

Individual Experience Alone Can Generate Lasting Division of Labor in Ants

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Summary

Division of labor, the specialization of workers on different tasks, largely contributes to the ecological success of social insects [1, 2]. Morphological, genotypic, and age variations among workers, as well as their social interactions, all shape division of labor [1–12]. In addition, individual experience has been suggested to influence workers in their decision to execute a task [13–18], but its potential impact on the organization of insect societies has yet to be demonstrated [19, 20]. Here we show that, all else being equal, ant workers engaged in distinct functions in accordance with their previous experience. When individuals were experimentally led to discover prey at each of their foraging attempts, they showed a high propensity for food exploration. Conversely, foraging activity progressively decreased for individuals who always failed in the same situation. One month later, workers that previously found prey kept on exploring for food, whereas those who always failed specialized in brood care. It thus appears that individual experience can strongly channel the behavioral ontogeny of ants to generate a lasting division of labor. This self-organized task-attribution system, based on an individual learning process, is particularly robust and might play an important role in colony efficiency.

Results and Discussion

Learning, the experience-dependent modulation of individual behavior, affects various traits of animal ecology and evolution, such as habitat and resource selection,

predator avoidance, mate choice, and social behavior [21–24]. Here, we explore the behavioral processes that might link individual learning and social organization. The decentralized work system [4, 25, 26] and the learning abilities [27–31] of social insects make them excellent candidates to investigate whether and how individual experience can lead to behavioral specialization. To date, a few theoretical studies have suggested that the experience gained from previous performances could influence individual decisions to engage in a particular task [13–16]. According to these studies, success would increase the worker's propensity for that task, whereas failure or the lack of opportunity would reduce it. Were this hypothesis to be proven, we would expect a division of labor to emerge from a worker population with varied experiences.

The ant *Cerapachys biroi* exhibits two singular traits—namely, phasic reproduction, whereby each new generation of workers emerge synchronously every 34 days [32, 33], and parthenogenesis [34, 35]. This allowed us to circumvent the other typical factors involved in labor division (see [Experimental Procedures](#), “Study Organism”); in our four experimental colonies, all individuals belonged to a same cohort of newly eclosed workers and were therefore exactly the same age, size, and shape and shared identical rearing conditions. Moreover, as parthenogens, they also displayed an extremely low interindividual genetic diversity. This exceptional colonial homogeneity offers an optimal ground to test the sole effect of individual experience on task specialization and its consequences on work organization.

First, we conducted training sessions on these naive workers who never had the opportunity to get out of the nest chamber and therefore had never experienced any foraging activity (defined here as the act of searching for food). During this period, half of the workers of each experimental colony (referred to as “successful explorers” for brevity) were artificially presented with prey at every foraging attempt. The second half (referred to as “unsuccessful explorers”) never found any prey (see [Experimental Procedures](#), “Training Period”). To evaluate the immediate effects of training on ant behavior, we compared (1) the mean foraging rate (i.e., the number of foraging attempts / number of training sessions) and (2) the mean exit delay (i.e., the time elapsed between the opening of the nest chamber and the exit of the workers) of the two experimental groups, throughout the training period. Despite the natural intrinsic variability in the responses of the different colonies, the analyses revealed significant differences between the two groups of workers ([Table 1](#)). In all colonies, individual worker behavior progressively diverged, depending on the experience gained from foraging performance. Successful explorers exhibited higher exit rates than did workers who systematically explored in vain (generalized estimating equations [GEE] with Procedure GENMOD, interaction experimental session × colony nested within group, $\chi^2 = 181.31$, $df = 126$, $p = 0.0009$, [Figure 1A](#)). Moreover, the exit delay also diverged

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Table 1. Results of the Statistical Analyses

	Model	Effects	Statistics		
Foraging Rate	GEE		Chi ²	df	p
		group	10.96	1	<0.0001
		colony(group)	20.45	6	0.0023
		session	113.67	21	<0.0001
		session × group	45.24	21	0.0016
		session × colony(group)	181.31	126	0.0009
Exit Delay	GLM		F	df	p
		group	20.84	1, 247	<0.0001
		colony(group)	3.41	1, 247	0.0030
		session	12.65	21, 5187	<0.0001
		session × group	5.31	21, 5187	<0.0001
		session × colony(group)	3.93	126, 5187	<0.0001
Long-Term Effects	MANOVA GLM		Wilks	df	p
		group	10.32	5, 197	<0.0001
		colony(group)	9.06	30, 790	<0.0001

