Ins. Soc. *42*: 267–277 (1995)

1015–1621/95/030267–11 $ 1.50 + 0.20/0

Congruency of hydrocarbon patterns in heterospecific groups of ants: transfer and/or biosynthesis?

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Key words: Hydrocarbons, mixed-species groups, cuticle, postpharyngeal gland, Formicidae.

Summary

In homospecific groups of ants, each species has its own hydrocarbon profile, on the epicuticle and in the postpharyngeal gland (PPG). When reared together in bispecific groups, workers of both species possess each other's hydrocarbons in both locations. The present study investigated two alternative mechanisms by which a mixed "odour" in artificial groups of *Formica selysi/Manica rubida* can be created. Using [1-^{14}C] sodium acetate as a precursor, *de novo* biosynthesis of hydrocarbons was demonstrated for both species whether reared in homospecific or mixed-species groups. The newly synthesized hydrocarbons occurred on the epicuticle, internally, and in particularly large amounts in the PPG. As expected from their PPG and epicuticular hydrocarbons composition, workers *F. selysi* synthesized alkanes and alkenes in comparable amounts irrespective of their rearing scheme. Likewise, *M. rubida* reared in bispecific groups synthesized mostly alkanes with only negligible amounts of alkenes, according to a ratio characteristic to *M. rubida* workers from homospecific groups and not to *F. selysi* workers. During dyadic encounters, a transfer of labeled hydrocarbons between nestmates (conspecific in homospecific groups and allospecific in mixed groups) was observed. These results suggest that the formation of the mixed hydrocarbon profile in artificial groups of ants is the result of a transfer of these chemicals between nestmates rather than *de novo* biosynthesis of the allospecific hydrocarbons. Behaviours like trophallaxis, grooming and body contact that occurred during the encounters mediated such a transfer.

Introduction

In ants, the profile of cuticular hydrocarbons are species and colony specific (Vander Meer, 1986; Howard, 1993). These chemicals are the dominant class of lipids found on the cuticle and are commonly considered as nestmate recognition cues, constituting the chemical signature of the colony (Bonavita-Cougourdan et al., 1987, 1989; Morel et al., 1988; Henderson et al., 1990; Nowbahari et al., 1990).

Each ant possesses its own cuticular hydrocarbon profile which is genetically determined and is influenced by its social and physical environment (reviewed by Carlin, 1989). This profile is common to all the members of the colony ("Gestalt odor", Crozier and Dix, 1979; Crosland, 1989), and in *Cataglyphis niger* it is achieved by an exchange of hydrocarbons between nestmates, mostly through trophallaxis and grooming (Soroker et al., 1994).

Cohabitation of two or more ant species in the same nest results, in most of the cases, in similarity in the epicuticular hydrocarbons between the allospecific workers. This chemical congruency was reported in natural heterospecific colonies, between a parasite and its host (Franks et al., 1990), or between slave-making ant and its host (Yamaoka, 1990; Kaib et al., 1993), as well as in artificial bispecific groups (Errard and Jallon, 1987; Bagnères et al., 1991; Vienne, 1993). The chemical signature in most of these groups is composed of hydrocarbons from both species and usually develops soon after emergence (Errard and Jallon, 1987; Errard, 1994). This mixed "odour" can explain the non-aggressive cohabitation between species and suggests that hydrocarbon profiles can be used as a marker for successful integration.

It was recently demonstrated in several ant species that the chemical profile of the cuticular hydrocarbons is congruent with that of the postpharyngeal gland content (Bagnères and Morgan, 1991; Do Nascimento et al., 1993). This congruency was also observed in artificial mixed-species groups of *Manica rubida/Formica selysi* (Hefetz et al., 1992). In a recent study, we suggested that PPG hydrocarbons can serve as a pool of recognition cues for their distribution within the colony (Soroker et al., 1994).

Several hypotheses were put forwards to explain the development of the mixed hydrocarbon profile found in naturally occurring heterospecific groups, e.g., the association of two species of ants (one is usually the parasite of the other), or an ant and its inquiline. The new allospecific chemicals (or their precursors) can be actively synthesized as in the case of *Microdon albicomatus* that parasitizes *Myrmica incompleta* (Howard et al., 1990), or can be actively or passively transferred between individuals as was suggested in several other studies (Vander Meer and Wojcik, 1982; Bonavita Cougourdan et al., 1989; Vander Meer et al., 1989; Franks et al., 1990 and Breed et al., 1992).

