populations of abnormal neurons, which indicates that the biochemical alterations are not simply secondary to neuronal dropout.

Although noradrenergic neurons were abnormal in brain as well as periphery in all the IOH patients, the nigrostriatal dopaminergic system was apparently affected only in the single patient with extrapyramidal signs and symptoms. It appears that not all catecholaminergic neurons manifest biochemical deficits in patients with IOH, and that noradrenergic and dopaminergic cells may have differing susceptibilities.

Although the data do not yet permit definition of the underlying mechanisms in IOH, the observations may be relevant to the general problem of the regulation of neurotransmitter biosynthesis. Considerable evidence from animal models suggests that in normal noradrenergic neurons TOH catalyzes the rate-limiting step in norepinephrine biosynthesis (*6*). Our observations, on the other hand, suggest that in sympathetic ganglia from patients with IOH, DBH activity may be undetectable while TOH activity is normal. This raises the possibility that in diseased human neurons DBH may become rate limiting in norepinephrine biosynthesis.

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# Tournaments and Slavery in a Desert Ant

*Abstract.* *Many species of ants engage in physical fighting when territorial borders are challenged. In contrast, colonies of the honeypot ant species* Myrmecocystus mimicus *conduct ritualized tournaments, in which hundreds of ants perform highly stereotyped display fights. Opposing colonies summon their worker forces to the tournament area by means of an alarm-recruitment system. When one colony is considerably stronger than the other, the tournament quickly ends, and the weaker colony is raided and its ants "enslaved." This is the first example of intraspecific slavery recorded in ants.*

Ritualized aggressive behavior, sometimes entailing tournaments and sometimes pure displays, has been described in many invertebrate and vertebrate animal species (*1*). That it has never been observed in ants is surprising, because many ant species are territorial and frequently conduct physical combats with conspecific neighboring colonies. One would expect to find a more ritualized form of aggression in those species that are furnished with strong mandibles or stings but are also vulnerable because of a thin cuticle. I now report such a case of ritualization in the ant *Myrmecocystus mimicus* during territorial combats with conspecific neighbors and describe how territorial aggression in an ant species can lead to intraspecific "slavery," of a kind hitherto unknown in the social insects.

*Myrmecocystus mimicus* is one of the honeypot ant species, which are abundant in the mesquite-acacia community in the southwestern United States. Like other members of its genus, *M. mimicus* has a thin cuticle, apparently a necessary adaptation to its special honeypot biology. The members of the honeypot caste function as living storage containers; and when their crops are heavily filled, their gasters can be expanded to almost the size of a cherry (*2*).

In some parts of our study area in Arizona (near Portal) foraging grounds of neighboring colonies of *M. mimicus* frequently overlap. As a result, there are often massive territorial confrontations. However, in contrast to most ant species studied, the territorial conflicts do not consist of deadly physical fights, but, rather, of elaborate tournaments in which few ants are injured. Hundreds of ants participate in these affairs, which take place along the challenged territorial border. They can last for several days, being

Table 1. Number of displays by *Myrmecocystus mimicus* to releasing stimuli. Various stimuli were offered at nest entrances of five different colonies (A–E). At 1-minute intervals during the subsequent 5 minutes, the number of ants displaying on stilt legs was counted. The entries are the pooled totals of the five 1-minute counts.

| Stimuli | Number of displays at each nest | | | | |
|---|---|---|---|---|---|
| | A | B | C | D | E |
| Live conspecifics* | | | | | |
| Test | 42 | 67 | 51 | 17 | 28 |
| Control | 0 | 2 | 0 | 0 | 0 |
| Killed conspecifics† | | | | | |
| Test | 12 | 6 | 4 | 0 | 6 |
| Control | 0 | 0 | 0 | 0 | 0 |
| Nest material‡ | | | | | |
| Test | 7 | 0 | 10 | 3 | 9 |
| Control | 0 | 0 | 0 | 0 | 0 |

*Test stimuli were 30 foreign conspecific ants; controls were 30 nestmates. †Test stimuli were 30 freshly killed foreign conspecifics; controls were 30 freshly killed nestmates. ‡Test stimulus was nest material from a nest of foreign conspecifics; control was nest material from a termite nest.

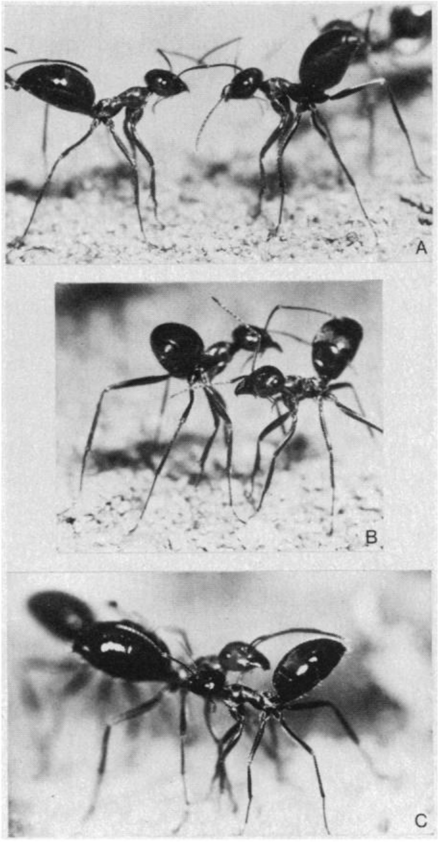

Fig. 1. The stereotype display patterns of *Myrmecocystus mimicus*. (A) Stilt-walking and head-on confrontation. (B) Beginning of lateral display. (C) Full lateral display and antennal drumming.

interrupted only at night when the species is normally inactive.

