Supporting Information

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SI Results and Discussion

Twenty-Five-Role-Environment Experiments. Our central experiment suggested that task-switching costs can lead to the evolution of strategies that use division of labor. We also explored whether the type of tasks present in the environment affects whether division of labor evolved. To study this question, we created a second environment that uses a different suite of tasks. The original experiment used nine logic tasks. This new environment uses 25 role-selecting tasks. To perform one of these tasks, an organism must select an integer value to indicate the role that it performs. The target role-IDs are 1 through 25. Thus, although there are more tasks in the environment, they are also easier to perform. Each role-selecting task has an associated limited resource with an initial amount of 100 resources, an inflow of 0.25 units of resource per update, and an outflow of 1% per update. When an organism performs a task, it can consume 5% of the available resources associated with that type of task. Because the colonies have more resources at their disposal, we also increased the amount of resources required for replication to 1,000 resources. We ran 50 replicates of each cost treatment (i.e., 0-cost, 25-cost, and 50-cost).

Fig. S1*A* depicts the results of the various treatments in the new 25-role environment. At the final time point in the treatment, the mean amount of Shannon mutual information between organisms and tasks performed is as follows: 0-cost: 1.877 ± 0.127; 25-cost: 2.368 ± 0.071; 50-cost: 2.495 ± 0.059. In this case, for all treatments, the colonies are performing ∼19–21 different roles (Fig. S1*B*). There is not a statistically significant difference in the number of roles performed by the control colonies compared with the treatment colonies. As a result, we can conclude that differences in division of labor result solely from organisms choosing to be generalists and specialists. For this experiment, we see that more division of labor is present in runs with task-switching costs than the control run (Kruskal-Wallis multiple comparison, $P = 0.05$), which supports our hypothesis that task-switching costs increase the amount of division of labor present in evolved strategies.

Intrinsic Task-Switching Costs. Within our experiments, in addition to our explicitly applied task-switching costs, there are also intrinsic task-switching costs that result from the work required to compute logic tasks. It is challenging to estimate these intrinsic costs because they vary depending on the specific tasks being performed, and organisms are under evolutionary pressure to reduce these costs by evolving clever algorithms. To provide some intuition for the magnitude of these costs, we selected a best-performing colony from each replicate across all control treatments and measured the number of central processing unit (CPU) cycles needed to change between different tasks. The median number of CPU cycles needed to change tasks was 7.166, 8.314, and 10.732 when 250, 500, and 1000 units of resource were required for colony replication, respectively. We use the median number of CPU cycles, rather than the mean, owing to the presence of outliers.

Intrinsic task-switching costs rose as the number of units of resources required for colony replication increased across treatments. This rise in intrinsic task-switching costs results from increased pressure for the colonies to perform a wider range of types of tasks. Specifically, when more units of resources are required to replicate, the colony must wait for resources to replenish to collect enough. If the colony performs only a small set of presumably simple tasks, owing to the limited nature of these resources, they must wait a longer period to collect enough resources to replicate. Thus, under these conditions they embrace a larger set of tasks, which includes some of the more complex tasks. These more complex tasks cause them to have to execute more instructions between successive exports of tasks.

As an additional test, we explored how division of labor was affected when we did not allow the colonies to perform the more-complex tasks and thus kept the intrinsic task-switching costs low. To assess this effect, we ran an experiment in which 1,000 units of resource were required for replication, but we limited colonies to performing the three least complex logic tasks, while maintaining the same amount of resources present in the environment as the other experiments. We found that the treatments with higher explicit task-switching costs evolved to exhibit a significantly larger degree of division of labor (0.163 ± 0.023 in the 0-cost treatment compared with 0.307 ± 0.031 and 0.477 ± 0.035 in the 25- and 50-cost treatments, respectively; Kruskal-Wallis multiple comparison, $P = 0.02$).

When intrinsic task-switching costs are high (i.e., experiments in which 1,000 units of resources are required to replicate and nine logic tasks are rewarded), the organisms are in a situation in which specialization becomes increasingly attractive and division of labor is more likely to evolve. It is not the case that division of labor is appearing without task-switching costs. However, it is the case that, under certain circumstances, the explicit costs we apply have a smaller relative effect due to the increase in intrinsic task-switching costs.