The objective of the present study was to discriminate between the two mechanisms mentioned above using mixed-species groups of *F. selysi/M. rubida*. These two species are specifically suited for such a study because *M. rubida* workers reared in mixed-species groups possess high amount of alkenes, whereas in *M. rubida* reared in homospecific groups, alkenes could not be detected by GC-MS (Bagnères et al., 1991, Hefetz et al., 1992).

Materials and methods

Collection and maintenance of ant colonies

Colonies of *F. selysi* (Formicinae) and *M. rubida* (Myrmicinae) were collected in Morillon (French Alps, 800 m of altitude) in July 1993 and June 1994. In the labo-

ratory, they were reared in artificial nests under controlled conditions: 20 ± 3 °C and the natural photoperiod of Paris. Colonies were provided with an identical diet of honey/apple mixture and mealworms three times a week. Homospecific control groups (either *F. selysi* or *M. rubida*) and bispecific groups were formed by isolating newly emerged workers (less than 5 hours old) from their mother colonies and placing them together. Experimental groups were reared in a glass tube (180 × 17 mm) with a water reservoir at one end. Control groups comprised 15 to 20 workers while heterospecific groups contained about 15 workers. The ratio between the workers of the two species was not always equal in all the mixed groups. A previous study showed that one allospecific worker is sufficient to promote the occurrence of allospecific hydrocarbons in workers of the other species (Hefetz et al., 1992). The ants were kindly provided by Dr. Christine Errard from the University Paris Nord, France. Voucher specimens of the ants are at the "Laboratoire d'Entomologie, Museum d'Histoire Naturelle, Paris".

Studies on hydrocarbon distribution in vivo using labeled sodium acetate

In order to follow the biosynthesis and distribution of the newly synthesized hydrocarbons in the ants, an in vivo radiochemical assay was used. Ants, about 7 months old, were each injected through the intersegmental membrane of the abdomen with 0.5 µl medium, prepared according to Katase and Chino (1984) and containing 1 µCi (56 mCi/mmole) of [1-^{14}C] sodium acetate (NEN Boston, USA) for *M. rubida* or 1.2 µCi for *F. selysi*. In the time course study, the incubation was stopped by freezing the ants at various time intervals (6 h, 24 h and 48 h) whereas for all other experiments, incubations lasted for 24 hours. The ants were dissected and monitored for the presence of labeled hydrocarbons on the epicuticle, in the PPG and internally as described below.

Hydrocarbon transfer between nestmates

Two to three weeks old ants were used for these experiments. In the experiments using ants from heterospecific groups, *F. selysi* workers were always used as donors. Donor ants were injected with 1 µCi [1-^{14}C] sodium acetate as described previously, and after 39 hours of incubation (25 ± 3 °C) one donor was encountered with one starved nestmate (recipient) in a Petri dish (4.8 cm diameter). Food transfer by trophallaxis was verified by feeding the donor ants with colored food and monitoring its occurrence in the recipient. All encounters were stopped 24 hours later by freezing the ants, and both donor and recipient were monitored for the presence of labeled hydrocarbons in the postpharyngeal gland and on the epicuticle. For comparison between the magnitude of labeled hydrocarbon transfer to the various recipients, the relative amounts of labeled hydrocarbons transferred from donor to recipient were calculated individually for each pair as the percentage of total labeling found in the donor.

Extraction and separation of the labeled hydrocarbons

Postpharyngeal glands were extracted in 100 µl of pentane. To separate cuticular from internal hydrocarbons, headless carcasses from which Dufour's gland was removed were first washed by immersion in 400 µl of pentane for 5 min and subsequently extracted in a new aliquote of 400 µl of pentane for 48 hours. The extracts used for the time course study were subjected to silica gel (polygram Sil G) thin layer chromatography (TLC). The running solvent was petrol ether:diethyl ether:acetic acid (95:5:1, v/v/v). For the other experiments, alkenes were separated from alkanes by TLC using silica gel that was impregnated with 10% silver nitrate in double distilled water. Plates were activated by heating for one hour at 110 °C. Plates were first developed in hexane to the top, air dried and then developed to 4 cm above the baseline with the running solvent described above. The various lipid classes were identified by comparing their Rf values with that of co-chromatographed standards purchased from Sigma (n-heptacosane, tricosene, triolein, oleic acid, and palmitoleic acid stearyl ester) and visualized by iodine vapor and/or a spray of 0.1% 2′,7′-dichlorofluoroscein in ethanol. The area corresponding to total hydrocarbons or to alkene and alkane fractions was cut and placed in scintillation fluid (Opti Fluor O, Packard). Its radioactivity was monitored using a scintillation counter (Packard Tri-Carb 4530).