During the contests the ants walk on stilt legs while raising the gaster and head. When two hostile workers meet, they initially turn to confront each other head-on (Fig. 1A). Subsequently they engage in a more prolonged lateral display (Fig. 1B), during which they raise the gaster even higher and bend it toward the opponent. Simultaneously, they drum intensively with their antennae on each other's abdomen (Fig. 1C). This is almost the only physical contact, although each ant seems to push sideways as if to dislodge its opponent. After 10 to 30 seconds, one of the ants usually yields and the encounter ends. The ants continue to move on stilt legs, quickly meet other opponents, and the whole ceremony is repeated.

In order to identify the cues by which the display behavior is released, two groups of 60 ants, each taken from a different colony, were placed together in an arena 50 cm in diameter. Different colors of paint were used to mark individuals of the two colonies. During 5-minute intervals, the number of displaying ants was counted. This test was replicated 26 times. Workers displayed significantly more frequently (at the .05 level) toward members of another colony than to nestmates ($\chi^2 = 177.29$; d.f. = 25). Encounters with nestmates lasted only 1 to 2 seconds and were usually terminated by brief jerking movements of the body. Encounters with "foreigners" lasted considerably longer (up to 30 seconds) and followed closely the stereotyped display sequence of (i) stilt-walking, (ii) head-on confrontation, and (iii) lateral display and sideward pushing. In the control experiments, in which an equal total number of ants, all from the same colony, were kept in the arena, prolonged stilt-walking was never observed.

Observations and experiments conducted in the field at nests of *M. mimicus* colonies confirmed that the presence of foreigners released the display behavior. It was first noted that contact with ants of neighboring colonies of other species (such as members of *Pogonomyrmex*, *Pheidole*, *Solenopsis*, and *Formica*) did not elicit stilt-walking in *M. mimicus*. But a single foreign conspecific worker often evoked the display behavior in a number of ants around the nest entrance. Not only live ants but also freshly killed ones or even nest material from a neighboring colony can evoke stilt-walking (Table 1). I concluded that a specific colony odor of the foreign workers releases the display.

I next investigated how the tournaments arise. When foragers venture into another territory, they frequently encounter foreign ants, whereupon they invariably begin to display on stilt legs. Subsequently some scouts return to their colony, dragging their abdominal tips over the ground. Upon arriving at the nest, they perform a conspicuous motor display in which they rush at nestmates over short distances and perform rapid jerking movements. The locomotor behavior of members of the colony immediately increases. Within a few minutes, a group of 100 to 200 ants moves out and progresses rapidly in the direction from which the scouts approached the nest. Analysis of films reveals that these groups are regularly accompanied by the scouts, which still drag their abdominal tips over the ground. Upon encountering foreign conspecific workers at the disputed territorial area, the ants invariably perform the display behavior. Real physical fights, which occur rarely, usually end fatally for both opponents. During the course of the tournament, scouts of both colonies repeatedly return to their nests and recruit reinforcements to the battleground. However, if the defending colony is considerably weaker and therefore unable to recruit a large enough worker force to the tournament area, the colony will be overrun by the intruders and raided. Of 28 observed territorial invasions, five ended with the raiding of the weaker colony. During these raids the queens were killed or driven off. The larvae, pupae, callow workers, and honeypots were carried or dragged to the nest of the raiders. This process required several days and terminated only when the raided colony ceased to exist. Surprisingly, even during these raids, physical combats occurred only at the beginning and were infrequent. After several days the display behavior ceased, as the surviving workers of the raided colony were wholly incorporated into the raiders' nest. Since, to my knowledge, all cases of slave-making in ants involve two different species, this is the first evidence for intraspecific slavery in ants.

The next experiments were designed to identify the cue by which the territorial raids in *M. mimicus* are organized. Since scout ants drag their abdominal tips over the ground during tournament organization, I hypothesized that a recruitment pheromone from one of the abdominal exocrine glands was involved. When extracts were made from whole gasters of workers and laid in artificial trails, ants at the nest entrance were alarmed and followed the trail for a short distance (up to approximately 100 cm), but no true raid was triggered by the stimulus. Similarly, raids were not induced by extracts from the mandibular glands, poison glands, Dufour's glands, and rectal bladders. These results suggested that a trail pheromone laid down by the scouts might function as the principal orientation cue which leads to the battleground.

