many traits exhibit continuous phenotypic variation underlain by many genes (14). In such cases, individual genes have minor effects on trait variation. Moreover, not only genes but also the environment influences trait expression.

Additionally, even apparent cases of single genes with strong effects on a trait may represent multiple genes that are tightly linked (i.e., physically located) on the same chromosome, as occurs in "supergenes" (13). Studying such complex genetic architectures is more challenging than studying single genes, as evidenced by difficulties in genetic mapping of human disease and complex behavioral traits (14). Testing how traits underlain by many genes affect ecological dynamics is a challenging, yet important, avenue for future work. A caveat is that even if major effect loci are relatively rare, they could be more likely than minor effect loci to exert marked ecological effects (1).

Further studies that combine disciplines such as ecology, genetics, and mathematical modeling are likely to invigorate the field of eco-evolutionary dynamics. Although simple systems are a powerful and useful starting point for such work, most eco-evolutionary systems are more complex because of the interactions and feedback among and within ecological and evolutionary processes, and complex communities and trait genetics (1-3). This complexity of eco-evolutionary systems must be unraveled to elucidate if these dynamics will be gradual or abrupt, and how the dynamics can be characterized by tipping points in ecosystems (15). Such knowledge will inform the importance of evolution for ecological dynamics and biodiversity.

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EVOLUTION AND COGNITION

Selective cultural processes generate adaptive heuristics

Less intuitive, hard-to-learn cognitive heuristics can thrive

By Joseph Henrich

ong before the arrival of astrolabes, compasses, or marine chronometers, Micronesian navigators guided canoes across hundreds of miles of open ocean by integrating information from stars, waves, coral reefs and more into a rich conceptual framework. Looking into the heavens, they saw a celestial compass and knew which rising and setting stars to follow. They used three distinct types of waves-originating from the south, east, and northeast-as directional references (1, 2). Equipped with such cognitive tools, the ancestors of these Micronesians spread across Oceania, sailing from the bustling islands of Southeast Asia to the remote reaches of Hawaii, Easter Island, and South America. How do such complex cognitive technologies emerge? On page 95 of this issue, Thompson et al. (3) describe taking an experimental approach to the question of how opportunities to selectively learn from successful role models can favor the spread of more adaptive, but less intuitive, cognitive heuristics over more intuitive and memorable alternatives.

To hunt, gather, farm, fish, and tackle countless other challenges, humans have relied on a dizzying array of complex, locally adaptive heuristics (4, 5). Yet the origins of such heuristics present a puzzle because the best protocols and practices are often not the easiest to learn, remember, and teach. Even when one manages to master a more effective, but less intuitive, technique, it will deteriorate as it's transmitted and transformed by the minds of others over generations (6). Researchers have long considered how ensembles of psychological biases, preferences, and inferences make certain ideas, stories, songs, and concepts catchier-easier to acquire, recall, and retransmit—and have deployed these "cognitive attractors" to account for the recurrent patterns found across societies in domains such as religion, literature, art, and folk biology (7-10). But given the

pervasiveness of such cognitive attractors. how can the impressive assemblages of nonintuitive heuristics and hard-to-learn cognitive abilities that have permitted humans to dominate Earth's major ecosystems be accounted for?

Approaching this puzzle, cultural evolutionary theorists were inspired by ethnographic accounts such as those for Micronesia, where all young males aspired to become master navigators—the pinnacle of local prestige-by apprenticing under the most respected masters (1). Few aspirants, however, succeeded in being initiated as masters because some of the most important skills were nonintuitive, difficult to learn, and unforgiving of mediocrity—miscalculating by a few degrees could mean sailing past an atoll and dehydrating or starving, lost in the Pacific's vastness. Using mathematical models, theorists have shown that if learners selectively attend to models or teachers based on cues of prestige, success, and skill, this can drive the spread of less intuitive heuristics by compensating for errors that creep in when complex heuristics are transmitted from person to person (6).

