al invariance, judged by the overall error rates (Fig. 3B). The differences may be due to unavoidable instruction, pretraining, and pay-off inequalities. However, the humans generated a reaction-time function that increased monotonically with the angular disparity between the sample and comparison forms, whereas the pigeons produced essentially flat functions (Fig. 3A). Analyses of variance of the pigeon reaction-time data did not show significant orientation effects (all P's $> .05$). The human data yielded a significant orientation effect [$F(4,84) = 22.76$, $P < .001$] due to a linear trend [$F(1,105) = 22.58$, $P < .001$].

The human function is in close agreement with those reported by others for similar experiments (*3*). It conforms to the interpretation that the invariance was achieved by mental rotation, an operation conceived as a serial process in which an engram of a form is rotated until the matching or nonmatching with the percept of another form can be directly assessed (*9*). Pigeons solved the problem differently and more efficiently, presumably through a parallel mode of information processing (*10*). The use of mental rotation by humans, however, appears to be almost exclusively restricted to situations involving the discrimination of mirror-image forms. When tasks require the discrimination of distinctly different forms, humans too yield fast and flat functions like those of our pigeons (*11*). The difference in performance may be ascribed to the possibility that for pigeons, but not for humans, mirror-image forms are as perceptually distinct as any arbitrarily different forms (*12*).

Although phylogenetically more primitive, pigeons solved a perceptual problem more efficiently than humans. Whether this is related to the primarily midbrain-based visual system of lower vertebrates and the mainly forebrain-based visual system of mammals is not known (*13*). We believe that the disparity may have originated because of different ecological demands. Pigeons operate visually predominantly on the horizontal plane where the orientation of objects is largely arbitrary, being relative to the position of the observer. Humans primarily view the frontal plane where their orientation and that of objects are highly consistent, being dependent on gravity.

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Chemical Mimicry in the Myrmecophilous Beetle *Myrmecaphodius excavaticollis*

Abstract. *The myrmecophilus beetle* Myrmecaphodius excavaticollis *(Blanchard) was found to have species-specific cuticular hydrocarbons acquired from one of its hosts, the ant* Solenopsis richteri *Forel. Removal from its ant host resulted in loss of the host hydrocarbons, leaving a cuticular pattern innate to the beetle. When beetles were transferred to colonies of three other* Solenopsis *species, they acquired the specific hydrocarbons associated with each of the new hosts. This passive integration mechanism is coupled with the beetle's armored exterior to enable it to cope with multiple aggressive hosts.*

Myrmecophiles, ant symbionts, have evolved numerous mechanisms for integrating themselves into host colonies. Among these mechanisms are morphological mimicry, defensive and appeasement chemical secretions, and behavioral mimicry (*1*). We report a novel integration mechanism used by *Myrmecaphodius excavaticollis* (Blanchard) in which passive, nonintegrative, defensive behavior is followed by the integrative acquisition of host-specific hydrocarbons. Individual beetles are able to shed the hydrocarbons of one *Solenopsis* species and acquire the pattern of a different host species. These data partially explain the multiple host capability of this myrmecophilous beetle.

Myrmecaphodius excavaticollis was probably introduced into the United States from South America with one of its imported hosts, *Solenopsis invicta* Buren or *S. richteri* Forel (*2*). The beetle has been reported in association with three indigenous species, *S. geminata* (F.), *S. xyloni* McCook (*3*) and *Iridomyrmex pruinosum* (Roger) (*4*), as well as with another import, *I. humilis* (Mayr) (*3*). All developmental stages of the beetles have been found within the mounds of the host ants. Adults move freely among host ants and obtain food directly from workers through trophallaxis, by predation on ant larvae, and by feeding on freshly killed or decomposed workers and ant booty (*5*). Dispersal flights can occur throughout the year, after which the beetles must find a suitable host

