

Task-switching costs promote the evolution of division of labor and shifts in individuality

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Edited by Joan E. Strassmann, Washington University in St. Louis, St. Louis, MO, and accepted by the Editorial Board July 11, 2012 (received for review February 9, 2012)

From microbes to humans, the success of many organisms is achieved by dividing tasks among specialized group members. The evolution of such division of labor strategies is an important aspect of the major transitions in evolution. As such, identifying specific evolutionary pressures that give rise to group-level division of labor has become a topic of major interest among biologists. To overcome the challenges associated with studying this topic in natural systems, we use actively evolving populations of digital organisms, which provide a unique perspective on the *de novo* evolution of division of labor in an open-ended system. We provide experimental results that address a fundamental question regarding these selective pressures: Does the ability to improve group efficiency through the reduction of task-switching costs promote the evolution of division of labor? Our results demonstrate that as task-switching costs rise, groups increasingly evolve division of labor strategies. We analyze the mechanisms by which organisms coordinate their roles and discover strategies with striking biological parallels, including communication, spatial patterning, and task-partitioning behaviors. In many cases, under high task-switching costs, individuals cease to be able to perform tasks in isolation, instead requiring the context of other group members. The simultaneous loss of functionality at a lower level and emergence of new functionality at a higher level indicates that task-switching costs may drive both the evolution of division of labor and also the loss of lower-level autonomy, which are both key components of major transitions in evolution.

digital evolution | problem decomposition | specialization | task partitioning | fraternal transition

Division of labor is a strategy used by a diverse set of biological groups, ranging in size and complexity from microorganisms to humans (1–13). Within human economies, Adam Smith considered the avoidance of task-switching costs to be a significant benefit resulting from division of labor (14). However, task-switching costs, such as cognitive overhead (12), travel time to a new location (9, 10), and costs associated with morphological alterations (15), are also present within other organic systems. As proposed by Dornhaus (16), we explore whether the avoidance of task-switching costs promotes the evolution of division of labor. This is a challenging topic to study in natural settings, owing to sparse phylogenetic data with missing intermediate states, as well as the inherent difficulty of inferring nonmorphological forms of division of labor from the fossil record (refs. 16 and 17; but see ref. 18). Although there have been pioneering laboratory selection experiments involving the propagation of large collections of groups of organisms (19–21), even microbes with short generation times are still difficult to track over long evolutionary periods.

Here, we perform experimental evolution on digital organisms, which compose a model system that exhibits open-ended evolutionary dynamics with rapid generations. Specifically, we use the Avida digital-evolution platform (22), previously used to study topics including the evolutionary origin of complex features (23), adaptive radiation (24), and the evolution of altruism (25). Within Avida, organisms are fully functional computer programs that must self-replicate to survive in a user-defined environment where they

are subject to mutations and natural selection. A digital organism executes its genome on a virtual central processing unit (CPU), allowing it to perform computations, self-replicate, and interact with its neighbors or environment in a variety of ways. Digital evolution enables us to start with a set of groups of organisms, impose task-switching costs upon individuals, and observe in real-time whether the groups evolve to exhibit more or less division of labor. Using Avida, we can also investigate how groups that perform division of labor evolved to coordinate tasks. Although we provide several potential coordination mechanisms, including spatial information and communication capabilities, the ways in which the organisms evolve to make use of these mechanisms, either individually or in concert, is open-ended.

We created worlds consisting of 400 competing “colonies,” each containing up to 25 clonal organisms. Colony fecundity is based on the speed at which its members accumulate resources. Nine types of resources are available, each associated with a distinct Boolean logic function (Table 1) (23) that the organism must export to uptake the resource. The resources are set up in a virtual chemostat. Each resource has a constant inflow rate of one unit per update (an update is the standard unit of time in Avida; organisms receive, on average, 30 CPU cycles per update and live for 5–20 updates), while at the same time 1% of the available resources flow out, limiting total accumulation to 100 units. When an organism exports the result of a function, it uptakes 5% of the available resource associated with that function. A colony that collects a designated number of units of resources (of any type) divides into two colonies, replacing a random competing colony. As a result of resource scarcity, colony performance is improved if, collectively, its members target multiple resource types. Organisms can evolve to accomplish this objective anywhere along the continuum from generalists to specialists. A perfect generalist organism could sequentially export each logic function, collecting multiple types of resources in series, whereas a perfect specialist organism repeatedly targets a small subset of available resources, relying on other colony members to acquire additional resource types. The specialist dynamic is analogous to honey bee colonies where bees specialize on collecting nectar from one type of flower but collectively gather nectar from all flowers in their habitat (9, 26). Experimental runs are seeded with organisms that grow into colonies capable of collecting just the resource associated with the NOT function, eventually gathering enough of it for the colony to replicate. Organisms within a colony are clonal; mutations occur only during colony division. Over time, colonies

Author contributions: H.J.G., A.D., B.K., and C.O. designed research; H.J.G. performed research; H.J.G., B.K., and C.O. analyzed data; and H.J.G., A.D., B.K., and C.O. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission. J.E.S. is a guest editor invited by the Editorial Board.