Behavioural recording

During the first 6 hours of each dyadic encounter, the behaviour of both ants was recorded simultaneously every five minutes. The behavioural items were classified into five categories: trophallaxis, selfgrooming, allogrooming, physical contact (antennal and body contacts) and indifference. During these encounters, agonistic interactions were rarely observed. Data were converted as observed frequencies relatively to a total of 72 records per encounter. We further grouped the items to determine the total of interactions (trophallaxis + allogrooming + contact) and non interactions (selfgrooming + indifference).

Statistics

In all the experiments individual ants were analyzed. Different groups were compared by Kruskal-Wallis test and Mann & Whitney U test, while data from the same individuals were compared by Wilcoxon's Signed-Ranks test. Analyses were performed using a Statview 4.01 package in a Macintosh computer.

Results

De novo *hydrocarbon biosynthesis*

Adult *F. selysi* synthesized hydrocarbons *de novo* from sodium acetate in a time dependent manner (Fig. 1). After six hours of incubation, the amount of labeling

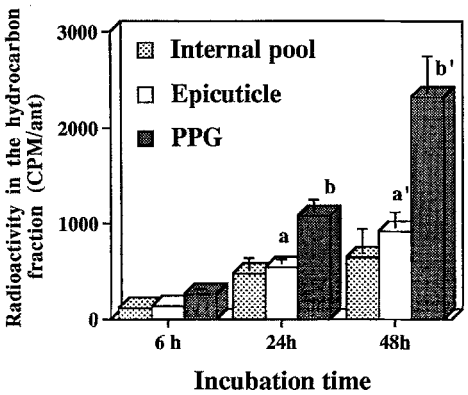

Figure 1. Time dependent changes in in vivo incorporation of [1-^{14}C] sodium acetate into the hydrocarbon fraction of different tissues in *Formica selysi* workers (Mean CPM/ant ± sem). Different letters (a vs b and a' vs b') represent the groups which differed significantly (Mann & Whitney U test)

Table 1. Total radioactivity in the hydrocarbon fraction in the postpharyngeal gland (PPG) and on the epicuticle of workers *Formica selysi* and *Manica rubida* reared in homo- and heterospecific groups (Mean CPM/ant ± sem). Numbers in parentheses denote the number of replicates

Groups	*F. selysi*		*M. rubida*	
	homospecific	heterospecific	homospecific	heterospecific
PPG	750 ± 124 (20)	1148 ± 356 (9)	9260 ± 2243 (7)	3218 ± 494 (12)
Epicuticle	543 ± 69 (22)	713 ± 147 (10)	5093 ± 535 (9)	3548 ± 33 (12)
PPG/Epicuticle	1.61 ± 0.25 (20)*	2.11 ± 0.6 (9)*	1.81 ± 0.34 (7)*	1.09 ± 0.19 (12)*

* No significant difference for all the comparisons (Mann & Whitney U test)

was similar in all tissues examined. Thereafter, this level remained stable in the internal pool (there were no significant differences between times) but increased on the epicuticle and in the PPG. At 24 hours, the amount of labeled hydrocarbons in the PPG (cpm/ant) was already significantly higher than on the epicuticle (cpm/ant) (a vs b, $p = 0.017$, a' vs b', $p = 0.027$, Wilcoxon's signed-rank test).