Division of Labor Knockout Data. To better understand how organisms were coordinating their roles within groups, we performed a series of knockout experiments, in which we replaced a coordination experiment with a neutral instruction. Table S1 presents the effect of the knockouts on division of labor. Examining these data indicates that only messaging had a substantial effect upon the amount of division of labor within the colonies. However, a closer examination of the performance of individual colonies indicates that some colonies did make use of other mechanisms. For example, Fig. S2 depicts the performance of colonies required to consume 250 units of resource to replicate whose spatial location capabilities were removed. Although the mean amount of division of labor present within the colonies remains close to zero, the scatter of points indicates that some colonies were using spatial location as part of their strategy.

Loss of Task Diversity Resulting from Communication Knockouts. We have demonstrated that colonies evolved under higher task-switching costs exhibited a greater degree of division of labor and that the primary mechanism they made use of was communication via messaging. In our case study, the evolved colony used messaging to send partial task results, which resulted in both division of labor and a loss of individuality at the lower level—the organisms within the colony could not perform tasks in isolation that they could perform as a group. To better understand whether other colonies were using similar tactics and also were exhibiting signs of a loss of individuality, we examined how knocking out the communication capabilities affected the diversity of tasks performed by the colonies.

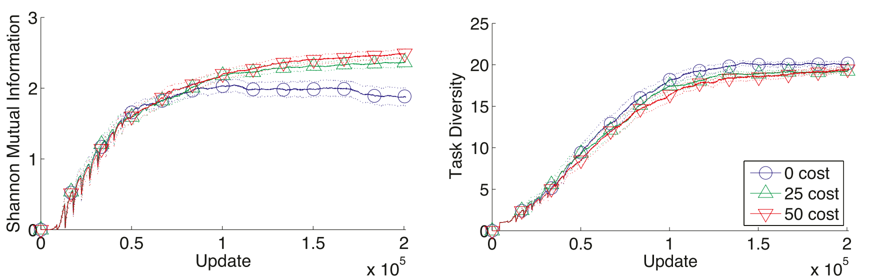
Fig. S3 presents the results of knocking out the communication capabilities for colonies in our central experiment in which colonies were required to consume 500 units of resource to replicate. As the task-switching costs increase, the effect of the loss of communication capabilities becomes more pronounced. In fact, for the high task-switching cost treatment, many of the colonies lose the ability to perform a large number of types of tasks. These data indicate that communication played such a central role in the strategies of these colonies that organisms were only able to perform very few types of tasks without it.

Perturbation of Colony Starting Conditions. An open question is whether the evolved colonies are collections of independent organisms or collectives (individuals at the higher level), where each part depends on the proper behavior (timing and location of states) of other parts. To assess this, we studied the behavior of four colonies—two generalist colonies and two specialist colonies evolved under the 0-cost and 50-cost treatments, respectively—when their starting conditions were perturbed. For these analyses, we used the amount of time it took for the colony to replicate as a measure of group performance.

We examined what happens when we modify the number of starting organisms (from one to two and 25) and the composition of the group (by combining individuals from different colonies). Data are presented in Table S2. The performance of generalist colonies reflects our expectations for a collection of organisms. When we increase the number of organisms in the group from one to two and then 25, the amount of time it takes a colony to replicate consistently decreases (i.e., performance improves). Moreover, when we start a group with organisms from different colonies the performance also improves, indicating that the organisms are able to function independent of their peers. In contrast, the performance of the specialist colonies is more sensitive to the initial conditions. When the colonies start with 25 organisms, the performance improves. However, the improvement is substantially less than that of the generalist colonies and, in the case of colony Specialist B, is a minor improvement. Additionally, when we seeded the colonies with two organisms, only the performance of Specialist A improved; adding a second organism to colony Specialist B decreases performance. When we combined organisms from Specialist A and Specialist B into a single colony, productivity decreases substantially.

Exploring the Conditions Under Which Division of Labor Evolves. In the article, we explore how task-switching costs affect the amount of division of labor that evolves as a part of the colonies' strategies. Thus, we selected conditions under which it was possible for division of labor to evolve. These conditions included using limited resources to reward colonies for performing multiple, different types of tasks and also maintaining the clonal integrity of the colony. Here we explore whether violating these conditions results in a decrease in division of labor. Specifically, we examine how division of labor is affected when (*i*) resources are unlimited (i.e., an organism receives the same reward for a task no matter how many times it is performed by itself or other colony constituents); (*ii*) the clonal nature of the colonies is disrupted by migration (i.e., 10% of the offspring organisms migrate to a different colony on birth); and (*iii*) the clonal nature of the colonies is disrupted by mutations that occur during individual replication within the colony. We explore these conditions with high task-switching costs (50 CPU cycles), where colonies require 500 units of resources to replicate.