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This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1202233109/-DCSupplemental.

Table 1. Logic functions that can be exported by organisms to accrue resources

Function name	Logic operation	Example A: 1001 B: 1010
NOT	$\neg A$; $\neg B$	0110; 0101
NAND	$\neg(A \text{ and } B)$	0111
AND	A and B	1000
ORNOT	$(A \text{ or } \neg B)$; $(\neg A \text{ or } B)$	1101; 1110
OR	A or B	1011
ANDNOT	$(A \text{ and } \neg B)$; $(\neg A \text{ and } B)$	0001; 0010
NOR	$\neg(A \text{ or } B)$	0100
XOR	$(A \text{ and } \neg B) \text{ or } (\neg A \text{ and } B)$	0011
EQU	$(A \text{ and } B) \text{ or } (\neg A \text{ and } \neg B)$	1100

Organisms have only NAND gates (a universal logic gate) from which to build the other logic operations. The logic operations are ordered in terms of the number of NAND operations required to complete them. More complex operations can be built using the results for simpler logic operations (e.g., XOR can be performed by ORing the results of two ANDNOT operations together). Although this example uses 4-bit numbers, organisms perform logic operations on 32-bit numbers.

evolve organisms that perform different types of logic functions, potentially engaging in strategies to coordinate task allocation and thus perform division of labor. Because of the clonal nature of the group, evolved division of labor strategies cannot rely on genetic heterogeneity. Instead, their polyphenism must arise from stochasticity or plasticity to environmental heterogeneity. Because organisms can send messages to one another, this environmental heterogeneity may be created by the organisms themselves.

Results and Discussion

We created three treatments that vary the penalty organisms pay for changing types of tasks (i.e., exporting solutions to different logic functions): a control (with no costs), a moderate-cost treatment (requiring organisms to wait 25 CPU cycles each time a different type of task is exported), and a high-cost treatment (requiring a delay of 50 CPU cycles). We replicated each treatment 50 times and used Shannon mutual information [as proposed by Gorelick et al. (27); see *Materials and Methods*] to measure the amount of division of labor that evolved within the colonies. Table 2 summarizes our results. For our initial treatments, we required colonies to collect 500 units of resource to replicate. Trials with higher task-switching costs evolved more division of labor (Kruskal-Wallis multiple comparison, $P = 0.005$). Fig. 1 depicts the phenotypes of three colonies: an ancestral colony, a typical colony that evolved a generalist strategy in the control treatment, and a typical colony that evolved specialist organisms exhibiting division of labor under high task-switching costs (hereafter referred to as our case-study colony). Fig. 2 depicts segments of the genomes of the organisms within

Table 2. Observed amounts of division of labor

Task-switch treatment	Task-switch cost	250 units required	500 units required	1,000 units required
Control	0	0.027 ± 0.01	0.400 ± 0.04	0.735 ± 0.05
Moderate	25	0.322 ± 0.04	0.813 ± 0.04	0.899 ± 0.05
High	50	0.639 ± 0.04	1.066 ± 0.04	0.915 ± 0.06

Level of division of labor observed for various individual-level task switching costs (rows) and colony-level resource requirements for replication (columns). Division of labor is gauged as the Shannon mutual information between the tasks exported and the individuals exporting them, measured across 50 trials for each experimental configuration. High task-switching costs or higher resource requirements were observed to increase evolved division of labor.

