

cases, thicker layers of fused grains form below these biofilms in response to microboring activities and precipitation, probably resulting from polymer degradation in boreholes.

These findings provide insight into the role of microbes in stromatolite accretion, lamination and lithification. Although most researchers agree that, “microbial mats and their associated sediments must be lithified early in order to be preserved in the record as stromatolites”²¹, the proposed mechanisms and precise timing of early lithification have been “vigorously debated”²¹. Historically, early lithification was attributed to abiotic processes of submarine cementation^{23,5} or to calcification of cyanobacterial sheaths²⁴ related to photosynthetic activity. More recently, attention has shifted to heterotrophic bacterial decomposition of cyanobacterial sheaths in subsurface, aphotic zones^{25,26}. Although field studies have documented bacterial precipitation of micrite on the sheaths of dead cyanobacteria in the subsurface of laminated microbial mats in tidal flats^{25,27}, these mats do not form fully lithified laminae and stromatolitic build-ups. We argue that growth of laminated microbial structures with topographic relief, such as those that dominated the fossil record for three billion years, depends on pencontemporaneous lithification of surface mats. This lithification process occurs by decomposition of an amorphous matrix of bacterial exopolymer (not sheath material) in the photic zone across the stromatolite surface. Similar processes of precipitation within the amorphous exopolymer matrix of biofilms, rather than on cyanobacterial sheaths, offer an additional mechanism to account for the paucity of preserved microfossils in Precambrian stromatolites, which is typically ascribed to recrystallization and/or rapid degradation of sheaths^{1,26,28}. The potential role that climax microbial communities, functionally equivalent to the endolithic coccoid cyanobacterial communities in modern marine stromatolites, may have played in the growth and lithification of ancient stromatolites remains to be evaluated. □

Methods

This study combined a range of geological, microbial and chemical analyses. An extensive field program was conducted during January and June 1997, and March and August 1998. Physicochemical indices of stromatolite mats were determined *in situ*, primarily with O₂, sulphide, pH needle electrodes (0.8 mm outer diameter)⁹, whereas microstructural, chemical and microbial analyses and incubations were done in the laboratory at the field site and in home institutions. Mat communities and microstructural features were identified using a variety of microscope techniques (light, scanning electron, transmission electron, and scanning laser confocal²⁹) and microbial populations were enumerated using epifluorescence microscopy counts⁹, most-probable number enumerations^{9,10} and molecular phylogenetic techniques. Microbial activities were assessed using depth profiles measured with microelectrodes⁹ and radioisotope incubations using ³H, ¹⁴C and ³⁵S (refs 9, 10 and 30). Heterotrophic activity was also studied with microautoradiography of labelled organic matter uptake³⁰. Microscale distribution of sulphate reduction was assessed using Ag foil coated with ³⁵SO₄²⁻ (ref. 18). Exopolymer distribution and production were evaluated by physical and chemical extractions and ¹⁴C-bicarbonate experiments, respectively¹¹. Other methods used are described elsewhere^{9,10,11,13,29,30}.

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Ant-like task allocation and recruitment in cooperative robots

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One of the greatest challenges in robotics is to create machines that are able to interact with unpredictable environments in real time. A possible solution may be to use swarms of robots behaving in a self-organized manner, similar to workers in an ant colony^{1–5}. Efficient mechanisms of division of labour, in particular series-parallel operation and transfer of information among group members⁶, are key components of the tremendous ecological success of ants^{7,8}. Here we show that the general principles regulating division of labour in ant colonies indeed allow the design of

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flexible, robust and effective robotic systems. Groups of robots using ant-inspired algorithms of decentralized control techniques foraged more efficiently and maintained higher levels of group energy than single robots. But the benefits of group living decreased in larger groups, most probably because of interference during foraging. Intriguingly, a similar relationship between group size and efficiency has been documented in social insects^{9–11}. Moreover, when food items were clustered, groups where robots could recruit other robots in an ant-like manner were more efficient than groups without information transfer, suggesting that group dynamics of swarms of robots may follow rules similar to those governing social insects.