To assess the role of selective cultural learning in creating adaptive heuristics, Thompson et al. paid experimental participants according to how efficiently they could complete a sorting task. Participants had to correctly order six tiles using the fewest number of paired comparisons and were told that the tiles themselves were uninformative-only the paired comparisons revealed ordering information. Participants had to sort nine different sextets of tiles. After completing their assignment, they each wrote up what they had learned for the next generation of sorters and passed it along with a demonstration of their sorting strategy. Sorters were further paid according to the success of those who tapped them as "teachers." After the first generation, which served as an asocial treatment in which sorters had no opportunity to learn from others, participants in generations 2 to 12 were randomly placed into either the selective social learning or random mixing treatments. In both treatments, naïve sorters could select up to three teachers from a set of eight partici-

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An illustration from the early 1800s depicts canoes near the Mariana Islands in Micronesia.

pants from the prior generation. The only difference was that sorters in the selective social learning treatment could observe the monetary payoffs ("success") of their eight potential teachers, whereas those in the random mixing treatment observed only their teachers' arbitrary identification numbers. When learners selected a particular model, they had an opportunity to read their teacher's write-up, observe their demonstration, and practice their strategy.

When individuals could preferentially learn from more successful sorters, their average performances increased across time such that, by the final generations, their scores exceeded those in the random mixing and asocial treatments by 24 and 70%, respectively. By the end, the randomly chosen participants who could selectively learn from others seemed smarter: They had better cognitive algorithms for solving this kind of problem. This not only confirms prior work (11, 12), illustrating how selective cultural learning can foster the evolution of more efficient artifacts (e.g., kayaks and bows), but also shows that it can generate better information-processing algorithms.

Closer inspections of the data reveal even more notable results. Although there are a vast number of possible ways to go about this sorting process, only eight distinct and identifiable algorithms emerged in the social treatments, and only two-selection sort and gnome sort-dominated the final three generations. Meanwhile, in the asocial treatment, most sorters used idiosyncratic approaches that didn't approximate any known algorithm and generally performed poorly. Thus, when social learning was possible, a method's transmissibility, fidelity, and memorability rapidly shaped the variation in sorting algorithms, creating quasi-discrete cultural units for selective learning to act on (6).

Of the two leading algorithms, selection sort was substantially easier to learn and/ or transmit-and thus represents a stronger cognitive attractor-but was 30% less efficient than gnome sort at the sorting task. The difficulty of transmitting and learning the gnome algorithm is seen by the more complex written instructions provided by gnome teachers and the more frequent errors made by those trying to imitate gnome during their practice round. Consequently, in the random mixing treatment, when gnome did sometimes emerge and begin to spread, errors introduced during the transmission process degraded its effectiveness, allowing selection sort to

out compete it. By contrast, when selective learning was possible, gnome not only survived but often diffused across the population and was sustained at sizable frequencies. Here, selective processes favored the more efficient, but harder to learn, cognitive attractor by allowing learners to pick models who hadn't inadvertently introduced errors, thus filtering out errors each generation. Indeed, only in the selective social learning treatment did a stable cadre of gnome "master sorters" emerge. As with Micronesian navigators, nearly all master sorters (>85%) had master sorters as teachers, though most students of master sorters did not become master sorters themselves. This experimental evidence elegantly converges with well-established ethnographic patterns (13, 14).

These results highlight a deeper point: Humans don't have culture because we're smart, we're smart because we have culture (3). The selective processes of cultural evolution not only generate more sophisticated practices and technologies but also produce new cognitive tools—algorithms that make humans better adapted to the ecological and institutional challenges that we confront. Thompson et al.'s results underline the need for the psychological sciences to abandon their implicit reliance on a digital computer metaphor of the mind (hardware versus software) and transform into a historical science that considers not just how cultural evolution shapes what we think (our mental contents) but also how we think [our cognitive processes (15)].

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