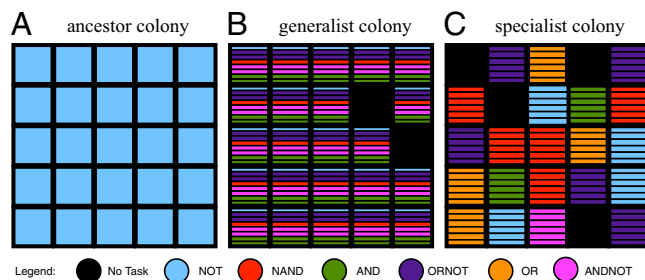


Fig. 1. A snapshot of the tasks exported (and thus the task-specific resources used) for three colonies. Each square represents the phenotype of an organism. Squares divided into segments represent multiple tasks exported; colors denote which tasks were exported. (A) An ancestral colony in which all organisms export the NOT task exactly once. (B) A colony that evolved a generalist strategy in which all organisms export five distinct tasks a total of eight times. (C) A colony that evolved a division of labor strategy in which each organism specializes on one of seven possible tasks that it exports a total of six times. (At the instant depicted, the organisms are not exporting NOR, which other colony members export at other times).

the ancestral colony (Fig. 2A) and the specialist case-study colony (Fig. 2B). We verified that the number of types of resources and the types of tasks did not drive our results in a second environment that used 25 resources associated with simpler tasks (*SI Results and Discussion, Twenty-Five-Role-Environment Experiments*).

Intrinsic Task-Switching Costs. To further confirm the robustness of these results, we performed two additional treatments in which the amount of resources required for the colony to replicate was set to 250 units (half the original amount) and 1,000 units (double the original amount). For the 250-requirement experiment, as task-switching costs increased, the colonies increasingly evolved division of labor strategies, which is consistent with our hypothesis (Kruskal-Wallis multiple comparison, $P = 0.005$). For the 1,000-requirement experiment, however, the levels of division of labor in the colonies evolved under treatments with distinct task-switching costs are not significantly different from one another. Instead, the control colonies (no cost) evolved to exhibit a high degree of division of labor that was almost equal to that exhibited by the higher-cost treatments. This behavior results from intrinsic task-switching costs (further details in *SI Results and Discussion, Intrinsic Task-Switching Costs*). As the resource requirements rose, colonies

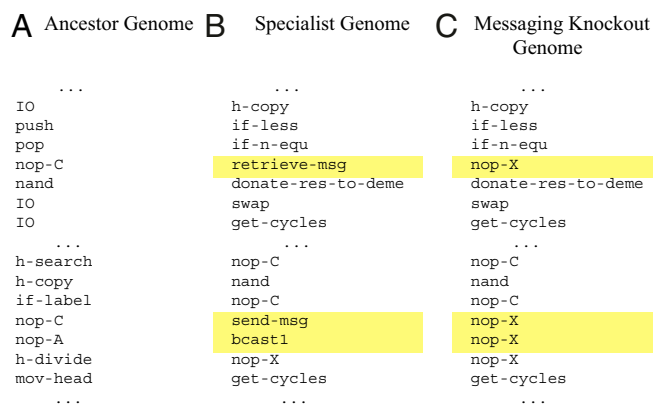


Fig. 2. Segments of code across a genome. (A) Portions of the ancestral genome for performing task NOT and self-replicating. (B) An evolved specialist genome from our case-study colony, with the messaging instructions highlighted in yellow. (C) The knockout version of the specialist genome described in B, where messaging instructions have been replaced with a neutral instruction (nop-X), highlighted in yellow. These knockout organisms cease to be able to perform any task at all.