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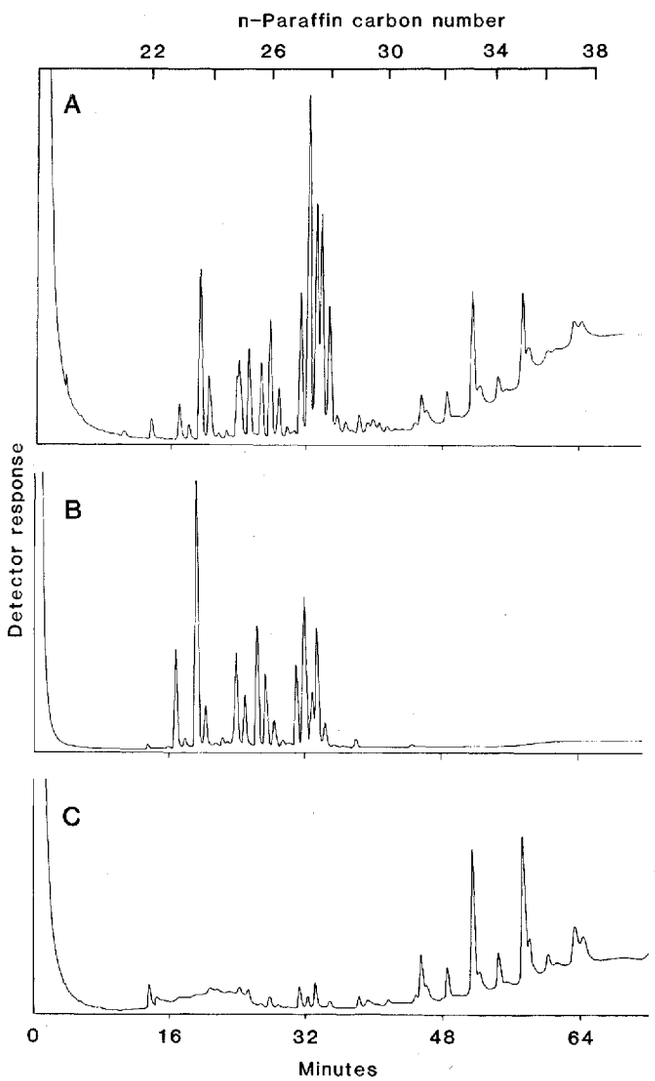
colony, which may not be the same species they originally came from (*6*, *7*).

The integration of *M. excavaticollis* into a host colony in spite of the absence of morphological mimicry and chemical defenses (*5*) led us to investigate the potential role of host colony odor and species odor in myrmecophile acceptance. Colony odor has both innate and acquired components (*8*). Ants recognize each other by touching of one's antennae to the other's cuticle, suggesting that the cuticle acts as a source of species-specific (innate) chemicals and provides a large surface for their release. The cuticle can also effectively function to absorb the acquired components of colony odor from the surrounding environment.

Hydrocarbons are cuticular components that are useful chemotaxonomic tools for species complexes in Diptera (*9*, *10*); they have physiological activity as sex attractants in Diptera and Lepidoptera and alarm pheromones in Hymenoptera (*11*). Cuticular hydrocarbons have been postulated to be semiochemical cues for caste and species recognition for termites (*11*), and the termitophilous beetle *Trichopsenius frosti* Seevers synthesizes a cuticular hydrocarbon pattern identical to that of its host, *Reticulitermes flavipes* (Kollar) (*12*). Hydrocarbons constitute 65 to 75 percent of the cuticular lipids of *S. invicta* and *S. richteri* (*13*, *14*) and are distinctly different for the four *Solenopsis* species hosts of *M. excavaticollis* (*15*).

The relation between the cuticular hydrocarbons of *M. excavaticollis* and its host was investigated when large numbers of beetles were found in association with *S. richteri* collected from northern Mississippi. The ants and myrmecophiles were isolated from the soil and maintained together in laboratory colony trays (*16*). Some beetles were separated from their ant hosts and maintained in nest cells where they were fed honey agar.

