Path selection in cockroaches

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Summary

In gregarious insects, the exploration and the use of the home range can involve both individual navigational abilities and/or chemical trails. Trail formation can result from an active laying of pheromones but can also derive from the incidental deposition of chemical cues. In this study, we investigated whether scent trails can influence path selection in the cockroach *Blattella germanica* (L.). Experiments were designed to separate the role of prior experience based on the orientation of the path and the presence of trails. In a first phase, cockroaches were able to access freely one or two branches of a platform during a 48 h period. In a second phase, cockroaches were offered a binary choice between one marked and one clean branch, or between two clean branches. In the absence of trails, cockroaches prefer the novel orientation but in the presence of a trail previously laid by the same group of individuals, they prefer the path with the trail, irrespective of orientation. However, cockroaches tended to avoid trails laid by a different group of cockroaches. Overall, our results indicate that both scent cues and response to novelty influence, weakly but significantly, path selection in cockroaches. The plausible nature of scent marks used by cockroaches is discussed. Our study suggests that the influence of incident trailing cues can be modulated by learning to support a flexible orientation strategy depending on individual experience.

Key words: cockroach, novelty, scent trail, *Blattella germanica*.

Introduction

In many species, the orientation within the vital domain and the exploitation of environmental resources benefit from several strategies ranging from individual navigation to the extensive use of collective scent trails. Individual orientation has been shown to rely either on path integration, whereby the position of an individual in relation to its starting point is determined by the mean of idiothetic (i.e. internal) references, or on the learning of salient environmental cues to navigate in the home range (Papi, 1992; Lehrer, 1997; Healy, 1998).

However, solitary or group-living individuals can benefit from trails to locate food and find mates or conspecifics. The successive passages of individuals can induce the formation of either physical [bears (Reimchen, 1998); humans (Helbing et al., 1997)] or chemical trails [snakes (Greene et al., 2001); gastropods (Chelazzi, 1992); rats (Galef and Buckley, 1996); naked-mole rats (Judd and Sherman, 1996)]. It is in insects that the contribution of trails to animal orientation has received the most attention. Well-known examples have been described in ants (Hölldobler and Wilson, 1990) or termites (Pasteels and Bordereau, 1988; Reinhard and Kaib, 2001). In swarm-founding polistine wasps, individuals drag their abdomen and lay spots of pheromones on the substrate to mark the route of migration toward new nest sites (Jeanne, 1981). In bumblebees, homing benefits from odoriferous trail deposited at the nest entrance (Pouvreau, 1996). Workers of the stingless bee *Trigona spinipes* lay scent trails to recruit and guide nestmates to food sources (Nieh et al., 2004). In caterpillars, pheromones associated with silk lead siblings to food patches (Fitzgerald, 1995).

Two modes of acquisition of social information are usually distinguished: cues providing incident information, frequently as by-products of individual activities (Lloyd, 1983; Seeley, 1995), and signals that have been shaped specifically by natural selection to convey information. Whereas trails can be formed with pheromones originating from specialized exocrine glands devoted to communication (Billen and Morgan, 1998; Bradbury and Vehrencamp, 1998), trail formation can also result from the passive deposition of various materials on the substrate. For instance, homing in the wasp *Vespula vulgaris* benefits from the use of scent trails formed by the passive deposition of cuticular hydrocarbons owing to the successive passages of workers between nest and cavity entrance (Steinmetz et al., 2003). In a social context, a passive trailing behavior can induce the formation of collective patterns. For instance, spiders produce silk draglines during their displacement to act as security threads. In groups of spiderlings of the solitary species *Larinioides cornutus*, silk threads lead to the collective selection of an aggregation site through

amplification processes owing to the successive passages of individuals (Jeanson et al., 2004).

In group-living animals, navigation can then rely on an individual memory based on previous experience and learning, but individuals can also orient through the use of an external memory supported by persistent traces of previous activities of conspecifics. Both modes of orientation can be used hierarchically, with the prevalence of one mode of orientation over another in case of conflicting information. For instance, the ant species *Linepithema humile* and *Lasius niger* use mass communication and orient along chemical trails to exploit newly discovered food sources. Whereas *L. humile* predominantly use chemical communication, workers of *L. niger* can switch to a more individual mode of orientation based on learned visual landmarks (Aron et al., 1993). In the giant tropical ant *Paraponera clavata*, foragers change cue hierarchies with experience: naïve foragers use pheromonal cues for orientation to food, whereas experienced foragers preferentially use visual landmark cues (Harrison et al., 1989).

