



Coevolution of intelligence, behavioral repertoire, and lifespan



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ABSTRACT

Across many taxa, intriguing positive correlations exist between intelligence (measured by proxy as encephalization), behavioral repertoire size, and lifespan. Here we argue, through a simple theoretical model, that such correlations arise from selection pressures for efficient learning of behavior sequences. We define intelligence operationally as the ability to disregard unrewarding behavior sequences, without trying them out, in the search for rewarding sequences. We show that increasing a species' behavioral repertoire increases the number of rewarding behavior sequences that can be performed, but also the time required to learn such sequences. This trade-off results in an optimal repertoire size that decreases rapidly with increasing sequence length. Behavioral repertoire size can be increased by increasing intelligence or lengthening the lifespan, giving rise to the observed correlations between these traits.

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1. Introduction

The main theoretical question of this paper is how selection for efficient learning shapes the evolution of a species' behavioral repertoire. At first sight, a large behavioral repertoire appears beneficial because it enables an animal to act upon its environment in many ways, thus broadening the spectrum of resources that can be exploited. A crab's claws, for example, can just grasp and crush, while the hands of primates can perform a large range of manipulations that contribute to impressive feeding behavior (Strier, 2010). Why, then, do not all species have large behavioral repertoires? Apart from constraints on the evolution of morphology and motor control (Arnold, 1992), we argue that a large repertoire incurs a hidden cost because it increases the time necessary to learn functional sequences of behaviors. Our argument rests upon two observations. First, behavioral repertoires are mainly genetically determined and are often limited to a small number of behaviors. Second, animals obtain rewards by combining these genetically determined behaviors into learned sequences (we use the term "reward" to indicate any positive contribution to fitness, such as food, shelter, safety from predators, temperature regulation, and so on).

All species have an inborn repertoire of behavior patterns that develop without any specific experiences (Hinde, 1970; Hogan, 2001; Berridge, 1994; Lorenz, 1981). These patterns, called *fixed action patterns* in ethology, are centrally generated and are typically performed by young animals without peripheral or external

feedback (Hinde, 1970; Hogan, 2001; Lorenz, 1981). Rat pups, for example, can suckle from birth without any need for learning (Hall et al., 1975). Similarly, movements used in dust bathing in chickens develop spontaneously during the first two weeks of life, before they are used in dust bathing (Larsen et al., 2000; Vestergaard et al., 1990). Ethologists have determined the inborn behavioral repertoire of many species and studied its evolution and genetic determination through comparative methods (Hinde and Tinbergen, 1958; Lorenz, 1981, 1941) and the observation of species hybrids (see Dilger, 1960; Buckley, 1969 for the selection of nest material in parrots, and Lingle, 1993, Lingle, 1992 for gait in deer). Of greatest relevance to this paper are studies about exploratory behavior and learning. Glickman and Sroges (1966) assessed exploration of novel objects in more than 100 mammal and reptile species, reporting great variation in the quantity and form of exploratory behavior. Primates and carnivores explored the most, followed by rodents, marsupials, insectivores and edentates; reptiles explored the least. Time spent exploring correlated with the number of exploratory behaviors. Rodents, for example, mainly sniffed and gnawed at novel objects, while many primates engaged in extensive manipulation and prolonged visual inspection. Consistent species differences in exploratory behavior have also been reported in foraging behavior (Mettke-Hofmann et al., 2002), including differences in how experience influences future exploration (Mettke-Hofmann and Gwinner, 2003).

Ethologists have also demonstrated that individual experience is important to organize inborn behaviors into functional sequences. A squirrel (*Sciurus vulgaris*), for example, uses several behaviors to open a nut, such as holding, gnawing, and prying (Eibl-Eibesfeldt, 1975). Young squirrels can hold, gnaw, and pry, but

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are inefficient nut openers because they use these behaviors randomly on the surface of the nut, until it cracks. By trial and error, they gradually learn how to assemble these behaviors into an efficient sequence (Eibl-Eibesfeldt, 1963, replicated in *S. lis* by Tamura, 2011). This example brings us to our second observation, and the crux of our argument. Learning, to contribute substantially to individual fitness, should not be limited to the acquisition of single behaviors in response to specific stimuli. Rather, fitness is most enhanced when coordinated sequences of behaviors are acquired. Learning sequences is much harder than learning single responses because of a combinatorial explosion in the number of sequences that can be tried out. The development of tool use in chimpanzees (*Pan troglodytes*) exemplifies this problem. Inoue-Nakamura and Matsuzawa (1997) studied how chimpanzees at Bossou, Guinea, learn to crack nuts with stone or wooden anvils and hammers, using a sequence of five behaviors: pick up a nut, place it on the anvil, pick up a hammer (requires a different grip than picking up a nut), hit the nut, and eat the nut. It takes the chimpanzees thousands of attempts over three or more years to learn this sequence. Apart from perfecting the necessary motor skills, we argue that a major difficulty in such learning is that the five actions must be chosen among many. Inoue-Nakamura and Matsuzawa (1997) observed the animals perform at least 35 different actions on stones and nuts. Chimpanzees can thus potentially perform at least $35^5 \approx 50$ million sequences of 5 behaviors involving stones and nuts. How to find the correct sequence among so many? There are at least two different ways, not mutually exclusively, to resolve this combinatorial dilemma and reduce sequence learning times.