A group of beetles were removed from *S. richteri* colonies and immediately washed with hexane. Hydrocarbons were isolated by applying the concentrated wash to a silicic acid column and eluting with hexane. The hydrocarbon fraction was analyzed by gas chromatography (*17*). A sample of *S. richteri* workers were treated in the same way to obtain a comparative chromatogram of their cuticular hydrocarbons. A comparison of chromatograms of beetle and *S. richteri* hydrocarbons (Fig. 1, A and B) shows that species-specific *S. richteri* hydrocarbons are also present on *M. excavaticollis*. In addition to host hydrocarbons, the beetles show significant amounts of higher molecular weight hydrocarbons. Analysis of cuticular hydrocarbons from beetles isolated from *S. richteri* for about 2 weeks (Fig. 1C) showed a dramatic decrease in host-related hydrocarbons; however, the high molecular weight components remained. The data suggested that *M. excavaticollis* acquired host-specific hydrocarbons and that the components shown in Fig. 1C are innate to the beetle. A less likely explanation is that the beetles are stimu-



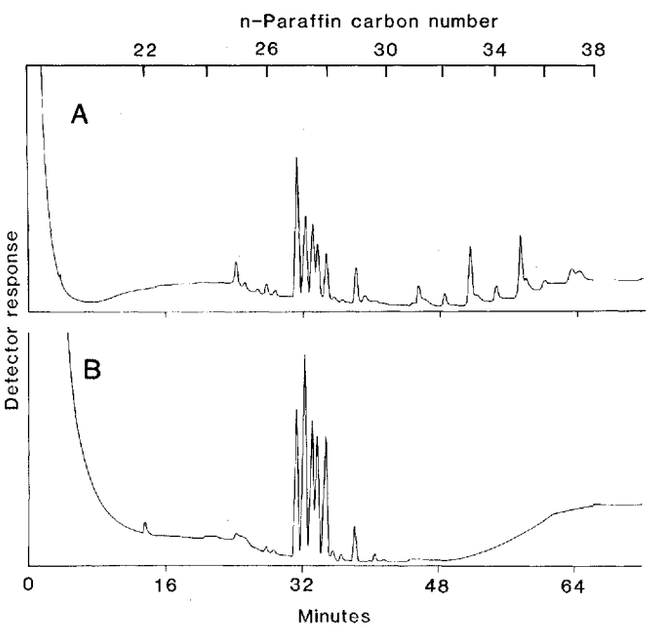


Fig. 1 (left). Gas chromatographic traces of (A) cuticular hydrocarbons from *M. excavaticollis* taken directly from a *S. richteri* colony, (B) cuticular hydrocarbons from *S. richteri*, and (C) cuticular hydrocarbons from *M. excavaticollis* 2 weeks after the beetles were removed from a *S. richteri* colony (*14*, *17*, *18*). Fig. 2 (right). Gas chromatographic traces of (A) cuticular hydrocarbons from *M. excavaticollis* 5 days after introduction to a *S. invicta* colony and (B) cuticular hydrocarbons from *S. invicta* (*14*, *17*, *18*).

lated to produce *S. richteri* hydrocarbons when in contact with the host. It is also evident that cuticular components are in a continuous state of flux.

If the host hydrocarbons are acquired, then this multiple-host myrmecophile should be able to change its hydrocarbon pattern to match that of the host species. To test this hypothesis, we collected beetles from *S. richteri* colonies, isolated them for 2 weeks, and then introduced them into laboratory colonies of *S. invicta*. After 5 days, the beetles were removed and analyzed for cuticular hydrocarbons as described. The data (Fig. 2, A and B) show that the *M. excavaticollis* taken from *S. richteri* colonies acquired the cuticular hydrocarbons of its new host, *S. invicta*. The same phenomenon occurred when previously isolated beetles were introduced into *S. geminata* and *S. xyloni* colonies. Although the switching of hydrocarbon patterns from one host to another weakens the likelihood that they are synthesized by the beetle, we also found that freshly killed isolated beetles had acquired *S. invicta* hydrocarbons within 2 days after exposure to the ant colony. These data eliminate biosynthesis as a possibility and support a passive mechanism of hydrocarbon acquisition. When initially introduced into a host colony, the *M. excavaticollis* were immediately attacked. The response of the beetles was to play dead and wait for the attacks to cease, or they moved to an area less accessible to the ants. Within 2 hours after introduction into a host colony, the beetles' cuticle contained 15 percent of host hydrocarbons. The accumulation of hydrocarbon continued up to 4 days until the beetles' cuticle contained about 50 percent host hydrocarbons. Beetles surviving this long were generally no longer attacked.