The following findings support this hypothesis. While a raid organized by scout ants was in full progress (that is, once the ants had become initially aroused, presumably by the jerking behavior of the recruiting ants), I drew artificial trails intersecting the natural trail at 90° to it. The raiding ants did not respond to artificial trails laid with extracts from poison glands or Dufour's glands, but a significant number of workers followed the trail laid with hindgut extract. The territorial raids of *M. mimicus* thus seem to be organized by an alarm-recruitment system. Behavior observations suggest that the ants are alerted by a jerking motor display performed by the recruiting scouts. Experimental results support the hypothesis that they are subsequently guided to the combat area by a hindgut pheromone trail laid by the scout ants. Some ant species employ an elaborate alarm recruitment system in defense against particular interspecific enemies (*3*). I demonstrate here that a similar system can also be used in intraspecific territorial defense (*4*).

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## Hippocampal Activity and Scopolamine

The report by Teitelbaum *et al.* (*1*) does not account for previous data which seem to invalidate their conclusion that behavior-related hippocampal rhythmical slow activity is abolished by injections of scopolamine. In a previous report (*2*) it was shown that hippocampal rhythmical slow activity persists during locomotion after a dose of scopolamine HBr of 10 mg/kg intraperitoneally. Teitelbaum *et al.* used a dose of 10 mg of scopolamine HCl per kilogram. The slight difference in the amount of base given by these two dosages is probably unimportant. The effects of atropinic drugs on hippocampal activity were clarified in another report (*3*) which concluded, in part, that "Preservation of reasonably clear RSA [rhythmical slow activity] during gross movements following atropinization could be demonstrated *only* at sites where the RSA, in the absence of any drug, had a large amplitude (preferably 1 mv or more) and little admixture of fast wave activity. This point requires emphasis since there have been reports, based on recordings lacking these features, that atropinic drugs essentially abolish RSA during behavior." Apparently I did not emphasize the point sufficiently, even though it was illustrated by a figure [figure 4 in (*3*)]. The tracings shown by Teitelbaum *et al.* contain considerable fast activity and have an amplitude of about 0.5 mv. Such tracings may continue to exhibit rhythmical slow activity after injection of atropinic drugs (*2*) but usually they do not.

There are two further points. First, despite the assertion by Teitelbaum *et al.* (*1*, p. 1115), I have not claimed a relation between atropine-sensitive rhythmical slow activity and "behavioral arousal." As I point out (*3*), hippocampal activity of this type can occur during surgical anesthesia, and its behavioral significance is largely unknown. Second, hippocampal rhythmical slow activity is present not only during the initiation of voluntary movement but also during its long-continued performance, for example during running in a wheel or walking on a treadmill (*4*).

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While our conclusions (*1*) were not based on scopolamine data alone, our findings with regard to the effects of this drug on hippocampal theta patterns are in agreement with those of Bennett (*2*) and Friedman and Wikler (*3*).

We were able to mimic the movement-related theta response with physostigmine and we showed that the same dose of scopolamine that blocked physostigmine-induced theta also blocked theta produced by treadmill running without affecting the rate or pattern of movement. Both the physostigmine response and the behaviorally induced hippocampal theta response were abolished with lesions of the medial septal nucleus.

The negative findings of Vanderwolf (*4*) with regard to the effects of muscarinic blocking agents were discussed in detail in our report (*1*). Apparently, Vanderwolf has seen this effect in his laboratory (as indicated above). Because our signal was a mere 500 $\mu$v in amplitude and contained "considerable" [we disagree, see figure 1 in (*1*)] high-frequency activity, he has arbitrarily decided to ignore such data. We are in no position to make such a decision—nor is he.

Winson (*5*) and Fox and Ranck (*6*) have provided evidence for the existence of at least two (possibly three) theta-generating layers in the dorsal hippocampus of the rat, one located high in $CA_1$ (the location of our recording electrodes), another located more ventrally in the dentate gyrus, and possibly a third in the suprapyramidal layer of $CA_3$. With their staggered bipolar electrode configuration, Vanderwolf *et al.* (*4, 7*) are recording differentially between two neurochemically distinct movement-related theta generators that are synchronous but phase reversed [see Winston (*5*) for a description of phase relationships between theta generators in hippocampus]. In recording such bioelectric activity from freely moving animals, movement artifacts and electrical noise are reduced with employment of differential amplifiers that have common mode rejection characteristics. According to Giles (*8*), the output voltage

$$E_{\text{out}} = (R_{\text{f}}/R_{\text{s}})\,(E_{\text{in}_2} - E_{\text{in}_1})$$

where $R_{\text{f}}$ = resistance in the feedback circuit and $R_{\text{s}}$ = resistance of source; $E_{\text{in}_2}$ is the peak potential at one electrode (for example, dorsal theta generator) and $E_{\text{in}_1}$ is the peak potential at the other source (for example, ventral generator). Since $E_{\text{in}_1}$ and $E_{\text{in}_2}$ are synchronous, but phase reversed, $E_{\text{in}_1}$ is a negative value that is multiplied by a