We chose foraging as the task assigned to robots to investigate whether ant-derived algorithms allow several robots to achieve tasks in a cooperative manner because foraging efficiency is a key factor influencing colony productivity^{7,12}, foraging is the task for which mechanisms of task allocation are best understood^{13,14}, and foraging is the task that has received the greatest attention in cooperative robotics⁵. The essential components of social organization governing ant colonies were used to program swarms of robots foraging from a central ‘nest’ (Fig. 1; see electronic movie, Supplementary Information).

First, ‘colony’-level information about colony energy was accessed and updated by the individual robots. While in the nest, the robots were informed of the colony energy by radio messages from a control station. This simulated colony-level information that social insects obtain by other means under natural conditions¹⁵. No further information on colony energy was provided to them during foraging missions. Upon return to the nest, each robot renewed its energy reserves (which corresponded to a decrease in colony energy) and unloaded the food item collected into a basket (if the foraging trip was successful), thereby increasing colony energy. This mimics a natural situation where ants share through trophallaxis food that they stored in their crops (social organ)¹⁵. Second, the robots were programmed to avoid each other to minimize collisions and avoid negative interactions. This directly follows from the observation that ants actively regulate their rates of encounters¹⁶ and because foraging ants, like robots, cannot occupy the same space simultaneously. Third, individual variation in the tendency to perform a task was implemented in the robots. This directly models the different individual stimulus thresholds for task allocation that are observed in ants and bees^{13,17–19}. Thus, robots did not leave the nest simultaneously, but only when the colony energy dropped below the pre-set threshold of a particular robot. The individual stimulus thresholds varied linearly, ranging between 75 and 100% of

the initial colony energy. The initial colony energy was proportional to the number of robots per colony. This resulted in good modulation of the number of individuals engaged in the two possible activities: staying in the nest (inactive) and foraging (active). Finally, for some trials robots were programmed to recruit another robot when they identified a resource-rich area, thus mimicking recruitment behaviour observed in many ant species¹⁵. Hence, the robots had generalized information about the overall colony energy, ways to avoid interfering with one another in space and time, and, in the last experiment, the ability to transfer useful information to others.

To determine the relationships between group size and efficiency, we compared groups of 1, 3, 6, 9 and 12 robots in 3 sets of experiments: uniform food distribution without recruitment; clustered food distribution without recruitment; and clustered food distribution with recruitment. Relative colony energy (expressed as the mean energy per robot) was recorded every 5 min during a 30-min trial period. For the analyses we averaged the last three recordings, as they represented most clearly the differences among experiments and the effect of robot number. The use of more than the last three measures did not affect the outcome of the statistical analyses.

In experiments with uniform food distribution, there was a significant effect of group size (analysis of variance (ANOVA): $F_{4,35} = 4.69$; $P = 0.004$) on the average relative colony energy (Fig. 2). A posteriori comparisons (Fisher’s procedures for learning systems design (PLSD) tests) showed that this difference was mainly due to single robots and groups of 12 robots having lower foraging efficiency than groups of intermediate size (differences were significant at $P < 0.05$ between groups 1 and 3, and between groups 12 and 3, 12 and 6, and 12 and 9). Groups of intermediate size performed better when food items were uniformly distributed, which is probably due to a trade-off between the positive and negative effects of robot–robot interactions. Because robots were programmed to avoid each other, groups of robots probably exhibited a more efficient coverage of the foraging arena than single robots. When the number of robots increased, however, negative interactions among robots (here defined as robots interfering with each other when trying to perform a task) also increased. In particular, larger groups of robots more frequently suffered from negative interference at the entrance of the nest, resulting in robots being slower in leaving and returning to the colony. In addition, food items were more frequently seized by two robots in larger groups. Overall, the proportion of time spent in such negative interactions was 0, 0.6, 0.5, 1.5 and 2.0% for 1, 3, 6, 9 and 12 robots,