At the final time point in these new control treatments, the mean amount of Shannon mutual information between organisms and tasks performed is as follows: unlimited resources: 0.002 ± 0.00; migration: 0.066 ± 0.02; mutations during individual-level replication: 0.638 ± 0.04. For reference, the amount of Shannon mutual information present in our original experiment was 1.066 ± 0.04. These data indicate that, as we would suspect, limited resources and the clonal nature of the colonies were important conditions for evolving division of labor. Extreme violations of these conditions (i.e., unlimited resources and high migration rates) result in colonies adopting different strategies. Further explorations of the effect of less extreme violations (i.e., various individual-level mutation rates) is an interesting area for future work.



(a) Mean Shannon Mutual Information

(b) Mean Number of Unique Tasks Performed by Replicating Groups

Fig. S1. Twenty-five-role results. (*A*) The mean Shannon mutual information averaged across 50 runs for colonies with varying amounts of task-switching costs within the 25-role environment. Dotted lines are used to indicate SE. Notably, treatments with higher task-switching costs evolve strategies that exhibit higher levels of division of labor. (*B*) The mean number of different tasks performed by the colonies under various treatments. The colonies all evolve to perform ∼19–21 types of tasks.

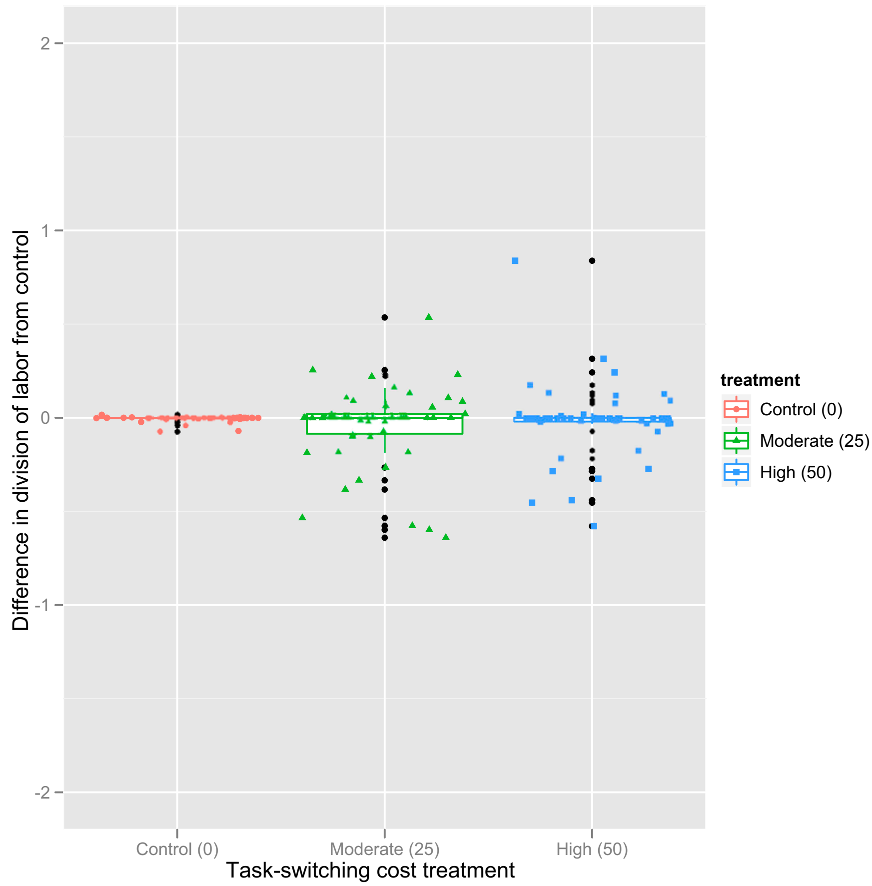


Fig. S2. Effect of spatial location knockouts (on colonies required to consume 250 units of resource to replicate) across three treatments that vary the task-switching costs. Results are presented as the difference between the behavior of a colony with spatial information knockouts and a control run of the same colony without any knockouts. Negative numbers indicate that less division of labor occurred. In general, although the amount of division of labor present within the group of colonies remains constant, the scatter of points indicates that some colonies are making use of spatial location as part of their division of labor strategy.