Here are summarized the immediate (foraging rate and exit delay) and long-term effects of the training sessions on the two groups (successful and unsuccessful) of explorers. The factor session was used as the repeated measure in the GEE and GLM procedures. Five behaviors (exploration, brood care, and immobility at three different locations) were considered in the MANOVA GLM.

increasingly between the two types of individuals (generalized linear model [GLM] with Proc. GLM, interaction experimental session × colony nested within group, $F_{126, 5187} = 3.93$, $p < 0.0001$, Figure 1B). Whereas successful explorers presented short exit delay, the unsuccessful ants were less and less likely to leave the nest with repeated foraging failures. The treatment we applied on this homogeneous worker population effectively led to interindividual variability in foraging propensities (Figures 1A and 1B). Here, workers differed only in the outcome of their exploration for food, even though none of them ever retrieved any food into the nest (prevented by the fluon-coated compartment walls). Successful explorers always found prey after an active search for food outside the nest, whereas unsuccessful explorers, although motivated, never did, even if they all had access to food when the colony was fed. Therefore, it is very likely that the internal state of workers when discovering the food influences their tendency to forage. Besides, had they been able to retrieve prey, their behavior would probably have diverged even more rapidly.

Interestingly, effects associated with the two treatments appeared relatively early in the training period, despite the fact that we only performed two sessions per day. Seven sessions (3.5 days) were sufficient to generate a significant difference between individuals in the mean exit delay (Tukey post-hoc comparison, session eight: $p < 0.0001$; $n = 125$ and $n = 130$ for successful and unsuccessful explorers, respectively). These post-hoc differences were significant ($p < 0.05$) for all subsequent sessions, except session 11 ($p = 0.99$), which immediately followed the second food supply, and session 13 ($p = 0.32$), for undetermined reasons. This delay might be overestimated because workers probably have more foraging opportunities under natural conditions.

Foraging experience might not be the only factor involved in the diverging behaviors observed among workers. Because workers who always explored in vain increasingly remained in the nest chamber, they were also more exposed to the brood. They could thus respond to brood stimulation and care for it more,

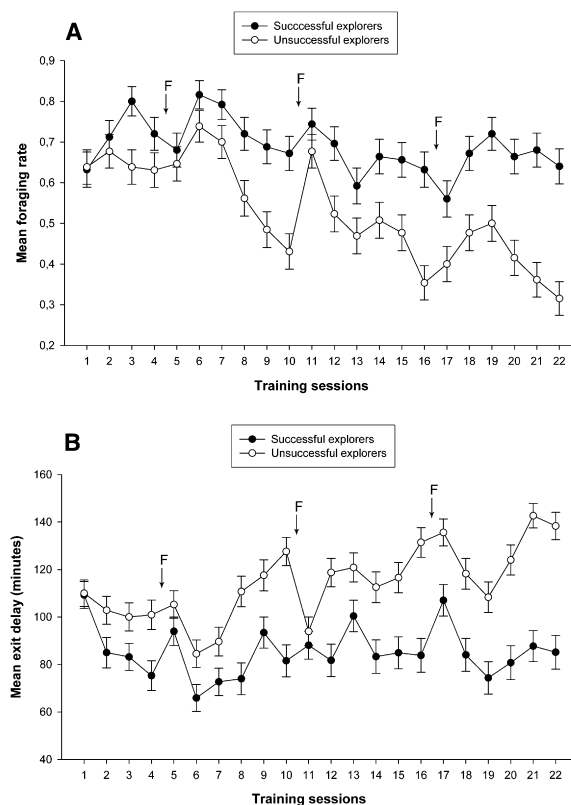


Figure 1. Immediate Effects of Training on Ants' Behavior
Evolution of (A) the mean foraging rate (\pm standard error [SE]) and (B) the mean exit delay (\pm SE) according to foraging experience: Successful explorers kept a high foraging rate and presented short exit delay, whereas unsuccessful explorers were less and less likely to leave the nest with repeated foraging failures. The curves illustrate the session × group interaction effects (for [A]: $\text{Chi}^2 = 45.24$, $\text{df} = 21$, $p = 0.0016$; for [B]: $F_{21, 5187} = 5.31$, $p < 0.0001$; successful explorers: $n = 125$; unsuccessful explorers: $n = 130$). "F" indicates days when food was supplied.