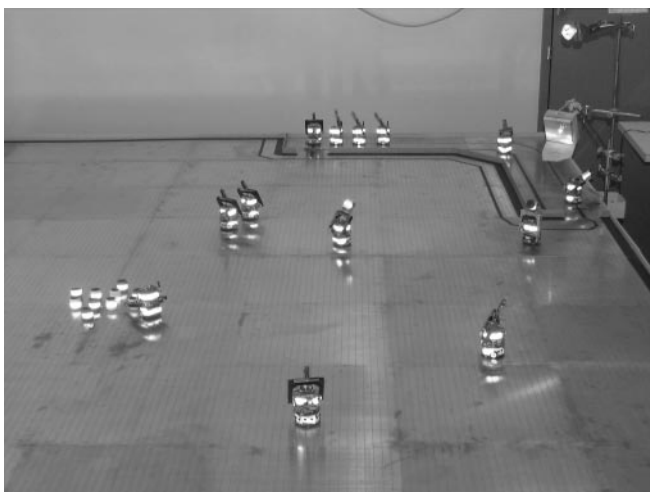


Figure 1 Khepera robots foraging and collecting food items which are then transported back to the nest.

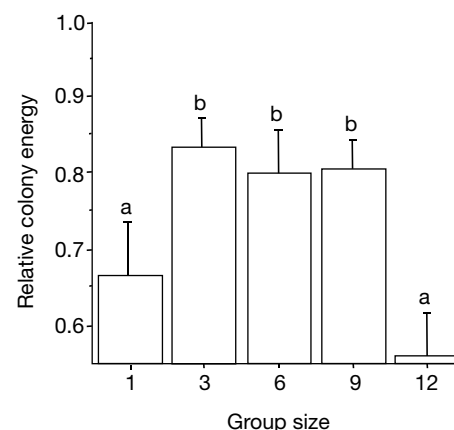


Figure 2 Relative colony energy (per robot) (mean ± s.e.) in groups of 1, 3, 6, 9 and 12 robots with uniform food distribution and no recruitment. Mean values with different lower-case letters differed significantly ($P < 0.05$, Fisher’s PLSD tests).

respectively (ANOVA: $F_{4,35} = 4.43$; $P = 0.005$). A post hoc analysis (Fisher's PLSD, 5%) revealed that negative interactions were more common in groups of 12 robots than in teams of 1, 3 and 6 robots, as well as in groups of 9 compared with 1. Although negative interactions accounted for only a limited amount of the robot's time budget, they significantly affected performance because they occurred predominantly in the vicinity of food items and nest entrance, hence directly affecting the localization and memorization of nest entrance and food items, respectively.

In the second set of experiments with clustered food distribution and no recruitment, we found a similar but nonsignificant relationship (ANOVA: $F_{4,35} = 1.11$; $P > 0.05$) between groups size and colony energy (Fig. 3). The smaller effect of group size in this experiment might have resulted from the decreased benefit provided by uniform coverage of the foraging arena when food items were clustered rather than uniformly distributed. Because robots were programmed to memorize and return to areas where they encountered more than one food item (that is, when they found clustered food items, see Methods), foraging efficiency should have been higher when food was clustered rather than uniformly distributed. Relative colony energy was indeed 10.9% higher when food was clustered (two-way ANOVA, effect of food distribution: $F_{1,70} = 8.69$; $P = 0.004$), a result consistent with the idea that robots were able to relocate patches where they had found more than one food item. The effect of group size was again significant ($F_{4,70} = 4.80$; $P = 0.002$) and the interaction between food item distribution and group size not significant ($F_{4,70} = 0.89$; $P > 0.05$).

The third set of experiments tested for potential benefits conferred by information transfer among the robots. In these experiments food was clustered, as in the second set of experiments, but robots could recruit another robot (see Methods) after their return to the nest. Recruitment significantly increased foraging efficiency compared with experiments where robots could not communicate (Fig. 4), as shown by the overall 9.4% higher mean relative colony energy (two-way ANOVA: effect of information transfer; $F_{1,56} = 9.49$; $P = 0.003$; only groups with two or more robots were considered in the analysis because no information transfer can occur when robots are alone). As in the previous experiments, colony energy was also influenced by group size ($F_{3,56} = 7.70$; $P < 0.001$), but there was no significant interaction between group size and whether or not robots could transfer information ($F_{3,56} = 0.16$; $P = 0.923$).