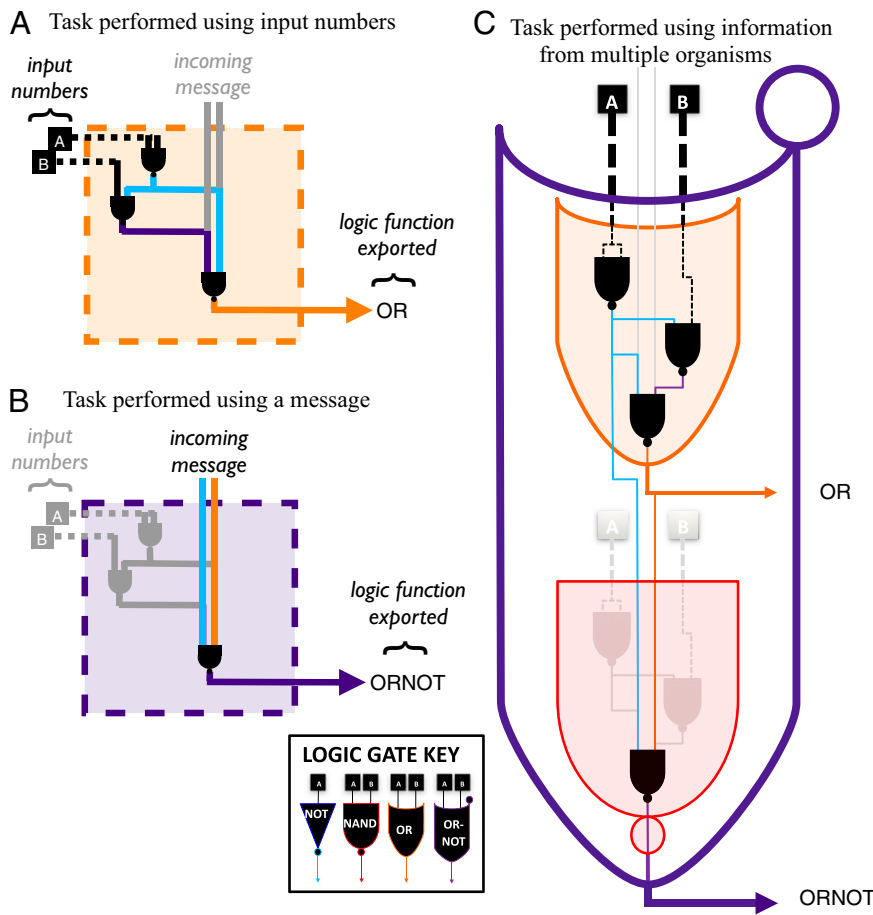


Fig. 5. Internal circuitry used by organisms in the case-study colony to export logic operations varies depending on whether they have successfully received a message. (A) An organism that exports operation OR on the input values. This individual does not receive a message (grayed-out lines) and processes inputs A and B through its logic circuitry of three NAND gates. Note $\{[(A \text{ NAND } A)] \text{ NAND } [(A \text{ NAND } A) \text{ NAND } B]\} = (A \text{ OR } B)$. Thus, this individual performs and then exports the OR task. (B) An organism that exports the results of an ORNOT operation using the contents of a received message. This organism performs the same initial steps as the organism depicted in A. However, it successfully receives a message that overwrites the partially processed input values. It NANDs together the received values to produce the result for ORNOT, which it exports. (C) A hierarchical perspective on how multiple organisms participate via messaging in performing a more-complex logic operation. Within this figure, we depict the same two organisms as in A and B. However, we vary their shape and color to represent the internal logic operations performed, rather than the task exported. The first organism highlighted in orange is the organism in part A. This individual ORs inputs A and B together and as such is represented by an OR gate. Additionally, it passes a message with two components to the second individual: (NOT A) and (A OR B). The second organism (from B) is highlighted in red and is represented by a NAND gate, because it receives the message (represented as blue and orange lines) sent by the first organism and performs a NAND operation on the components of the message. Because of the message contents, which were created by organism A, the resulting operation is (A ORNOT B), which is exported by the organism. Note that $[(\text{NOT } A) \text{ NAND } (A \text{ OR } B)] = (A \text{ ORNOT } B)$. Combined, these two individuals serve as an ORNOT gate, as depicted by the large purple gate surrounding the pair of individuals.

We provide the standard set of Avida instructions (detailed in ref. 23) to enable organisms to perform basic computational tasks (addition, subtraction, bit-shifts, etc.), control execution flow, and allow for replication. Our instruction set also included communication and location-sensing instructions (summarized in Table 3).

Organisms can perform tasks that enable them to accumulate resources from their environment and contribute to colony replication. Resources within this environment are limited. (Further details on how violations of this assumption affect division of labor are given in *SI Results and Discussion*,

Exploring the Conditions Under Which Division of Labor Evolves.) For the majority of experiments, we required the organisms to perform bitwise Boolean logic operations on 32-bit integers. [Lenski et al. (23) provide detailed examples of these operations.]

To study how the presence and magnitude of task-switching costs affect the evolution of division of labor, we created a configurable task-switching penalty. Specifically, if an organism changes the type of task it is performing, then it incurs a time penalty that is applied before the resources for the second task are collected. We implement this time penalty as wasted CPU