We investigated further the magnitude of hydrocarbon biosynthesis after 24 hours of incubation in workers reared in homo- and heterospecific groups. As in the time course study, there was a tendency in most cases for hydrocarbon accumulation in the PPG, but the variance in these experiments was too high to demonstrate statistical significant difference (Table 1). The ratio of the labeling in the PPG vs labeling on the epicuticle was not different between *F. selysi* and *M. rubida* workers, as well as within species between homo- and heterospecific groups (Table 1, Mann & Whitney U test). Alkenes/Alkanes ratio was significantly different between individuals of the two species, both in the PPG and on the epicuticle ($p = 0.0001$,

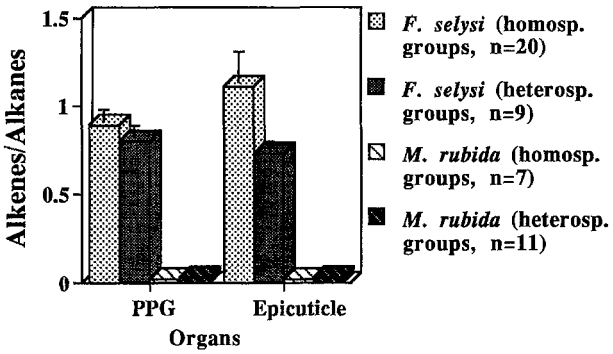

Figure 2. Ratio of newly synthesized alkenes and alkanes in *Formica selysi* and *Manica rubida* workers reared in homo- and heterospecific groups (Mean ± sem)

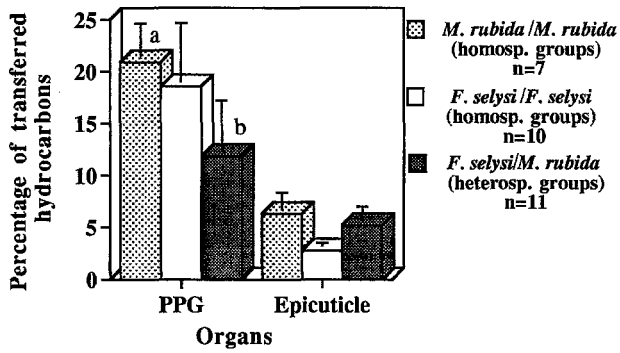

Figure 3. Transfer of labeled hydrocarbons between allo- and conspecific nestmates (Mean ± sem). Different letters represent the groups which differed significantly (Mann & Whitney U test)

Mann & Whitney U test) (Fig. 2). As expected from their hydrocarbon composition in the PPG or cuticular washes, *F. selysi* workers synthesized alkanes and alkenes in comparable amounts, whereas *M. rubida* workers were able to synthesize only negligible amounts of alkenes. There were no significant differences in the rates of alkenes synthesis between individuals of the same species, irrespective of their social environment. Most importantly, *M. rubida* workers reared in mixed-species groups with *F. selysi* did not augment the production of alkenes, despite the fact that they possess appreciably higher amounts of alkenes as compared to their conspecifics reared in homospecific groups (Hefetz et al., 1992).

Dyadic encounters between nestmates

Hydrocarbon transfer. After 24 hours of encounters, a transfer of labeled hydrocarbons was observed between conspecific as well as between allospecific nestmates (Fig. 3). However, the amount of labeled hydrocarbons in the PPG of recipient

Table 2. Percentages of transferred alkenes and alkanes between nestmates during homo- and heterospecific dyadic encounters

Donor/recipient	*F. selysi/F. selysi* (n = 10)		*F. selysi/M. rubida* (n = 11)	
Hydrocarbon class	alkenes	alkanes	alkenes	alkanes
PPG	18.2 ± 6.1	20.3 ± 6.6	12.2 ± 6.7	12.9 ± 3.9
Epicuticle	2.7 ± 0.7	2.9 ± 0.9	3.7 ± 1.5	4.9 ± 1.4

Table 3. The ratio of radioactive Alkenes/Alkanes in the postpharyngeal gland (PPG) and on the epicuticle of the recipient ants after 24 h of encounters with an allo- and a conspecific donor (mean ± sem). In each row, different letters indicate groups which differ significantly: a vs b, $p < 0.0005$; a' vs b', $p < 0.003$ (Mann & Whitney U test)

Recipient ant	Homospecific groups		Heterospecific groups
	M. rubida (n = 7)	*F. selysi* (n = 10)	*M. rubida* (n = 11)
PPG	0.01 ± 0.00 *a*	2.1 ± 0.3 *b*	2.1 ± 0.8 *b*
Epicuticle	0.03 ± 0.01 *a'*	9.1 ± 5.8 *b'*	2.1 ± 0.9 *b'*