A similar relationship between group size and group efficiency has been documented in social insects. For example, a detailed study of the wasp *Polybia occidentalis* showed that per capita output

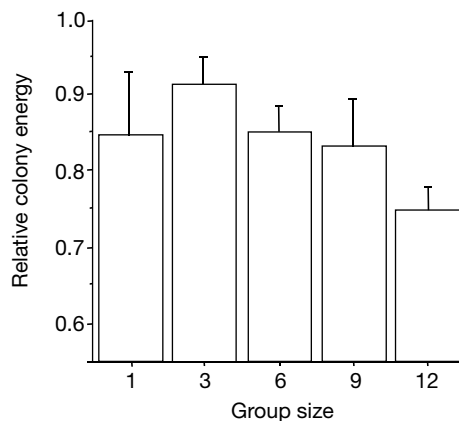


Figure 3 Relative colony energy (per robot) (mean \pm s.e.) in groups of 1, 3, 6, 9 and 12 robots with clustered food distribution and no recruitment.

increases with group size⁹ but levels off in large colonies in a manner similar to that observed with our experimental robots. Decreased individual worker efficiency in large colonies has also been documented in several ant species^{10,11}. One possible reason for this effect is increased rates of negative interference among group members in larger colonies, as has been suggested by theoretical models²⁰ and shown in our experiments with robots. Notably, ants have been shown actively to regulate the rate of encounters as a function of colony size, perhaps to limit the rate of negative interferences at high density and optimize task allocation¹⁶.

Our results show that an ant-inspired system of task allocation based on variation in individual stimulus thresholds provides a simple, robust and efficient way to regulate activity within teams of robots (in our case, collecting food items when robots have no initial information on the environment and group size). Furthermore, relatively complex tasks can be efficiently performed by relatively simple (and autonomous) robots regulated in a decentralized way. This has important implications in robotics, particularly in situations where agents must perform tasks in stochastic environments and where risks of system failures must be avoided, for example during missions on Mars or other planets. A further advantage of controlling robots with individual stimulus thresholds is that it provides great flexibility with regard to team size. As shown in our experiments, single as well as groups of robots can be controlled with the same threshold mechanism. This has also important implications for robotics because it allows for an increase in the number of robots in a system without modifying the control program of individual robots. Likewise, this permits a swarm of robots to continue to work efficiently in case of the number of robots being reduced by individual failures or by allocation of some robots to other work areas or tasks.

Our experiments also show that, similar to a pattern observed in social insects, groups where robots could recruit other robots in an ant-like manner were significantly more efficient at exploiting clustered resources than groups without information transfer. The implementation of an ant-like mechanism of recruitment offers an interesting perspective in robotics when tasks to be performed vary in an unpredictable manner in space and/or time. In conclusion, this study illustrates that similar self-organizing behaviours emerge from groups of agents, be they robots or actual insects, and shows that transfer of knowledge about social insects to the field of intelligent system design is indeed possible. □

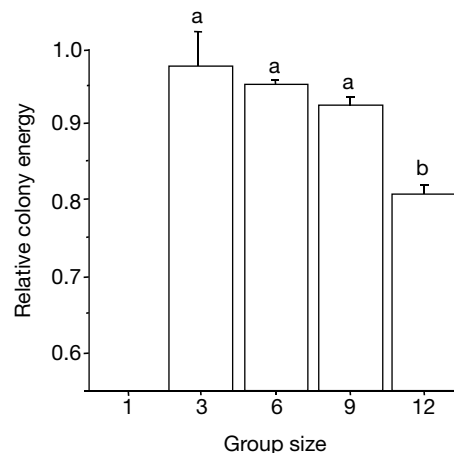


Figure 4 Relative colony energy (per robot) (mean \pm s.e.) in groups of 3, 6, 9 and 12 robots with clustered food distribution and recruitment (no experiments were conducted with single robots as at least 2 robots are necessary for recruitment to occur). Mean values with different lower case letters differed significantly ($P < 0.05$, Fisher's PLSD tests).