Although most of the studies on chemical trails have been performed in eusocial species using sophisticated means of communication, few works have examined whether gregarious organisms can form and use trails to orient within their home range [with the noticeable exception of social caterpillars (Fitzgerald, 1995)]. The cockroach *Blattella germanica* forms mixed clusters of males and females with generation overlap in its natural environment. During daytime, cockroaches rest in a common shelter often located in cracks or crevices and forage mainly at night. *Blattella germanica* is a relevant biological model to examine whether organisms characterized by simple social organization and the absence of any sophisticated means of communication can form and use incident scent trails. Experimental evidence suggests that cockroaches have the ability to use chemical trails. Indeed, previous studies have shown that a pre-applied solution of fecal extracts on the substrate can induce trail-following in cockroaches (Miller and Koehler, 2000; Miller et al., 2000). However, navigation in *Blattella germanica* relies also on multiple sensory channels, implying the use of idiothetic cues or learned visual landmarks (Durier and Rivault, 1999; Durier and Rivault, 2000; Rivault and Durier, 2004). During outward trips, the exploratory behaviors of cockroaches are affected by the presence of novel objects introduced in their familiar home range (Durier and Rivault, 2002) and they can build a representation of rewarding events to locate food sources during foraging trips (Durier and Rivault, 2000). In this study, we ask whether cockroaches (*Blattella germanica*) can form and use scent trails produced by the successive passages of conspecifics and we examine how cockroaches can balance conflicting information provided by experience and the presence of scent trails to select a path.

Materials and methods

Study species

Cockroaches [*Blattella germanica* (L.)] were collected in human dwellings in Brussels (Belgium) during winter 2004–2005. After their collection, cockroaches were mixed to form groups of 500 adults (250 males and 250 females) and 1500 larvae of all instars, which were housed in transparent plastic boxes (24×18×10 cm). Shelters (folded cardboard and paper), food (dog food pellets) and water were provided in each container. A 1 cm hole was drilled in the middle of the longest side of the box, at 1 cm from the bottom to allow access to a platform for behavioral assays. Boxes were kept in a climate room (23°C, ~35% RH, 13 h:11 h L:D). In total, 10 containers were formed. Ideally, all cockroaches should have been identified individually with a unique combination of marks to determine whether some individuals accessed the platform repeatedly and to distinguish naïve from experienced individuals. However, the large population in each container (2000 individuals), the small size of larvae and their molting cycle impeded any individual marking or tagging.

Experimental procedure

Before the beginning of a trial, the top of the container housing cockroaches was removed and the lateral hole opened. The box was placed on four stands (height: 2.5 cm) within a tank with Fluon® (Whitford France, Pontault-Combault, France)-coated walls. Cockroaches had access to a horizontal platform that was screwed to a Y-shaped aluminium stand (height: 2.7 cm). Depending on experimental conditions, the platform included a white Plexiglas stem (length, 6 cm; width, 1.6 cm) and/or one or two white Plexiglas branches (length, 30 cm; width, 1.6 cm) (Table 1). The angle between both branches equaled 90°. The stem, branches and stand were washed with soapy water and a solution of 97% ethanol:3% ether between trials.

The experimental platform was placed in the front of the lateral hole. To encourage cockroaches to walk on the platform and to prevent them from escaping, the tank was filled with water. The water level reached 0.5 cm below the platform. During daytime, two lamps were placed symmetrically above the set-up on each side of the platform. During the night, a lamp covered with a red filter (Rosco colour filter, E-Colour #19; Rosco Ltd., London, UK) was positioned above the container to provide luminosity for video recording. A webcam (Philips ToUCam Pro; Eindhoven, The Netherlands), placed above the platform, was coupled to a computer for image recording.