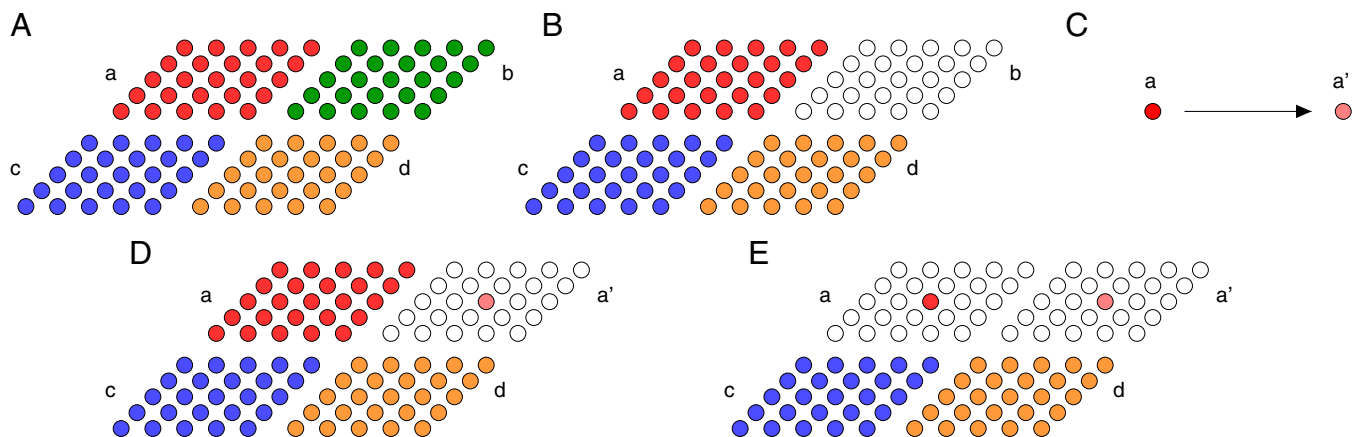


Table 3. Coordination instructions for this study

Instruction	Description
send-msg	Send a message to a neighbor of the caller.
retrieve-msg	Load the contents of a received message into the caller's virtual CPU.
rotate-left-one	Rotate this organism counterclockwise one step.
rotate-right-one	Rotate this organism clockwise one step.
get-role-id	Set register <i>BX</i> to the value of the caller's role-id register.
set-role-id	Set the caller's role-id register to the value in register <i>BX</i> .
bcast1	Send a message to all neighboring organisms.
get-cell-xy	Set register <i>BX</i> and <i>CX</i> to the (<i>x</i> , <i>y</i>) coordinates of the caller.

cycles, whereby a CPU cycle is the amount of time it takes an organism to execute one instruction.

For each experiment, we conducted 50 trials to account for the stochastic nature of evolution. Within each trial, the Avida world consists of 400 colonies. All genotypes are fixed at a length of 100 instructions. Mutations occur to a genotype when the colony replicates; the mutation rate is set to an average of one mutation per genome per replication event. The trials last for 201,000 updates. After the first 200,000 updates, the colonies go through a 1,000-update ecological period, in which the mutation rate is set to zero. The ecological period prunes dysfunctional colonies that occur as the result of deleterious mutations that are not able to fix in the population. In this case, the ecological phase enables us to better analyze and assess the behavior of the colonies.

Measuring Division of Labor. To measure the amount of division of labor present within a colony, we use Shannon mutual information as proposed by Gorelick et al. (27). Shannon mutual information is defined as:

$$I(N, M) = \sum_{i \in N, j \in M} p_{ij} * \ln \left(\frac{p_{ij}}{p_i * p_j} \right)$$

where *i* is an organism, *N* is the set of organisms that performed a task within the colony, *j* is a type of task, and *M* is the set of types of tasks. *p_i* is the probability of picking individual *i* at random. For this study, we treat the

probability of all individuals (*p_i*) as equal. *p_{ij}* is the joint probability of a random unit of work being individual *i* working on task type *j*. For this measurement, we normalize by individual productivity, to determine the percentage of time an individual spends on a specific type of task. Thus, we set *p_{ij}* equal to the percentage of time each individual spent on task type *j* divided by the total number of organisms. *p_j* is the probability that individuals are working on task *j*. To compute *p_j*, we sum *p_{ij}* across all organisms.

Intuitively, Shannon mutual information captures two reciprocal pieces of information: given an individual, how much information do we have about the type of task it spends its time performing, and given a type of task, how much information do we have about the individual that is most likely to be working on performing it? Information will be high when individuals specialize on performing one type of task but the group as a whole contains specialists that focus on performing a diverse set of tasks. Specifically, Shannon mutual information (and division of labor) will be maximized for a given population size and number of tasks performed when each organism is a perfect specialist and the organisms within the colony are evenly divided among the tasks. If all members of a colony are performing the same set of tasks with the same proportions, then information is zero.

ACKNOWLEDGMENTS. We thank F. C. Dyer, D. B. Knoester, N. Serra, and members of the Devolab for their insights during discussions of this work. This work has been supported in part by National Science Foundation Grants CCF-0643952, DBI-0939454, CCF-0820220, OCI-1122620, DEB-0952825, and R3D381.

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