M. rubida from mixed groups was significantly lower than in *M. rubida* recipients of homospecific groups (11.9% vs 20.9%, $p = 0.0075$, Mann & Whitney U test). The distribution of transferred hydrocarbons between the PPG and the epicuticle was to the benefit of the PPG for all the encounters (average for all the encounters: 17% vs 5%, $p < 0.018$, Wilcoxon's signed-ranks test). Considering the percentages of transferred alkenes and alkanes separately, it appeared that these two classes of hydrocarbons were transferred in similar proportion to the recipients' PPG or its epicuticle in both homospecific encounters of *F. selysi* workers and heterospecific encounters (Table 2). It should be emphasized that Alkenes/Alkanes ratio in *M. rubida* recipients from heterospecific groups in both the PPG and the epicuticle was significantly higher from that of *M. rubida* recipients from homospecific groups but similar to that of *F. selysi* recipients (Table 3).

Behavioural observations. Workers displayed essentially the same behavioural repertoire in homo- and heterospecific encounters but with some significant differences in their respective frequencies (Table 4). Physical contacts between the encountered pairs was the most frequent event in all encounters. It was especially frequent in the encounters involving homospecific pairs of *F. selysi*, who remained in touch twice as long as either homospecific pairs of *M. rubida* or heterospecific pairs of *M. rubida/F. selysi* ($p < 0.035$ and $p < 0.0045$ respectively, Mann & Whitney U test). The frequency of selfgrooming was higher during the homospecific encounters between *M. rubida* workers than between *F. selysi* (Mean value between donor and recipient: 4.5% vs 1.2% $p < 0.01$, Mann & Whitney U test). *F. selysi* donor of the

Table 4. Behavioural observations during 6 hours of homo and heterospecific encounters between a prelabeled (donor) and a non labeled (recipient) ant. Data are expressed as the observed frequencies of each behavioural item (Mean ± sem) relative to a total of 72 records per encounter

	Homospecific groups				Heterospecific groups	
	F. selysi donor	*F. selysi* recipient	*M. rubida* donor	*M. rubida* recipient	*F. selysi* donor	*M. rubida* recipient
Trophallaxis	0.14 ± 0.14	0.14 ± 0.14	0	0	0.23 ± 0.16	0.23 ± 0.16
Selfgrooming*	1.95 ± 0.6	0.7 ± 0.2	5.5 ± 1.4	3.4 ± 0.8	0.8 ± 0.3	1.6 ± 0.5
Allogrooming	0.96 ± 0.5	0.7 ± 0.2	2.0 ± 0.7	1.6 ± 0.6	1.4 ± 0.7	3.8 ± 2.2
Physical contact*	61.9 ± 6.8	62.6 ± 6.8	35.3 ± 9.2	36.9 ± 9.3	31.1 ± 6.1	28.5 ± 4.4
Indifference*	35.0 ± 6.4	35.8 ± 6.7	57.2 ± 9.7	57.3 ± 9.6	66.5 ± 9.9	65.9 ± 6.0
Total interactions	63.0 ± 6.8	63.5 ± 6.7	37.3 ± 9.6	38.5 ± 9.4	32.7 ± 5.9	32.5 ± 5.8
Total non interactions	37.0 ± 6.8	36.5 ± 6.7	62.7 ± 9.6	61.5 ± 9.4	67.3 ± 5.9	67.5 ± 5.8
Number of replicates	10	10	7	7	12	12

* Behavioural items significantly different among donors and among recipients ($p < 0.05$, Kruskall-Wallis Test)

heterospecific encounters exhibited a similar frequency of selfgrooming (0.8%) as in homospecific encounters (1.95%), but it was significantly lower than that of a *M. rubida* donor in homospecific encounters (0.8% vs 5.5%, $p = 0.0023$, Mann & Whitney U test). Indifference in heterospecific encounters occurred at a similar frequency as in encounters between *M. rubida* workers. Trophallaxis was observed between *F. selysi* conspecifics and between heterospecific nestmates, but not between *M. rubida* workers.

Discussion

Workers of *F. selysi* and *M. rubida* synthesized hydrocarbons *de novo* from sodium acetate as described previously in other insects (Howard and Blomquist, 1982; Soroker et al., 1994). The distribution of labeled hydrocarbons between the PPG and the epicuticle was similar in both species independently of their social environment. The time course study conducted with *F. selysi* workers revealed a progressive increase in the amount of newly synthesized hydrocarbons. The labeled hydrocarbons were not equally distributed among the tissues examined and seemed to accumulate preferentially in the PPG. These results confirm our recent results with *Cataglyphis niger* concerning the function of this gland in hydrocarbon storage (Soroker et al., in press).