Experiments took place in a climate room (23°C, ~35% RH) with a photoperiod of 13 h:11 h L:D (beginning night at 21.00 h). Each trial had two phases: a marking phase (48 h) immediately followed by a test phase (13–13.5 h). Each phase began between 18.30 h and 19.00 h. Cockroaches were totally deprived of food and water during both phases to enhance their motivation to explore the platform and consequently increase the number of passages on the platform. During the entire duration of a trial, cockroaches could freely access the platform.
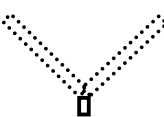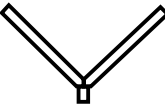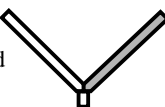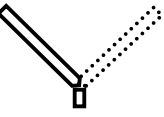
Experimental conditions
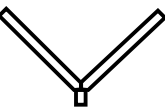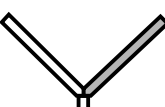
Each experimental trial included two successive phases: a marking phase with cockroaches accessing only the stem or the

stem plus one or two branches and a test phase with cockroaches facing a binary choice between two unmarked branches or between one marked and one unmarked branch (Table 1). In total, seven experimental combinations were designed to study the potential contribution of scent trail and learning.
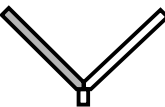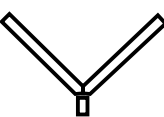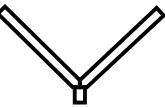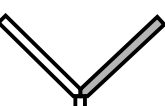
For each experiment, the stem used during the marking phase was reused during the test phase for the same group of cockroaches. Two experimental set-ups were used. When groups of cockroaches faced two branches during the marking phase, one branch was subsequently used for the same group during the test phase (Table 1: Experiment G) while the other branch was used as a marked branch for another group (Table 1: Experiment B). When only one branch was available, its position (left or right) was selected randomly. The stand was replaced by a clean one between the marking and test phase. The unmarked branches used for the test phase were placed above water in a tank placed beside the experimental set-up

Table 1. *Experimental design and results*

Experimental design		Mean number of passages ± s.d.		Total proportion (±95% CI) of cockroaches on each branch during test phase		
Marking phase	Test phase	Marking phase	Test phase	Test phase		χ^2 test
Stem, but no branch	Two unmarked **Expt A** (N=9)	–	541±202	Unmarked = 0.50±0.01	Unmarked = 0.50±0.01	χ_1=0.28, P=0.97
	One marked (by another group) and one unmarked **Expt B** (N=9)	315±98	576±284	Marked = 0.47±0.01	Unmarked = 0.53±0.01	χ_1=19.37, P<0.001
Stem + one branch	Two unmarked **Expt C** (N=8)	–	632±382	(same side to marking) 0.47±0.01	(opposite side to marking) 0.53±0.01	χ_1=12.80, P<0.001
	One marked (opposite side to marking) and one unmarked **Expt D** (N=9)	222±137	527±211	Marked = 0.55±0.01	Unmarked = 0.45±0.01	χ_1=44.07, P<0.001
	One marked (same side to marking) and one unmarked **Expt E** (N=9)	306±119	567±232	Marked = 0.54±0.01	Unmarked = 0.46±0.01	χ_1=25.84, P<0.001
Stem + two branches	Two unmarked **Expt F** (N=9)	–	596±295	Unmarked = 0.50±0.01	Unmarked = 0.50±0.01	χ_1=8×10^{-4}, P=0.60
	One marked and one unmarked **Expt G** (N=9)	226±102	720±300	Marked = 0.52±0.01	Unmarked = 0.48±0.01	χ_1=9.27 P<0.001

Experimental design: broken and solid lines represent the absence and presence, respectively, of a branch on the platform; white and grey branches represent the presence of unmarked and marked branches, respectively. Results: mean number of passages during the marking phase on the branch subsequently used as the marked branch, mean number of passages on both branches during the test phase and proportion of cockroaches following each branch during the test phase for the seven conditions (A–G).

during the marking phase. Groups of cockroaches were randomly assigned to an experimental condition. At least 10 days elapsed between two successive trials for each group.

Image processing

A movement detection program was developed with the video-processing freeware Videoscript (www.videoscript.com) to estimate the number of passages on each branch during the marking phase. For technical constraints, a threshold was set so that only fifth- or sixth-instar larvae and adults reaching the stem could launch the recording of pictures of the platform. During the marking phase, we aimed to assess the intensity of marking in counting the number of passages on each branch. Thus, cockroaches coming either directly from the stem or after visiting the alternative branch were considered to compute the flow on each branch.