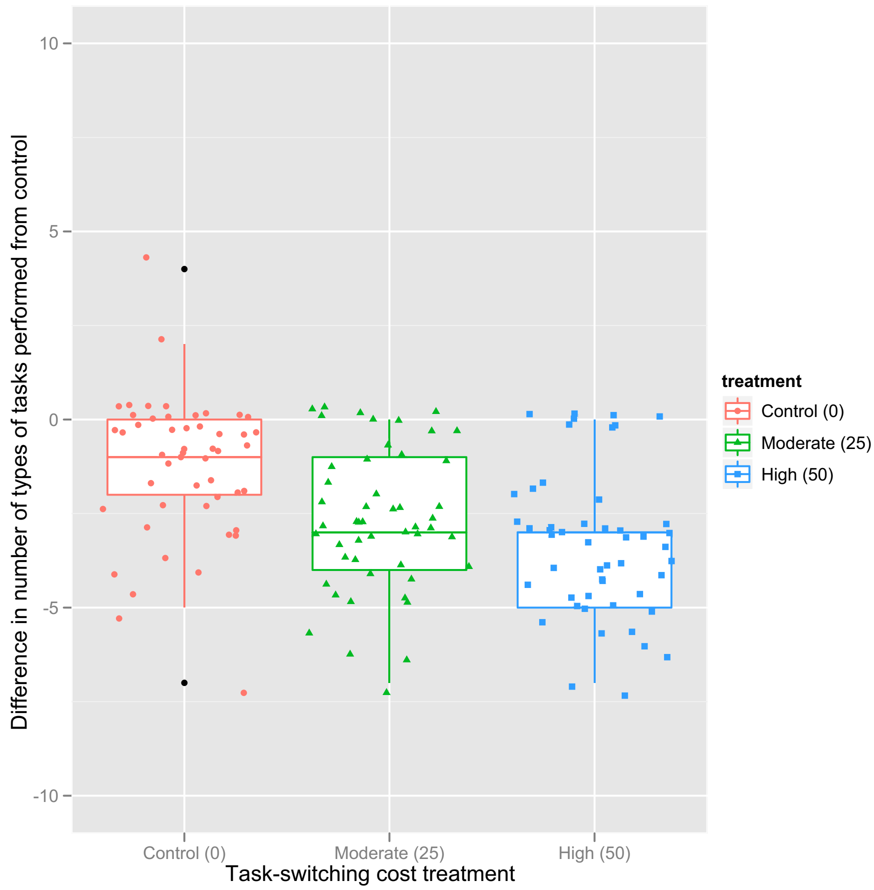


Fig. S3. Effect of communication knockouts (on colonies required to consume 500 units of resource to replicate) across three treatments that vary the task-switching costs. Results are presented as the difference between the behavior of a colony with communication knockouts and a control run of the same colony without any knockouts. The *y* axis represents how the number of types of tasks performed by the colony changed with the loss of communication capabilities. In general, colonies evolved under high task-switching costs lost the ability to perform more tasks than other colonies.

Table S1. Effect of knockouts on division of labor within evolved colonies

Units required for colony replication	Task-switch cost	Stochasticity	Spatial information	Communication
250	0	0.000 ± 0.002	−0.005 ± 0.002	0.081 ± 0.021
	25	0.013 ± 0.034	−0.044 ± 0.031	−0.123 ± 0.045
	50	0.059 ± 0.035	−0.016 ± 0.029	−0.315 ± 0.074
500	0	0.025 ± 0.023	0.001 ± 0.025	−0.144 ± 0.051
	25	0.050 ± 0.033	0.034 ± 0.026	−0.537 ± 0.065
	50	−0.002 ± 0.025	−0.030 ± 0.034	−0.804 ± 0.069
1,000	0	−0.007 ± 0.032	−0.021 ± 0.029	−0.461 ± 0.050
	25	−0.053 ± 0.026	−0.017 ± 0.034	−0.580 ± 0.076
	50	0.005 ± 0.033	−0.068 ± 0.052	−0.700 ± 0.082

Results are presented as the difference between the behavior of a colony with knockouts and a control run of the same colony without any knockouts. Negative numbers indicate that less division of labor occurred under knockout conditions. In general, the removal of communication capabilities had the most substantial effect on division of labor.

Table S2. Performance data for perturbation analyses of four colonies

Treatment description	Colony	Performance	Change in performance from control
Control	Specialist A	63	—
	Specialist B	64	—
	Generalist C	78	—
	Generalist D	75	—
Full colonies	Specialist A	39	−24
	Specialist B	60	−4
	Generalist C	39	−39
	Generalist D	37	−38
Two starting individuals	Specialist A	61	−2
From the same colony	Specialist B	73	+9
	Generalist C	61	−17
	Generalist D	58	−17
Two starting individuals	Specialist A & B	72	+8.5
From different colonies	Generalist C & D	59	−17.5