1. Limiting the behavioral repertoire. If chimpanzees could only perform on stones and nuts the 5 actions they actually need to open the nuts, they would only need to try $5^5 = 3125$ sequences. This would, of course, limit what they can do in other situations.
2. Intelligence. We define intelligence as the ability to disregard, without explicitly trying them out, behavior sequences that are not profitable (this definition includes both individual and social learning, see Section 4). Chimpanzees could, for example, understand that placing the nut on the anvil is the first thing to do. This would reduce the number of sequences to try to $35^4 \approx 1.5$ million. If chimpanzees further understood that picking up the hammer should come next, the number of sequences to try would decrease to $35^3 \approx 40,000$.

In the following, we introduce a simple mathematical model to study the coevolution of behavioral repertoire and intelligence under the selection pressure for efficient learning of functional sequences of behavior. The model predicts that large behavioral repertoires should be observed only in intelligent and long-lived species. We evaluate this prediction in a concluding Discussion.

2. The model

We introduce a model environment and a model animal that learns from interacting with the environment, and then calculate the optimal repertoire size for the animal. The environment is described by the following assumptions:

1. There are A actions that can be used to act upon the environment (e.g., grasp, push, pull, lift, twist, and so on). An animal's behavioral repertoire may comprise any number of actions between 0 and A .
2. The environment delivers a reward of 1 to the animal each time a specific sequence of l actions is performed. Other sequences yield zero reward—this is actually a cost because the time spent performing an unrewarding sequence could have been spent earning a reward.

3. Each action has the same probability to be part of the rewarding sequence. That is, the probability that an action is the correct one at any point in the sequence is $1/A$.
4. The rewarding sequence does not change over an animal's lifetime.

We make the following assumptions about animal behavior:

5. The behavioral repertoire is genetically determined, but the animal must learn which actions to use to obtain rewards.
6. The animal can perform a total of T actions in its expected lifetime (all actions take the same time).
7. The animal explores the environment by performing sequences of l actions at random until it stumbles upon the rewarding sequence and collects a reward. Thereafter, the animal continues to perform the rewarding sequence until it dies.
8. Actions can be added freely to the behavioral repertoire (there are no morphological or genetic constraints).

These assumptions are clearly a simplification of actual learning strategies. Animals, for example, usually take more than one experience to learn. They also do not try actions randomly, but use a variety of mechanisms to explore the environment in a more targeted way. Our model environment is also highly simplified. In a realistic environment some behaviors may have a higher probability of entering profitable sequences (a departure from assumption 3), and in general there are many profitable sequences which differ in length and value (a departure from assumption 2). After discussing this simple model, we will show how to generalize it to different learning strategies and more realistic environments.

3. Evolution of repertoire size

We want to calculate the reward, $r_l(n)$, that an organism with a repertoire of n behaviors expects to collect under the hypotheses above, when attempting to learn a sequence of length l . Conditioning on the probability that the repertoire contains all l actions required to collect a reward, we write

$$\begin{aligned} r_l(n) &= E(\text{reward}) \\ &= E(\text{reward} \mid \text{all actions in repertoire}) \\ &\quad \times \Pr(\text{all actions in repertoire}). \end{aligned} \quad (1)$$

The first term is the number of times the animal is expected to complete the profitable sequence. If the animal devoted all of the available T actions to performing the rewarding sequence, it would collect $\lfloor T/l \rfloor$ rewards ($\lfloor x \rfloor$ is the integer part of x). Some of the T actions, however, are used to learn, i.e., to search for the rewarding sequence among all possible sequences. We can thus write

$$\begin{aligned} E(\text{reward} \mid \text{all actions in repertoire}) \\ &= \left(\left\lfloor \frac{T}{l} \right\rfloor - \text{sequence search time} + 1 \right). \end{aligned} \quad (2)$$

where we add 1 because the learning phase terminates with a successful performance of the rewarding sequence. The sequence search time is calculated based on assumptions 5–7 as follows. With a repertoire of n actions, the animal can try out n^l sequences of length l . Each such attempt requires l time steps. If sequences are tried out at random, with no memory of what has been tried before, the expected time to find the profitable sequence is

$$\text{sequence search time} = ln^l \quad (3)$$

resulting in

$$E(\text{reward} \mid \text{all actions in repertoire}) = \left(\left\lfloor \frac{T}{l} \right\rfloor - ln^l + 1 \right). \quad (4)$$

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