During the test phase, we used the freeware VirtualDub v.1.6 (www.virtualdub.org) to record the platform at a sample rate of one frame every 1.5 s. The movie was then analyzed frame by frame to count the number of cockroaches (irrespective of sex and age) following each branch. To determine the proportion of cockroaches following either branch, individuals were considered to follow a given branch only when they came directly from the stem (we did not count cockroaches following a branch after leaving the other branch).

Since cockroaches were mostly active during the night, we only counted the number of passages on the platform during night-time (duration: 11 h) both for the marking and test phases.

Data analysis

The total flow of cockroaches on both branches of the platform was compared between experimental conditions with a one-way analysis of variance (ANOVA). For each experimental condition, the total proportion of cockroaches following each branch was compared with χ^2-tests. Pearson correlation tests were used to test the relation between the number of passages during the marking phase and the total proportion of individuals following the marked branch during the test phase. For each experimental condition, repeated-measures ANOVA was used to test whether the choices of cockroaches changed over time.

To determine whether the choice of cockroaches was random or oriented, we compared the experimental results with theoretical data assuming a random distribution of individuals on both branches. For each experimental condition, we computed the total flow of cockroaches on both branches every hour for each replicate. The mean and standard deviation of each distribution were obtained from either a normal (Experiments B, D, E and G) or a log-normal distribution (Experiments A, C and F). From the mean and standard deviation of each distribution, we used Monte Carlo simulations to generate theoretical distributions of the expected hourly flow on each branch assuming an equal individual probability to choose either branch. For each condition, we ran 1000 simulations of 11 h. The theoretical and empirical distributions of the hourly proportions of individuals following each branch were compared with one-way repeated-measures ANOVA after arcsine transformation.

All statistical tests were two-tailed and performed with SPSS for Windows (v.11; SPSS Inc., Chicago, IL, USA).

Results

Flow of cockroaches

The total number of passages during the marking phase on the branch subsequently used as a marked branch for the test phase were not different between experimental conditions (Experiments B, D, E and G) (one-way ANOVA, $F_{3,32}=1.71$, $P=0.18$) (Table 1). The total flow of cockroaches during the test phase did not differ between experimental conditions (one-way ANOVA, $F_{6,55}=0.51$, $P=0.8$) (Table 1).

Proportion of cockroaches following each branch

For each experimental condition, we pooled the data of all trials to compute the total proportion of cockroaches following each branch. Experiments A and F were control experiments to test for the homogeneity of the experimental set-up. In the presence of two unmarked branches, cockroaches used both branches evenly (Table 1), which confirms that the choice of cockroaches was not biased by spatial heterogeneities. Experiment C tested the contribution of novelty in path selection. When cockroaches encountered only one branch during the marking phase and two unmarked branches during the test phase (Table 1), they selected more frequently the unmarked branch located on the opposite side to the one available during marking. Experiments D and E examined, respectively, the synergy and conflict between the response to novelty and the presence of a branch conditioned by the same group of cockroaches. In both cases, cockroaches chose more frequently the marked branch when faced with choices between an unmarked branch and a branch conditioned by themselves (Table 1). In the absence of novelty, Experiment G tested the preference of cockroaches between a branch conditioned by themselves and an unmarked branch. Individuals selected preferentially the marked branch (Table 1). Finally, Experiment B examined the influence of scent marks deposited by another group of cockroaches. In this case, cockroaches selected more frequently the unmarked branch (Table 1).

Comparison between empirical and theoretical distributions

For each condition, we computed the theoretical distribution of the proportion of individuals following the left branch (arbitrarily chosen) assuming a binomial distribution with an equal probability to follow each branch. These theoretical distributions were then compared with the hourly experimental proportion of individuals following either branch. For all conditions, except for experiments A and F, the experimental distribution significantly differs from a binomial distribution (Table 2, Fig. 1). This indicates that cockroaches did not select branches randomly but were influenced by novelty and scent trails.