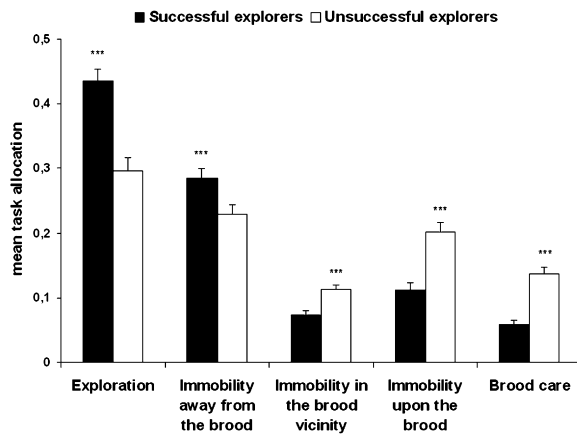


Figure 2. Long-Term Effects of Training on Ants' Behavior

The ants *Cerapachys biroi* generate a long-term division of labor based on individual experience of foraging (mean task allocation [\pm SE] of the two groups of workers according to their respective experience). The results show a simple effect of the factor group for the five behaviors, as revealed by the MANOVA (Wilks' lambda = 10.32, $df = 5, 197$, $p < 0.0001$; successful explorers: $n = 107$; unsuccessful explorers: $n = 102$). Scanning observations revealed that, long after the end of the training sessions (18–32 days later), workers who previously found prey at every foraging attempt presented higher exploratory activity and were more distant from the brood than were workers who always explored in vain. Conversely, the latter performed most of the brood care and stood closer to the brood (GLM with Proc. GLM [SAS], *****) indicates $p < 0.001$).

another type of experience that in turn might have modulated their propensity to nurse. It is very likely that both kinds of stimuli were at work at the same time and in synergy to generate heterogeneity among workers. Another factor temporarily modulating the task-specialization process might be the actual presence of food in the nest, as shown by the apparent reduced difference between groups after each time food was supplied (Figure 1A and 1B). Indeed, the feeding of the colonies could lead to a renewal of the motivation of unsuccessful workers to forage or to a change in foraging stimuli associated to brood satiation.

We then evaluated the long-term effect of the treatment on labor division by characterizing the behavioral profile of the same workers from the 18th to the 32nd day after the end of the training sessions (see [Experimental Procedures](#), "Long-Term Effects of Training"). While individuals were free to search for food, a significant difference in the task allocation of both groups of workers was observed (multivariate analysis of variance [MANOVA] with Proc. GLM, effect of colony nested within group, Wilks' lambda $F_{30, 790} = 9.06$, $p < 0.0001$, Figure 2). Workers that were previously led to discover prey explored both their nest chamber and the surrounding area more than the unsuccessful ones did ($F_{6, 201} = 9.35$, $p < 0.0001$, and $n = 107$ and $n = 102$ for successful and unsuccessful explorers, respectively). Conversely, the latter performed most of the nursing activity ($F_{6, 201} = 2$, $p = 0.067$). This difference in individual-task allocation was further illustrated by the location occupied by the resting workers of both groups: Successful explorers rested further from the brood (immobility away from the brood: $F_{6, 201} = 18.11$, $p < 0.0001$) and were more likely to forage. Workers who always

explored in vain during the training period were located closer to the brood (immobility in the brood vicinity: $F_{6, 201} = 2.87$, $p = 0.011$; immobility upon the brood: $F_{6, 201} = 9.73$, $p < 0.0001$) and were thus more likely to perform nursing activities [36]. Finally, experimental colonies succeeded in rearing a new generation of pupae, showing that a stable division of labor can emerge among workers differing only in early foraging experience.