The possibility that workers reared in mixed-species groups actively synthesize the allospecific hydrocarbons was subsequently investigated. In our paradigm,

M. rubida workers reared in heterospecific groups synthesized *de novo* mostly alkanes and a very low level of alkenes, according to a ratio characteristic to *M. rubida* workers from homospecific groups. This result indicates that the hydrocarbon metabolism of *M. rubida* workers reared in mixed groups, was not modified towards that of its nestmates *F. selysi* by producing more alkenes. This is quite different from the case of the myrmecophile fly *Microdon albicomatus* which biosynthesizes *de novo* the host specific hydrocarbons (Howard et al., 1990). This ability of an inquiline to synthesize the hydrocarbons of its host could have developed during their coevolution, while such coevolution could hardly take place in artificial mixed groups.

The importance of hydrocarbon exchange in the creation of a mixed "odour" in the artificial mixed-species groups emerges from the results of the dyadic encounters. The Alkenes/Alkanes ratio on the epicuticle and in the PPG of *M. rubida* workers reared in heterospecific groups and presented to their prelabeled *F. selysi* nestmates was different from that of their conspecifics from homospecific groups but similar to that of *F. selysi* workers. This result can be explained only by a transfer of labeled hydrocarbons, in particular with respect to alkenes. Moreover, the level of transfer between allospecific nestmates was similar to that occuring between the conspecific *F. selysi* nestmates and did not differ for alkenes and alkanes. The fact that most of the transferred hydrocarbons were found in the PPG of the recipient ants implies the latter's involvement in the creation of the mixed "odour". The relatively low level of radioactivity found on the recipients' epicuticle can be explained by the short time of exposure and with only one nestmate.

It is expected that hydrocarbon transfer would occur during interactions between nestmates. Intensive grooming of the host by their inquilines was previously reported in several cases of chemical mimicry (Dettner and Liepert, 1994). In some of them, trophallaxis was also observed (Henderson and Akre, 1986; Franks et al., 1990). Our behavioural observations revealed the occurrence of interspecific interactions (trophallaxis, allogrooming and close physical contacts) in non negligible frequencies, which is in contradiction to the results of Corbara and Errard (1991). Frequencies of the different behavioural items during heterospecific encounters were similar to those in homospecific *M. rubida* encounters suggesting that *M. rubida* is the dominant in this association with *F. selysi*, generally imposing its behaviour on the latter, except for the trophallaxis. Trophallaxis was usually initiated by *F. selysi* workers by offering food to *M. rubida* workers, thence can be considered as an appeasement behaviour of *F. selysi* towards *M. rubida* (Hölldobler and Wilson, 1990). Trophallaxis and allogrooming observed during the heterospecific as well as homospecific *F. selysi* encounters, could explain the presence of labeled hydrocarbons in the PPG, while body contacts and self- and mutual grooming explain their transfer to the epicuticle of the recipient ants as we have already demonstrated in *Cataglyphis niger* (Soroker et al., in press). Since during cohabition, both ant species continue to synthesize their own hydrocarbons and exchange them continuously, the mixed "odour" of the group is created and maintained. The transfer of hydrocarbons between ants of both species is bi-directional but not necessarily equal as a consequence of different qualitative and/or quantitative behaviour.

The results of our experiments suggest that the formation of the mixed hydrocarbon profile in heterospecific groups of ants is the consequence of a transfer of these chemicals between nestmates rather than *de novo* biosynthesis of the allospecific hydrocarbons. Since we observed the exchange of hydrocarbons between nestmates by trophallaxis and grooming within, as well as between two different subfamilies of ants, we propose to generalize this process and the role of the PPG as a source for the production of a colony Gestalt "odour" to all the Formicidae.

Acknowledgements

We are very grateful to Dr. Christine Errard for providing the ants. We thank Ms. Naomi Paz for revising the English. This research was supported in part by grants from the Foundation Singer-Polignac (Paris, France) and Tel-Aviv University (Georges S. Wise postdoctoral fellowship) to Catherine Vienne and by the Foundation of Higher Council in Israel to Victoria Soroker.

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Received 28 September 1994;
revised 1 February 1995;
accepted 9 February 1995.