Table 2. *Summary of one-way repeated-measures ANOVA testing for the effect of condition (experiments vs simulations) and time on the hourly proportion of cockroaches following each branch*

	d.f.	Experiment A		Experiment B		Experiment C		Experiment D		Experiment E		Experiment F		Experiment G	
		F	P	F	P	F	P	F	P	F	P	F	P	F	P
Condition	1	0.37	0.54	7.02	0.008	20.36	<0.001	42.59	<0.001	9.90	0.002	1.55	0.21	9.17	0.003
Time	10	1.03	0.22	1.44	0.16	2.72	0.002	2.19	0.02	1.43	0.16	2.57	0.04	1.21	0.28
Condition × time	10	1.21	0.27	1.53	0.12	2.55	0.005	2.11	0.02	1.33	0.21	2.29	0.01	1.00	0.43

Correlation between marking intensity and choice asymmetry

For trials with choices between an unmarked and a marked branch, there was no correlation between the number of passages during the marking phase and the total proportion of cockroaches following the marked branch during the test phase (Pearson correlation test, Experiment B, $r_9=0.12$, $P=0.75$; Experiment D, $r_9=-0.08$, $P=0.84$), except for Experiment E (Pearson correlation test, $r_9=0.67$, $P=0.046$; slope of linear regression, 0.02% per passage, $r^2=0.45$) and Experiment G (Pearson correlation test, $r_9=0.78$, $P=0.014$; slope of linear regression, 0.03% per passage, $r^2=0.60$). This suggests that the probability for a cockroach to select a path increased with the intensity of the traffic on this branch (Experiment G) and that a high number of passages on the marked branch can partly overcome the response to novelty (Experiment E).

Influence of time on choice asymmetry

We performed repeated-measures ANOVA to test whether the proportion of cockroaches following either branch changed over time (Table 2). For Experiment C, the proportion of individuals following the branch located on the opposite side to the one available during the marking phase decreased linearly during the course of the test phase (repeated-measures ANOVA, $F_{10,70}=2.72$, $P<0.001$). During the first two hours of experiment C, the mean proportion of cockroaches following the opposite side to the one available during marking was approximately 40%.