In insect societies, a worker is presumed to engage in a particular task as soon as the associated stimulus exceeds its internal response threshold. Interindividual variability in response thresholds, and thus in task selection, arises through many factors (i.e., age, size, genotype, and social interactions [1–12]). Consequently, a flexible, self-organized division of labor can emerge from a heterogeneous worker population. Here we have shown that individual experience also can affect the dynamics of task specialization by shaping ants' behavior, probably through a lasting modification of their internal response thresholds. The strength of experience lies in the fact that workers allocate their efforts according to their task performance, modulating division of labor through simple reinforcement mechanisms. This work, combined with others emphasizing the role of experience in improving individual and collective performance [18, 37, 38], suggests that individual experience can play a prominent role in colony efficiency through its effects on the task-attribution system.

The present study further suggests that, to achieve resilience, insect colonies can also benefit from quick task reallocations by experienced individuals with lower response thresholds. Results show that workers can use their experience to select a task after only a few attempts. Under natural conditions, a few opportunities might thus be sufficient to select a new set of specialized individuals and counterbalance a sudden change in the colony needs or the differential death of individuals engaged in risky labor. This mechanism, whereby a worker population diversifies its task propensities through the process of individual experience, appears therefore to be a stable and robust way to organize labor division.

Moreover, a large amount of studies on various animal taxa, including insects, have demonstrated a causal link between experience and modifications of the brain structure [39, 40]. In ants, age-related changes in biogenic amines, as well as in synaptic structure, have been suggested to underlie repertoire expansion, the ontogenetic extension of the list of behaviors exhibited by a worker [41, 42]. We therefore suggest that experience-dependent changes in the worker brain can be a major force in modulating individual responses to task stimuli, in turn shaping the colony task-allocation system. Considering that the amount of experience increases with age, it could thus explain most patterns of temporal polyethism without the need for a deterministic age-based model to account for changes in individual response thresholds [16].

Experimental Procedures

Study Organism

In Taiwan and Okinawa (Japan), colonies of *Cerapachys biroi* are characterized by a phasic reproductive cycle composed of two

alternating phases of activity. During the foraging phase (16 days), workers explore for food (brood of myrmicine ants), and a single cohort of larvae develop synchronously. Then, during the following starchy phase (18 days), larvae pupate and a new cohort of eggs is laid. After the eggs hatch and the young workers emerge, also synchronously, a new foraging phase begins [32, 33]. Thus, individuals from the same cohort are rigorously the same age and develop in the same conditions during preimaginal stages (cf. [Supplemental Experimental Procedures](#) and [Figure S1](#) in the [Supplemental Data](#) available online for more details on the species). Moreover, in these queenless colonies, diploid eggs are laid by unmated female individuals through obligatory thelytokous parthenogenesis [34, 35]. There is no sterile caste: Egg laying is evenly distributed among all individuals, with no social hierarchy. Reproduction is linked to a temporal polyethism in which older workers stop laying eggs as they become foragers, after three to four reproductive cycles on average [34]. As a consequence of thelytokous parthenogenesis, an extremely low genetic diversity is expected to occur between nestmates, even though an unequivocal estimation of genetic variance within colonies is still lacking for this species. The entire experiment (maturation, training, and observation) took place over an 84 day period ([Figure S2](#)).

Maturation Period: From Day 0 to Day 34

Four experimental colonies were prepared with the following procedure: On the day prior to their synchronous emergence, 80 pupae from each of four stock colonies (three collected in Taiwan and one in Okinawa) were settled in plastered nests. They were confined in a closed nest chamber, together with 25 workers from their respective stock colony who helped with the emergence process by licking the pupal velum. Three days later, the 80 newly emerged workers were individually color labeled for subsequent identification and transferred in a new nest, together with 15 larvae from their respective stock colony. Older foragers were discarded. During an entire reproductive cycle (i.e., the current foraging phase and the following starchy phase, around 30 days in total), nest chambers remained completely closed to prevent any foraging experience and provide young workers with time for physiological and behavioral maturation. Food was provided directly into the nest chamber through a special trap door. Before the onset of the next foraging phase, pupae developing from the introduced larvae were removed before emergence to prevent the setup of an age-based polyethism; only the focal cohort of workers remained in the nest. The pupae were replaced by 15 young larvae because workers cannot lay eggs on their first cycle [34]. In addition, ten older foragers originating from the respective stock colonies were introduced in the nest chamber to elicit recruitments and stimulate foraging activity during the training procedure.