Methods

Robots

Detailed information on the robots and programs used are available on request and general information on the system is available on the movie (see Supplementary Information). Essentially, we used Khepera miniature mobile robot designed as a research tool at the 'Laboratoire de micro-informatique' of the Swiss Federal Institute of Technology at Lausanne²¹ (now produced by K-Team SA). Three additional modules, a gripper turret, a custom-made detection module and a radio turret were added (Fig. 1).

Experiments

The experiments were carried out in a 9.24 m² arena surface covered with copper strips alternatively connected to the two poles of a direct current power supply. The food items consisted of small plastic cylinders (3 × 3 cm) with narrow strips of infrared reflecting tape. Depending on the experiment, they were either grouped in two patches (mean distance to nest 1.94 ± 0.06 m, n = 26) or placed singly at six locations (mean distance to nest 1.98 ± 0.71 m, n = 6). Food items were replaced immediately after being collected by a robot. Robots were programmed so that they randomly foraged in the arena until they either collected a food item or used their energy reserve (autonomy ~4 min), at which time they returned to the nest. Robot energy consumption was low when they were immobile, increased linearly with speed, and was maximal when robots carried a food item.

Once they collected a food item, robots searched the vicinity (within a radius of 7.5 cm, during ~30 s) to determine whether other food items were present. If they found another food item the robots recorded the return path to the nest (through integration of wheel movements) and used this information to return to the patch on the next foraging trip. To allow robots to locate and return to the nest after their foraging trips we placed a lamp close to the nest entrance, allowing robots to use visual cues (as real ants typically do¹⁵) to home-in on the nest.

In the third set of experiments, robots were able to recruit another robot if they had found a second food item (which was generally the case when food was clustered). Once back in the nest, the successful robot recruited the robot at the head of the waiting line in the nest. This experiment investigated potential benefits provided by active recruitment and information transfer^{22,23} and was directly inspired by the process of tandem recruiting behaviour that occurs in ants^{24,25}. The leader robot's speed was lowered during tandem walking to ensure successful arrival of both robots at the food patch which mimics the natural situation in the ants^{24,25}. Once arrived at the food patch, the leader robot decoupled the tandem allowing the follower to begin foraging.

The three sets of experiments were repeated 8 times for each group size (112 experiments in total). To test the effect of group size, we performed one-way ANOVAs²⁶. Comparisons between sets of experiments were performed with two-way ANOVAs to control for the effect of group size.

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Supplementary information is available on Nature's World-Wide Web site (<http://www.nature.com>).

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The relative metabolic demand of inhibition and excitation

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By using the (¹⁴C)2-deoxyglucose method¹, inhibition has been shown to be a metabolically active process at the level of the synapse^{2,3}. This is supported by recent results from magnetic resonance spectroscopy that related the changes in neuroenergetics occurring with functional activation to neurotransmitter cycling⁴. However, inhibitory synapses are less numerous and strategically better located than excitatory synapses, indicating that inhibition may be more efficient, and therefore less energy-consuming, than excitation. Here we test this hypothesis using event-related functional magnetic resonance imaging in volunteers whose motor cortex was inhibited during the no-go condition of a go/no-go task, as demonstrated by transcranial magnetic stimulation. Unlike excitation, inhibition evoked no measurable change in the blood-oxygenation-level-dependent signal in the motor cortex, indicating that inhibition is less metabolically demanding. Therefore, the 'activation' seen in functional imaging studies probably results from excitation rather than inhibition.

Anatomical studies have shown that the cortex consists of about 70–85% spiny neurons (mostly pyramidal cells) and about 15–30% non-spiny non-pyramidal cells^{5,6}. Spiny neurons are excitatory, whereas non-spiny cells constitute different classes of inhibitory interneurons. The relative number of synapses is also different—that is, on average there is about one inhibitory synapse for every five to six excitatory synapses⁷. Inhibitory synapses are located on or near the soma of pyramidal cells as well as on dendritic shafts, whereas excitatory synapses are mainly located on dendritic spines⁸.

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