Discussion

Our results indicate that scent cues and response to novelty influence path selection in cockroaches. Cockroaches tended to follow a branch on which individuals of the same groups had previously walked. However, the preference for a marked branch was reversed when individuals faced a clean branch and a branch marked by another group of cockroaches. Besides the influence of scent trail, our study suggests that path selection was also affected by previous individual experience on the platform. Indeed, cockroaches confronted with a binary choice between unmarked branches exhibited a preference for the branch located on the opposite side to the only one available during marking (Experiment C). This probably originates from the tendency of cockroaches to explore novel objects introduced in their home range (Durier and Rivault, 2002). Moreover, in association with the perception of novelty, the absence of food during the marking phase might act as a negative reinforcement increasing the likelihood of cockroaches to visit the alternative branch to the one available during marking. In the latter case, it is worth noting that choice asymmetry decreased with time. On average, 600 passages were counted on the platform during the test phase for groups of approximately 2000 cockroaches. It is thus likely that individuals made several trips on the platform during the same night. Therefore, the choice of cockroaches was not only influenced by their initial experience acquired during the marking phase but was also updated during the course of the
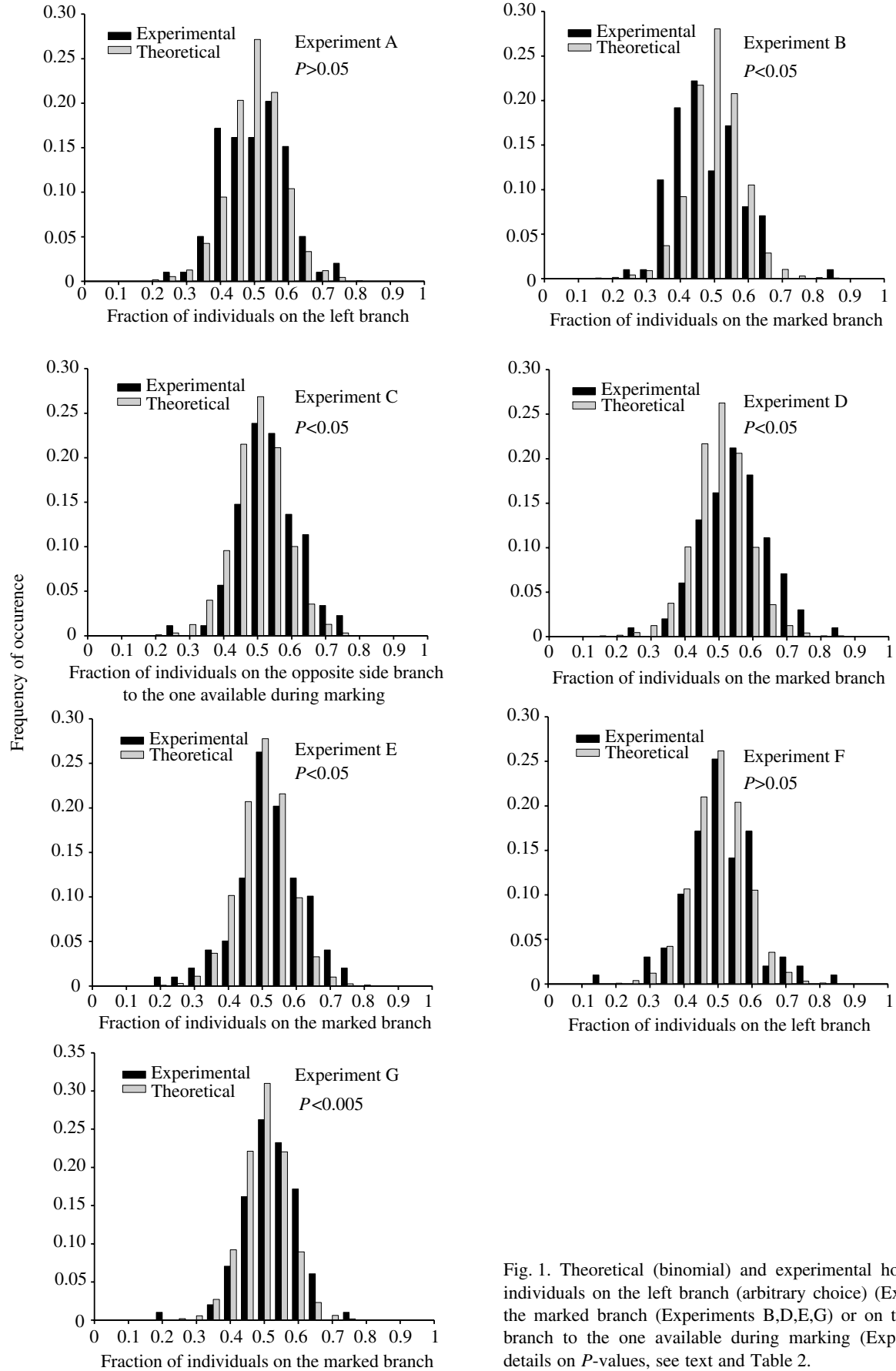
Fig. 1. Theoretical (binomial) and experimental hourly fraction of individuals on the left branch (arbitrary choice) (Experiments A,F), the marked branch (Experiments B,D,E,G) or on the opposite-side branch to the one available during marking (Experiment C). For details on *P*-values, see text and Table 2.

test phase. When marking and novelty provided conflicting information (Experiment E), the attraction of the marked branch increased with the intensity of marking. This suggests that the presence of a trail can partly overcome the response to novelty. Finally, in agreement with the other experimental conditions, the greatest asymmetry in choice was observed when trail and novelty acted in synergy (Experiment D).