The beetles can acquire the host cuticular hydrocarbons by ant-beetle contact, grooming behavior, regurgitation of ant postpharyngeal gland contents (which contain large amounts of species-specific hydrocarbons), and by ingestion. However, the overall mechanism used for integration of *M. excavaticollis* into its host colonies involves the initial passive defensive behavior that must enable it to survive long enough to acquire the species odor of its host as well as the environmental part of the host's colony odor.

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Lesion-Induced Sprouting in the Rat Dentate Gyrus Is Inhibited by Repeated Ethanol Administration

Abstract. *The effect of ethanol on hippocampal axonal sprouting was studied with a histochemical technique for identifying acetylcholinesterase. Unilateral lesion of the entorhinal cortex in adult rats produced an increase in the density of acetylcholinesterase staining in the outer molecular layer and a concomitant increase in the width of the pale-staining commissural-associational zone of the dentate gyrus. Other rats were given ethanol (11.3 ± 0.45 grams per kilogram) for 2 weeks before and 9 days after receiving the lesion. Ethanol abolished the expansion of the commissural-associational zone. The effect of ethanol on sprouting axons suggests that it may inhibit recovery of function after brain injury.*

Each year about 297,000 persons are hospitalized for initial stroke (*1*) and another 422,000 for head injury (*2*). Ethanol is a significant factor associated with central nervous system dysfunction and recovery (*3–8*). Since about 9 percent of Americans are heavy drinkers (*9*), there is a compelling need to understand the effects of ethanol on recovery from injury to the central nervous system.

The behavioral deficits that follow brain injury often show some recovery with time. Reactive synaptogenesis (axon sprouting) has been proposed as one mechanism underlying such recovery (*10*). The dentate gyrus is ideal for determining the effects of ethanol on lesion-induced sprouting. The precision with which afferents of the dentate gyrus are organized into laminar terminal fields has permitted accurate documentation of the changes that follow brain lesions. After infliction of an entorhinal cortical lesion (*11, 12*), most of the remaining afferents of the dentate gyrus sprout into the deafferented area of the molecular layer. Some of these afferents have been shown to form functional connections (*13, 14*).

Alterations in the cholinergic innervation of the molecular layer can easily be monitored by acetylcholinesterase (AChE) histochemistry. Within 4 to 6 days after infliction of an entorhinal lesion, a marked intensification of AChE staining is observed throughout the outer molecular layer. Biochemical studies have demonstrated increased activity of AChE and choline acetyltransferase following such lesions (*12, 15*). In addition, the pale-staining commissural-associational (CA) zone in the inner molecular layer widens and exhibits a concomitant decrease in the density of AChE staining. The expansion of the CA zone corresponds closely to the extent of commissural sprouting (*16*). A variety of studies recently provided evidence that long-term exposure to ethanol damages the hippocampal formation (*3, 17*). We now report that heavy consumption of ethanol inhibits the typical post-lesion sprouting response of the CA zone in the rat dentate gyrus.

Adult Sprague-Dawley rats of both sexes were maintained on a 12-hour light-dark cycle, with the period of light beginning at 700 hours. Nine days after unilateral lesion of the entorhinal cortex, the presence of axonal sprouting was determined by analyzing alterations in the laminated pattern of AChE staining in the molecular layer of the dentate gyrus. The ethanol-fed lesioned group

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