Training Period: From Day 35 to Day 50

In the four experimental nests, a single exit, experimentally controlled, allowed workers to leave the chamber and explore the surrounding area ([Figure S3](#)). Two training compartments were placed in this area. These compartments were made of a small plastic cup that was half filled with plaster and coated with fluon to prevent escapes. One contained abundant prey (brood of myrmicine ants), whereas the second was empty. Additional prey was placed in a part of the foraging area. Once older foragers discovered this subsidiary food resource, they could elicit the recruitment of nestmates within the nest chamber.

Training sessions started with the opening of the nest chamber. Older foragers were always prone to getting out, exploring the foraging area for food, and recruiting nestmates. Every color-labeled worker leaving the nest chamber was withdrawn with soft forceps and assigned to one of the two compartments, the same as every new foraging attempt, either becoming "successful explorers" or not thereafter. Because older foragers always lacked the necessary workforce to retrieve prey, they gradually recruited most of their nestmates. This allowed full control of the foraging activity of the treated workers. After 3 hr, the nest chamber was closed again and all individuals were reintroduced through the trapdoor. During all the foraging phase, we performed two training sessions per day, with a minimum of 2 hr between consecutive sessions. Neither old foragers (lacking sufficient workforce) nor successful explorers

(prevented by the compartment's wall) could retrieve prey into the nest chamber. This allowed us to carry out several training sessions on experimental colonies that remained motivated for foraging. Instead, the colony was fed every 3 days (i.e., after training sessions 4, 10, and 16) directly through the trapdoor (during these periods, workers were not actively searching for food). No session was performed on the day after the food was supplied, to take into account the resulting decrease in colony foraging motivation. Compartments and prey were replaced after each training session. The treatment ceased at the end of the foraging phase, after 22 sessions. The older foragers were discarded and the nest chamber remained closed during the following starchy phase (18 days) to prevent any uncontrolled foraging attempt.

Long-Term Effects of Training: From Day 68 to Day 84

Because workers were then reproductively mature, a new batch of eggs was laid during the starchy phase. At the end of this period, all pupae ensuing from the introduced larvae were removed before emergence to retain only the trained cohort of workers. At the onset of the following foraging phase, the nest chamber was reopened. It was never closed again until the end of the experiment. In each experimental colony, worker activity was recorded by the performance of 40 scanning observations throughout the entire foraging phase. Five behaviors were observed: exploration (both in and out of the nest chamber), brood care, and immobility at three different locations (spatial fidelity zones [36])—away from the brood, in the brood vicinity, and upon the brood. The time interval between two consecutive scans was at least one hour. Food was supplied directly into the nest chamber via the trapdoor to prevent uncontrolled foraging experience. No observation was performed on the day after the feeding.

Statistical Analyses

To evaluate the immediate effects of training on ants' behavior, we compared (1) the mean foraging rate and (2) the mean exit delay between successful and unsuccessful explorers. The foraging rate was analyzed with a logistic regression with repeated-measures design, by GEE. This model was fitted with the GENMOD procedure of SAS 9.14 (SAS Institute). Because the dependant variable was binary (exit or not), a logit link function with binomial errors was chosen. The exit delay was analyzed with repeated-measures models in Proc. GLM of SAS. For each analysis, we assessed the relationship between the dependant variables and the following factors: group, session (the repeated variable), and colony nested within group, as well as interactions.

Then, the behavioral profiles of successful and unsuccessful explorers during the next foraging phase were compared with a MANOVA (SAS, Proc. GLM). The MANOVA included group and colony nested within group as explanatory variables, and exploration, brood care, and immobility at three different locations as response variables. Post hoc analyses were performed with a Tukey-Kramer procedure (SAS Institute [Cary, North Carolina]: 2005. SAS/STAT Software Version 9.1).

Supplemental Data

Additional Discussion Experimental Procedures, three figures, and one table are available at <http://www.current-biology.com/cgi/content/full/17/15/15-21/DC1/>.

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F.R. designed the project. E.L. realized the experiments. F.R., E.L., and G.K. performed the statistical analyses. F.R., E.L., and N.C. wrote the paper. All authors discussed the results and commented on the manuscript.

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