Based on previous studies in cockroaches and other insects, we can speculate that the chemical cues used by cockroaches derived from the incident deposition of hydrocarbons that were transferred passively from the cuticle to the substrate through the multiple passages of individuals. In the wasp *Vespula vulgaris*, it has been shown that an extract of cuticular hydrocarbons can induce similar trail-following behaviors to trails naturally formed by walking foragers (Steinmetz et al., 2003). The preference for a marked branch over a clean one was reversed when cockroaches faced a branch marked by another group of cockroaches. This suggests that cockroaches can discriminate their own group odor from scent trails laid by alien groups. In our experiments, groups were randomly formed (i.e. non-kin groups) and cockroaches were fed with the same food. Such divergence of chemical profiles has been reported in queenless subgroups originating from the same colonies and reared under identical treatments in the ants *Cataglyphis iberica* (Dahbi and Lenoir, 1998) or *Cataglyphis niger* (Lahav et al., 2001). The existence of a group odor evidenced in our experiments seems consistent with results obtained in another context in which *Blattella germanica* were shown to distinguish odors of strains originating from different locations. In these experiments, larvae aggregated preferentially on shelters conditioned by conspecifics of their own strain rather than by alien strains (Rivault and Cloarec, 1998) and it has been shown that extracts of cuticular hydrocarbons induce aggregation in cockroaches (Rivault et al., 1998). The potential role of cuticular hydrocarbons in scent-trail formation could be amplified by the presence of feces, of which extracts have been shown to elicit trail following in cockroaches (Miller and Koehler, 2000). Further work should examine whether extracted cuticular hydrocarbons applied on the substrate can elicit trail-following behaviors.

In the wild, one might then ask how efficient scent trails can be formed. As in termites (Jander and Daumer, 1974) and ants (Klotz et al., 2000), cockroaches present a tendency to orient along structural guidelines provided by walls and edges when introduced in a new environment (Creed and Miller, 1990; Camhi and Johnson, 1999; Durier and Rivault, 2003; Jeanson et al., 2003). In the early stages of colonization of new harborages, wall-following behaviors can increase the number of passages of individuals in the vicinity of the heterogeneities and consequently favor the formation of efficient trails close to edges (Dussutour et al., 2005).

It might be argued that choice asymmetry was too weak to draw any conclusions on the trail-following abilities of cockroaches. In our opinion, the influence of scent trail on path selection was underestimated in our experimental design. In the absence of individual marking (e.g. paint dots), it was not possible to determine whether all individuals accessed the branches during the marking phase and/or their number of trips on the platform. During the test phase, the choice of individuals that have experienced the platform during the marking phase might be influenced by novelty, whereas naïve cockroaches might orient primarily in response to the presence of a trail. Moreover, the absence of food probably motivated cockroaches to visit both branches, and individuals might have accessed the platform several times during the same night. Assuming that the initial individual decision was affected by the presence of a trail, their subsequent choices might benefit from the update of the knowledge of their environment and encourage them to follow the other branch. Thus, the interplay between the negative reinforcement (i.e. absence of food) and trail attraction tends to induce a symmetrical distribution of cockroaches between branches. Further experiments should investigate how the presence of positive reinforcement affects the selection of either branch by cockroaches. Overall, our results indicate that scent trails, the influence of which was probably underestimated, contribute to path selection in cockroaches.

In some species, the same substances can act as both an aggregation and a trail pheromone, such as in the wasp *Polybia sericea* (Jeanne, 1981; Clarke et al., 1999). In the haematophagous bug *Triatoma infestans*, feces deposited on the substrate can induce both aggregation and orientation through positive anemotaxis (Lorenzo Figueiras et al., 1994). In the velvet worm *Euperipatoides rowelli*, the aggregation pheromone is also believed to be involved in trail formation (Barclay et al., 2000). Depending on the contexts and probably on pheromone concentration, the same chemical cues can exert an arresting action favoring clustering but also guide individuals within their vital domain. In *Blattella germanica*, aggregation pheromones are thought to be composed of a mixture of volatile principles acting as attractants and of nonvolatile compounds exerting an arresting action favoring clustering (Sakuma and Fukami, 1991; Sakuma et al., 1997; Scherkenbeck et al., 1999). In group-living species with resting site fidelity we can speculate that aggregation pheromone might be used not only to ensure group formation and cohesion but also as an incident means of conveying information through trail formation. Scent trails could contribute to optimal homing strategies and efficient exploitation of environmental resources and could be of particular relevance for the orientation of naïve individuals, such as inexperienced juveniles, during their first foraging trips.

In conclusion, our results indicate that cockroaches can rely on the interplay of individual navigational abilities acquired by experience and collective external memory developed incidentally by conspecifics to orient in their home range. In many gregarious species, byproducts of individual activities can be used as trailing cues in diverse contexts to ensure foraging (Galef and Buckley, 1996), aggregation (Chapman, 1998), collective migration (Saffre et al., 1999) or homing (Chelazzi et al., 1990).

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